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Climate controls over the net carbon uptake period and amplitude of net ecosystem production in temperate and boreal ecosystems

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1 **Climate controls over the net carbon uptake period and amplitude of net**
2 **ecosystem production in temperate and boreal ecosystems**

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37 **Abstract**

38 The seasonal and interannual variability of the terrestrial carbon cycle is regulated by the interactions
39 of climate and ecosystem function. However, the key factors and processes determining the
40 interannual variability of net ecosystem productivity (NEP) in different biomes are far from clear.
41 Here, we quantified yearly anomalies of seasonal and annual NEP, net carbon uptake period (CUP),
42 and the maximum daily NEP (NEP_{max}) in response to climatic variables in 24 deciduous broadleaf
43 forest (DBF), evergreen forest (EF), and grassland (GRA) ecosystems that include at least eight
44 years of eddy covariance observations. Over the 228 site-years studied, interannual variations in
45 NEP were mostly explained by anomalies of CUP and NEP_{max} . CUP was determined by spring and
46 autumn net carbon uptake phenology, which were sensitive to annual meteorological variability.
47 Warmer spring temperatures led to an earlier start of net carbon uptake activity and higher spring
48 and annual NEP values in DBF and EF, while warmer autumn temperatures in DBF, higher autumn
49 radiation in EF, and more summer and autumn precipitation in GRA resulted in a later ending date of
50 net carbon uptake and associated higher autumn and annual NEP. Anomalies in NEP_{max} s were
51 determined by summer precipitation in DBF and GRA, and explained more than 50% of variation in
52 summer NEP anomalies for all the three biomes. Results demonstrate the role of meteorological
53 variability in controlling CUP and NEP_{max} , which in turn help describe the seasonal and interannual
54 variability of NEP.

55

56 **Key words:** net ecosystem productivity; interannual variation; net carbon uptake period; maximum
57 carbon uptake amplitude; phenology; climate

58 **1. Introduction**

59 Climate controls the terrestrial carbon cycle by regulating plant physiological processes, including
60 phenology. Climate thus determines both ecosystem carbon uptake capacity as well as the length of
61 the carbon uptake period, which are important determinants of ecosystem carbon sequestration
62 (Falge et al., 2002b; Gu et al., 2009; Xia et al., 2015; Zhou et al., 2016). It is far from clear how
63 climatic or meteorological changes impact net ecosystem production (NEP) by changing carbon
64 uptake phenology and physiology, given that models are largely unable to simulate the interaction
65 between climate and ecosystem carbon dynamics to date (IPCC, 2013).

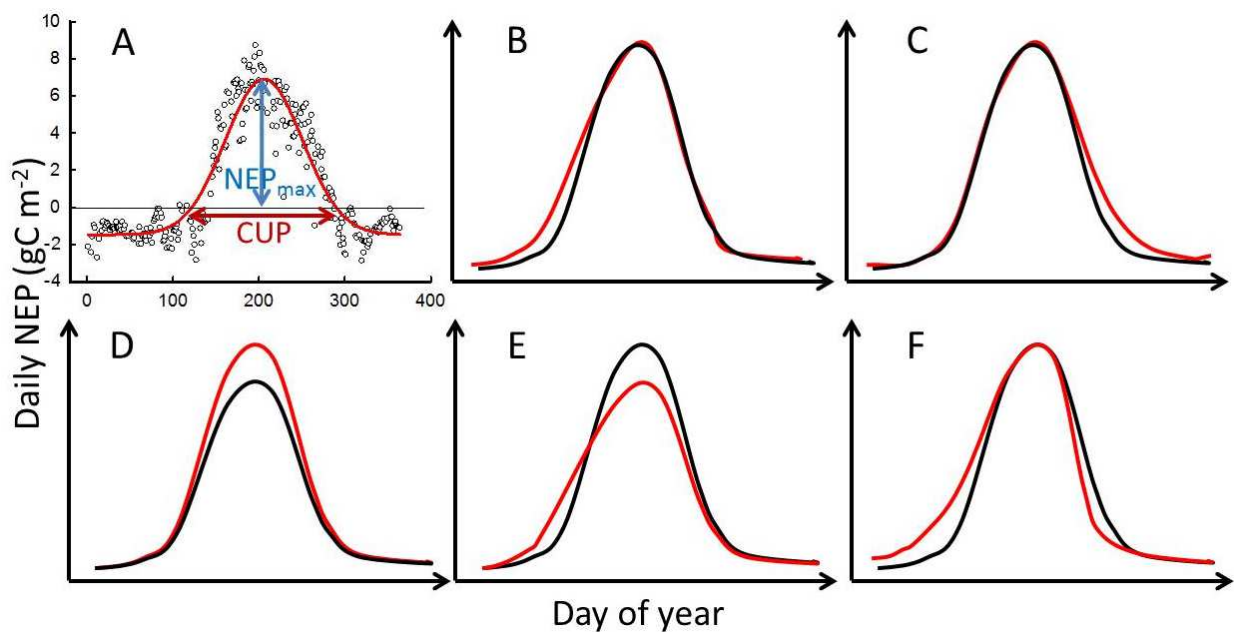
66 Previous studies on the relationship between carbon uptake phenology and NEP primarily
67 focus on growing season length (GSL). A longer GSL due to climate warming (Delpierre et al., 2015;
68 Linderholm, 2006; Peñuelas and Filella, 2001) usually stimulates NEP (Baldocchi, 2008; Baldocchi
69 and Wilson, 2001; Churkina et al., 2005; Dragoni et al., 2011; Richardson et al., 2013). Yet other
70 studies have found no relationship between GSL and NEP (Dunn et al., 2007), or lower NEP with
71 longer GSL (Hu et al., 2010b; Piao et al., 2007; Sacks et al., 2007). The reasons for this disparity are
72 twofold; gross ecosystem productivity may be offset by concurrent increases in ecosystem
73 respiration as NEP is the difference between the two, and longer GSLs may increase the likelihood
74 of drought limitations to productivity.

75 With the advantage of quasi-continuous measurements of the net CO₂ exchange by the eddy
76 covariance method, strong relationships between net carbon uptake period (CUP) and annual NEP
77 have been characterized (Baldocchi et al., 2001; Baldocchi et al., 2005; Richardson et al., 2010;
78 Richardson et al., 2013; Wu and Chen, 2013; Wu et al., 2013). Overall, annual NEP is more strongly
79 correlated with CUP than GSL (Piao et al., 2007; White and Nemani, 2003; Wu et al., 2013). While
80 climate controls on GSL have been well studied (Chmielewski and Rötzer, 2001; Delpierre et al.,

81 2015; Matsumoto et al., 2003; Richardson et al., 2013), our understanding of climate controls over
82 CUP and thus NEP across different ecosystems is still limited.

83 In addition to the CUP, the maximum daily ecosystem NEP (NEP_{max} , Fig. 1A) is another
84 strong predictor of annual NEP, especially in temperate and boreal ecosystems that have obvious
85 seasonal dynamics (Falge et al., 2002b; Xia et al., 2015; Zhou et al., 2016). With the same CUP,
86 ecosystems that have a higher NEP_{max} tend to have larger annual NEP (Fig. 1D) (Churkina et al.,
87 2005). Although a longer CUP may increase annual NEP, associated warmer and drier summers may
88 suppress summer NEP_{max} , potentially offsetting any annual NEP increase (e.g. Fig. 1E) (Angert et al.,
89 2005; Ciais et al., 2005; Cleland et al., 2007). Moreover, a longer CUP may decrease annual NEP
90 because an earlier onset of the growing season may result from a shallow snowpack or increased
91 transpiration, leaving less available water in the soil in summer and limiting plant growth later in the
92 growing season (Hu et al., 2010a; Kljun et al., 2006; Sacks et al., 2007). Niemand et al. (2005)
93 linked phenology observations to flux measurements in a Norway spruce forest and found that
94 earlier spring phenology correlated well with increased NEP only when the drought year of 2003
95 was excluded, suggesting that water availability influences the relationship between CUP and annual
96 NEP. These results indicate that the effects of summer water limitation on NEP_{max} may potentially
97 offset positive spring warming influences on spring NEP, leading to smaller changes in annual NEP
98 than otherwise expected (Fig. 1E). In addition, autumn warming may also advance the ending of
99 carbon uptake and decrease autumn NEP, resulting in a small change in annual NEP in response to
100 climate warming (Fig. 1F). We tested the hypothesis that, by separating annual NEP variability into
101 CUP and NEP_{max} , we can better disentangle how meteorological drivers impact NEP variability in
102 deciduous broadleaf forests (DBF), evergreen forests (EF), and grasslands (GRA) that experience
103 pronounced seasonality in temperate and boreal climate zones.

104 In this study, we analyzed eddy covariance-measured CO₂ flux and micrometeorological
 105 variables from 24 flux tower sites that have long-term (multi-year) quasi-continuous measurements.
 106 The specific questions addressed in this study include: (1) how are CUP and NEP_{max} related to
 107 annual NEP in different biomes; (2) what are the climate factors that determine NEP_{max} and the
 108 beginning (BDOY) and end (EDOY) of the CUP; and (3) how are seasonal NEP anomalies related to
 109 annual NEP anomalies?



110
 111 Fig. 1. Hypothesized changes in the regulation of annual NEP by net carbon uptake period (CUP)
 112 and the maximum daily net ecosystem productivity (NEP_{max}), and their roles in regulating annual
 113 NEP changes. Panel A defines the terminology used throughout the manuscript. Red lines in
 114 subsequent panels represent the change in a hypothetical warmer year *versus* the mean seasonal
 115 pattern in black. Panels (B) and (C) represent the phenological regulations by advancing net carbon
 116 sink beginning day (BDOY) or by delaying net carbon sink ending day (EDOY); (D) represents a
 117 change in NEP_{max}; (E) represents the larger spring NEP with an advancing BDOY but smaller
 118 summer NEP by decreasing NEP_{max}; and (F) represents larger spring NEP by early beginning of

119 BDOY, but smaller autumn NEP with earlier EDOY. We only showed the representative scenarios
120 rather than all possible interactions between NEP_{max} , BDOY and EDOY.

121

122 **2. Data and Methods**

123 **2.1. Site selection and data processing**

124 Surface-atmosphere CO_2 flux and micrometeorological data used in this analysis were downloaded
125 from standardized files of the FLUXNET LaThuille database released in 2007 (Baldocchi, 2008;
126 Baldocchi et al., 2001). The data have been quality-controlled and gap-filled by consistent methods
127 (Moffat et al., 2007; Papale et al., 2006; Reichstein et al., 2005). From the available 253 sites, we
128 identified and examined temperate and boreal ecosystems (38-62 °N, -125-24 °E; Table A1) that
129 have clear seasonal dynamics. We only chose sites that have eight or more years of data for a total of
130 24 sites with 228 site-years to investigate the interannual variability of climate and CUP and NEP_{max} ,
131 as well as seasonal and annual NEP (Table A1). Daily data for each site were used to calculate the
132 seasonal and annual values of incoming solar global radiation (R_g), air temperature (T_a),
133 precipitation (PPT), and daily CO_2 fluxes (i.e., NEP, also called the net ecosystem exchange, NEE).
134 These sites were divided into three groups based on International Geosphere-Biosphere Programme
135 (IGBP) land cover classifications: deciduous broadleaf forests (DBF), evergreen forests (EF), and
136 grasslands (GRA).

137 For each year, we calculated the seasonal and annual mean values of T, PPT, R_g , and NEP.
138 The whole year was separated into the climatological seasons of winter (December–February),
139 spring (March–May), summer (June–August), and autumn (September–November) in order to study
140 seasonal changes in NEP in response to changes in CUP and NEP_{max} . When the missing daily data
141 exceeded 10% of the entire season (or year), the seasonal (or yearly) value was indicated as missing.

142 On average, for the 24 sites, 8% of the years were rejected due to insufficient data. The years
143 rejected varied from 7% (US-Ha1) to 45% (IT-Col) among sites.

144

145 **2.2. Definition and analysis**

146 We used a 10-day moving average to determine the beginning (BDOY) and ending (EDOY) day of
147 positive ecosystem NEP for each year for each site (Fig. 1A, Table A2). Consistently, BDOY
148 occurred in spring and EDOY appears in autumn at all the sites. We defined the net carbon uptake
149 period (CUP) as the number of days between the BDOY and EDOY (Fig. 1A). Daily ecosystem
150 carbon uptake exceeds carbon release during the CUP. CUP is related to, but need not be identical to,
151 GSL. For example, the beginning of CUP may start later than leaf onset when the leaves
152 photosynthesize at a rate that outweighs ecosystem respiration. The CUP ends when ecosystem
153 respiration is higher than photosynthesis although plant growth and CO₂ uptake may continue. GSL
154 in most cases will be longer than CUP because the balance between total ecosystem respiration and
155 photosynthesis determines CUP (Churkina et al., 2005). The maximum daily NEP (NEP_{max}) is
156 defined as the maximum value of daily NEP, which was derived from the moving average curves of
157 NEP seasonal dynamics (Fig. 1A). Interannual variation as a yearly anomaly was calculated for each
158 site-year for each variable.

159

160 **2.3. Data analysis**

161 To examine the relationships between climate anomalies and the anomalies of BDOY, EDOY, and
162 NEP_{max}, as well as the anomalies in seasonal and annual NEP, we analyzed the data using simple
163 linear regression. For testing the inequality of regression slopes among different vegetation types,
164 the slopes between BDOY and EDOY anomalies, and seasonal or annual NEP anomalies for

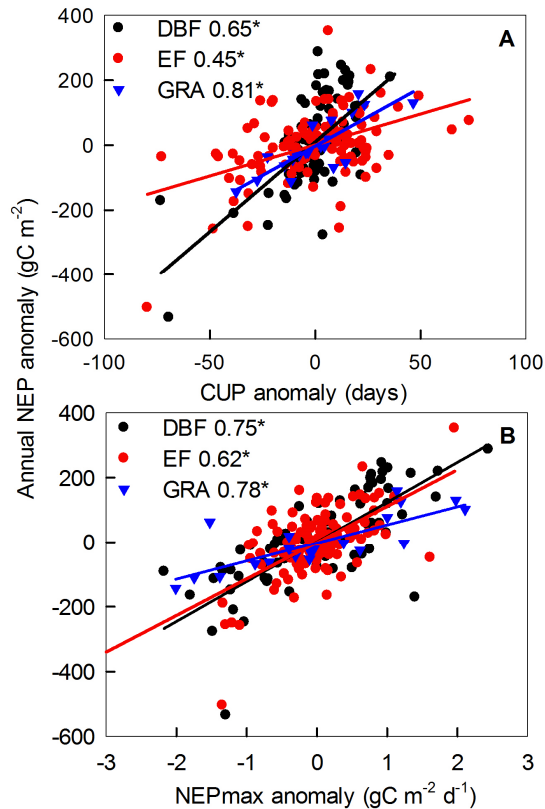
165 different seasons, we calculated t^* using $t^* = (b_1 - b_2) / \sqrt{(s_1^2 + s_2^2)}$, where b_1 and b_2 are regression
166 slopes, and s_1 and s_2 are the standard errors of regression slopes for the vegetation types or different
167 seasons. The null hypothesis is that the slopes b_1 and b_2 are not significantly different at $\alpha=0.05$. We
168 also used structural equation models to partition the total effect of variables on annual NEP into
169 direct and indirect effects (Schumacker and Lomax, 2004; Vargas et al., 2010). A path model was
170 developed to relate the anomalies of NEP to the anomalies of CUP and NEP_{max} , as well as the
171 anomalies of seasonal climate factors in different ecosystems. The model was fitted using the
172 'lavaan' package (Rosseel, 2012) in R3.0.2 for Windows.

173

174 **3. Results**

175 **3.1. CUP and NEP_{max} in controlling NEP**

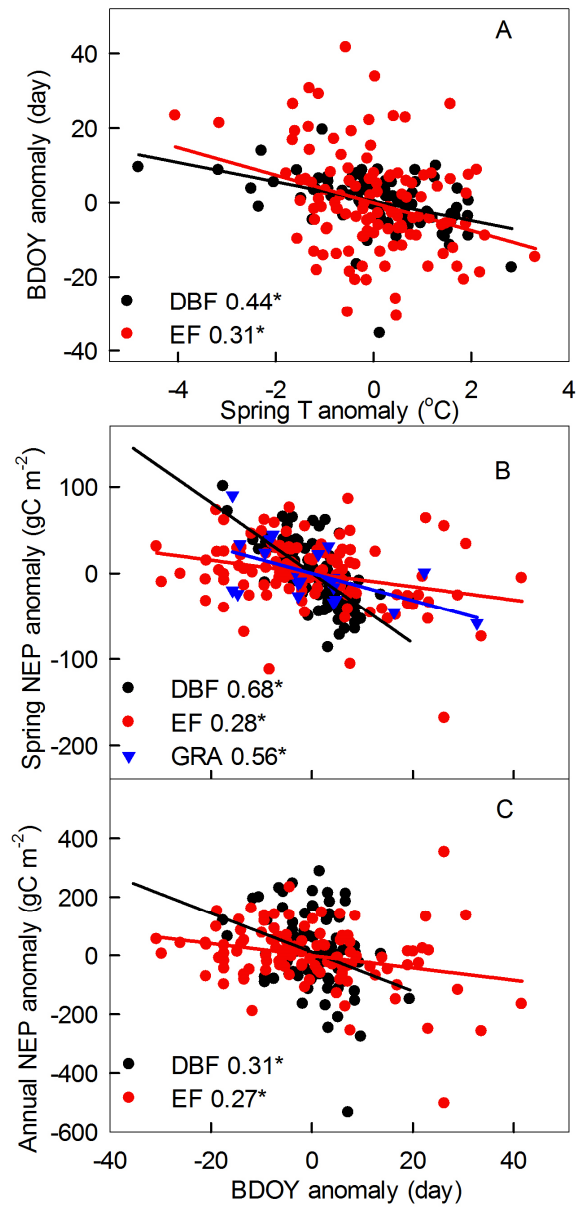
176 Across all the site-years, annual NEP anomalies were positively correlated with anomalies of CUP
177 and NEP_{max} across all three ecosystem types ($P < 0.001$, Fig. 2A). The slope between CUP and NEP
178 was significantly higher in DBF (5.5 g C m⁻² per day) and GRA (3.6 g C m⁻² per day) than in EF (1.9
179 g C m⁻² per day, Fig. 2A). Across all site-years, annual NEP increased by 107 g C m⁻² per unit
180 increase of NEP_{max} (g C m⁻² d⁻¹) (Fig. 2B). The relationship between NEP_{max} and NEP was similar
181 between DBF (123.2 g C m⁻²) and EF (112.9 g C m⁻²) per unit increase of NEP_{max} (g C m⁻² d⁻¹), and
182 both were higher than that in GRA (56.3 g C m⁻²) (Fig. 2B). NEP_{max} and CUP in combination
183 explained 73, 54, 63% of the variation in annual NEP anomalies in DBF, EF, and GRA, respectively,
184 as quantified using the structural equation models (Fig. A1).



185
 186 Fig. 2. (A) The changes in annual NEP anomalies with the anomalies of net carbon uptake period
 187 (CUP), and (B) the anomalies of maximum daily net ecosystem productivity (NEP_{max}) in temperate
 188 and boreal deciduous broadleaf (DBF), evergreen forest (EF) and grassland (GRA) ecosystems. The
 189 numbers in the legends are r values; all are significant at $P < 0.001$.

190
 191 **3.2. Spring phenology and NEP**
 192 BDOY was significantly correlated with spring temperature in DBF and EF (Fig. 3A), but not with
 193 spring precipitation or radiation in any biome ($P > 0.05$). BDOY advanced by 2.6 and 3.7 days per
 194 degree increase of spring temperature for DBF and EF, respectively (Fig. 3A). Early BDOY led to
 195 an increase in spring NEP in the three biomes, and annual NEP in DBF and EF (Fig. 3B and C). For
 196 example, spring NEP increased by 4.0, 0.8 and 1.6 g C m⁻² per day advance of BDOY for DBF, EF,
 197 and GRA, respectively (Fig. 3B), while annual NEP increased by 6.6 and 2.1 g C m⁻² per day

198 advance of BDOY for DBF and EF, respectively (Fig. 3C). All the spring climate factors in
199 combination explained 37% and 16% of the variation in BDOY in DBF and EF, respectively, but
200 explained only 3% in GRA (Fig. A1).



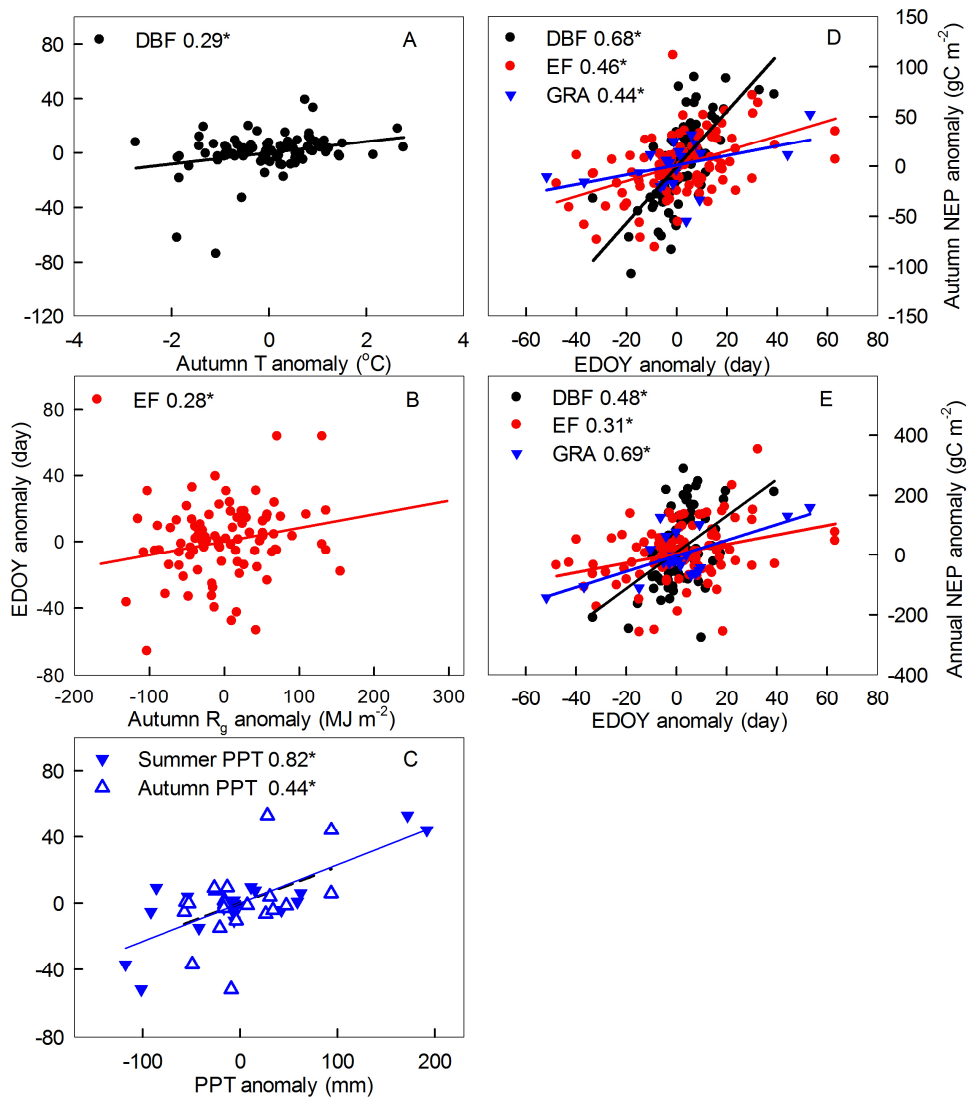
201
202 Fig. 3. (A) Spring phenology (net carbon sink beginning day, BDOY) in response to spring
203 temperature change, and its contribution to spring (B) and annual (C) NEP anomalies in temperate

204 and boreal deciduous broadleaf (DBF), evergreen forest (EF) and grassland (GRA) ecosystems. The
205 numbers in the legends are r values; all are significant at $P < 0.01$.

206

207 **3.3. Autumn phenology and NEP**

208 EDOY anomalies were positively correlated with autumn temperature anomalies in DBF ($P < 0.001$,
209 Fig. 4A), with autumn radiation anomalies in EF ($P < 0.01$, Fig. 4B), and with summer and autumn
210 precipitation anomalies in GRA ($P < 0.01$, Fig. 4C). EDOY was later by 4.1 days per degree increase
211 of autumn temperature in DBF (Fig. 4A), by 8 days per 100 MJ m⁻² increase of radiation in EF, and
212 by 2.3 days per 10 mm increase of summer or autumn precipitation in GRA. Later EDOY led to an
213 increase of autumn and annual NEP in the three biomes (Figs. 4D, E). Autumn NEP increased by 2.8,
214 0.8 and 0.5 g C m⁻² per extra day of EDOY for DBF, EF and GRA, respectively (Fig. 4D), while
215 annual NEP increased by 6.2, 1.6 and 2.6 g C m⁻² per day, respectively (Fig. 4E). The autumn
216 climate factors in combination explained 21% and 48% of the variation in EDOY in DBF and GRA,
217 respectively, but explained only 10% in EF (Fig. A1).



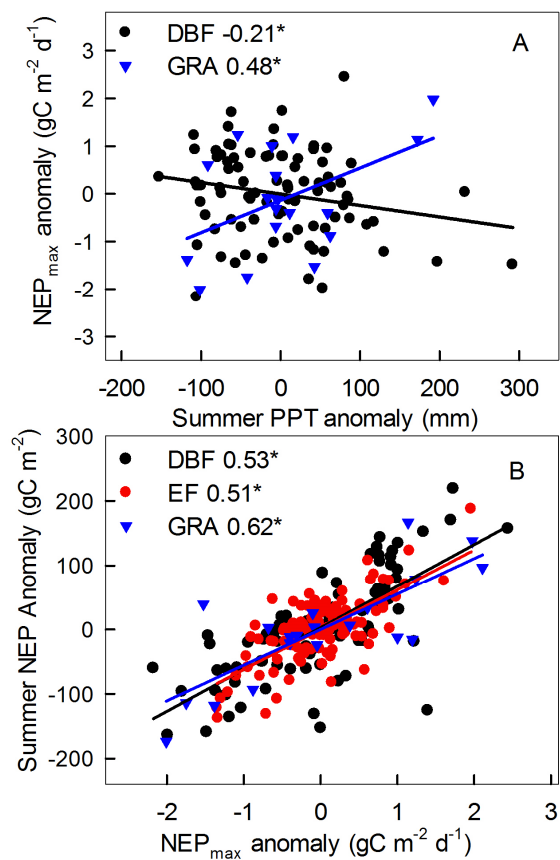
218

219 Fig. 4. (A-C) Significant relationships between meteorological variables and the day at which
 220 ecosystem net CO₂ uptake ends (EDOY) in temperate and boreal deciduous broadleaf (DBF),
 221 evergreen forest (EF) and grassland (GRA) ecosystems. The contributions of EDOY anomalies to
 222 autumn (D) and annual (E) NEP anomalies. The numbers in the legends are r values; all are
 223 significant at $P < 0.05$.

224

225 **3.4. NEP_{max} and NEP**

226 NEP_{max} had no significant relationship with summer temperature or radiation in any biome ($P > 0.05$),
 227 but was negatively correlated with summer precipitation anomalies in DBF and positively correlated
 228 with summer precipitation anomalies in GRA (Fig. 5A). NEP_{max} anomalies were related to summer
 229 NEP anomalies for all the three biomes with similar slopes (Fig. 5B). Summer climate factors in
 230 combination explained most (62%) of the variation of NEP_{max} in GRA but explained only 12% and 5%
 231 in DBF and EF (Fig. A1).

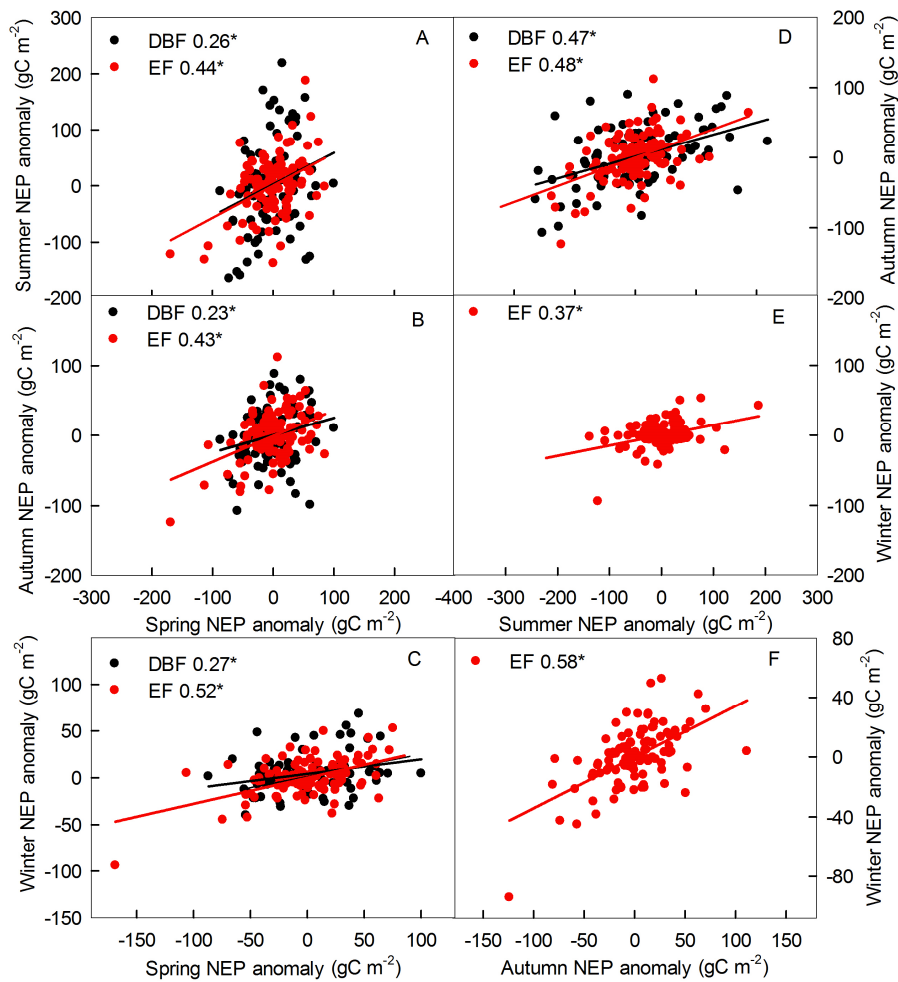


232
 233 Fig. 5. (A) The relationship between summer precipitation (PPT) and maximum daily net ecosystem
 234 productivity (NEP_{max}) in temperate and boreal deciduous broadleaf (DBF) and grassland (GRA)
 235 ecosystems. (B) The contribution of NEP_{max} anomalies to summer NEP anomalies at all three study
 236 biomes. The numbers in the legends are r values; all are significant at $P < 0.05$.

237

238 **3.5. Relationships among seasonal NEP**

239 Spring NEP anomalies were positively correlated with the summer, autumn, and winter NEP
240 anomalies in DBF and EF, and the slope of this relationship did not differ between biomes (Figs. 6A,
241 B, C). Summer NEP anomalies were correlated with autumn NEP anomalies in DBF and EF, and
242 with winter NEP anomalies in EF (Figs. 6D, E). Autumn NEP anomalies were positively correlated
243 with winter NEP anomalies only in EF (Fig. 6F). There were no significant relationships between
244 seasonal NEP anomalies in GRA.



245
246 Fig. 6. Relationships among the seasonal net ecosystem productivity (NEP) anomalies in temperate
247 and boreal deciduous broadleaf (DBF), evergreen forest (EF) and grassland (GRA) ecosystems. (A)

248 The relationships between spring NEP anomaly and summer NEP anomaly; (B) the relationships
249 between spring NEP anomaly and autumn NEP anomaly; (C) the relationships between spring NEP
250 anomaly and winter NEP anomaly; (D) the relationships between summer NEP anomaly and autumn
251 NEP anomaly; (E) the relationships between summer NEP anomaly and winter NEP anomaly; (F)
252 the relationships between autumn NEP anomaly and winter NEP anomaly. The numbers in the
253 legends are r values; all are significant at $P < 0.05$.

254

255 **4. Discussion**

256 We first discuss relationships between meteorological variables and the CUP, followed by a
257 discussion of the relationships between CUP, NEP_{max} , and NEP on the annual and seasonal bases.

258 **4.1. The relationship between climate and the beginning of the net carbon uptake period**

259 Our results show that interannual variability in ecosystem net carbon uptake phenology was sensitive
260 to climate factors. Spring temperature drives the variability in BDOY, with an average advance of
261 2.6 - 4.5 days $^{\circ}C^{-1}$ in warmer years (Fig. 3). The advancement of vegetation phenology in response
262 to temperature is well documented in previous studies (Jeong et al., 2011; Julien and Sobrino, 2009;
263 Keenan et al., 2014; Menzel and Fabian, 1999; Menzel et al., 2006; Piao et al., 2006; Schwartz et al.,
264 2006). In an analysis of direct observations of plant phenology over Europe for 1971–2000, Menzel
265 *et al.* (2006) detected an average advance of 0.25 days $year^{-1}$ in spring onset. Using satellite-
266 measured normalized difference vegetation index, Jeong et al. (2011) demonstrated that the start of
267 the growing season advanced by 5.2 days during 1982–1999 over the Northern Hemisphere due to
268 observed warming. Most of these previous studies used satellite-derived data to directly infer
269 vegetation phenological parameters (Jeong et al., 2011; Julien and Sobrino, 2009).

270 Vegetation phenology may not necessarily reflect ecosystem net carbon uptake phenology
271 (Bauerle et al., 2012; White and Nemani, 2003), but we found that BDOY responded to temperature
272 anomalies in DBF and EF (Fig. 3). The phenology of DBF emerged to be more sensitive to the
273 spring air temperature anomalies when compared with EF and GRA, likely because of the
274 fundamental differences in phenological strategies among the biomes. For example, leaf flush in
275 deciduous trees can occur rapidly compared to the reestablishment of photosynthetic mechanisms in
276 conifers (Gu et al., 2008; Monson et al., 2005; Richardson et al., 2010), resulting in a smaller
277 sensitivity of BDOY in response to a warmer spring in EF than in other biomes.

278

279 **4.2. The relationship between climate and the end of the net carbon uptake period**

280 Previous studies examining autumn phenology often focus on the impact of temperature on autumn
281 phenology of vegetation. For example, Keenan et al. (2014) reported that warmer autumn
282 temperatures lead to later senescence. The sensitivity of autumn phenology to a change from the
283 mean temperature was similar across forest types, with a 1 °C difference from the mean temperature
284 leading to a 1.8 day change in autumn senescence for DBF and a 6.3 day change in EF (Keenan et al.,
285 2014). Using satellite NDVI data, Stockli and Vidale (2004) reported a delay of senescence in
286 autumn by an average of 0.42 days year⁻¹ over Europe with observed climate warming, while
287 Tucker et al. (2001) found an earlier onset of autumn in Eurasia in a warmer environment. The
288 above-mentioned results suggest large uncertainties in estimating the key climate factors for
289 vegetation phenology changes in autumn (Menzel et al., 2006).

290 Vegetation phenology does not necessarily reflect net carbon uptake phenology, and we
291 found that the variability of EDOY was determined by different environmental factors in different
292 biomes. EDOY occurred later with higher autumn temperature in DBF, higher radiation in EF, and

293 more summer and autumn precipitation in GRA (Fig. 5). Our results indicate that precipitation and
294 radiation, in addition to temperature, play important roles in regulating the EDOY in temperate and
295 boreal ecosystems. More precipitation could improve soil water supply that enables longer carbon
296 gain into autumn, while higher radiation may enable more net carbon gain as days are getting shorter
297 and radiation is often limiting in autumn (Niu et al., 2011).

298

299 **4.3. The joint roles of CUP and NEP_{max} in regulating NEP**

300 The interannual variation in NEP was attributed to yearly anomalies in CUP and NEP_{max} (Figs. 2),
301 which in combination explained 54–73% of changes in annual NEP in the three biomes (Fig. A1). In
302 line with our findings, Xia et al. (2015) and Zhou et al. (2016) recently proposed that more than 90%
303 of annual gross primary productivity (GPP) can be explained by the combination of growing season
304 length and the maximum daily GPP in temperate, boreal, and arctic ecosystems. These findings
305 highlighted the important role of GPP_{max} and phenology in controlling production and emphasize the
306 importance of extending such an analysis to account for NEP in addition to GPP.

307 We found that an early onset of net carbon uptake enhanced spring and annual NEP (Fig. 3),
308 while a delay of EDOY increased autumn and annual NEP (Fig. 4), indicating the importance of
309 CUP in regulating carbon sequestration in temperate and boreal ecosystems. The observed link
310 between CUP and annual NEP in temperate and boreal ecosystems are consistent with the results of
311 Baldocchi *et al.* (2001), Baldocchi (2008), and Wu and Chen (2013). Compared to previous studies,
312 this study emphasized different sensitivities between climate and NEP among biomes and between
313 seasons. Spring, autumn, and annual NEP changed more in DBF than in EF and GRA with the same
314 change in BDOY or EDOY. This suggests a higher sensitivity of NEP to phenology changes in DBF
315 than other biomes. Some previous studies also reported that ecosystem productivity in DBF was

316 more sensitive than EF to carbon uptake period (Churkina et al., 2005; Wu et al., 2013). Using flux
317 data, Wu et al. (2013) quantified that a one-day increase in CUP led to a 3.3 and 1.5 g C m² y⁻¹
318 increase in annual NEP in DBF and EF, respectively. These results indicate that DBF tends to have a
319 higher productivity during the growing season than EF due to the fundamental differences in
320 physiological strategies between the two biomes (Barr et al., 2009; Falge et al., 2002a; Givnish, 2002;
321 Richardson et al., 2009). Deciduous broadleaf tree species evolved millions of years after conifers
322 and are much more efficient in assimilation per unit leaf surface—the luxury of shedding leaves in
323 winter. DBF are well known for having a higher maximum photosynthetic capacity, which is be
324 offset by a shorter vegetation period (Roser et al., 2002; Schulze et al., 1977). The observed
325 differences between EF and DBF in phenology-productivity relationships have ecological
326 implications, especially in the light of climate change effects on phenology, as phenology models
327 should predict ecosystem response to climate change in different ways for different biomes.

328 In addition to CUP, NEP_{max} also contributed to the interannual variability of ecosystem NEP,
329 especially during summer (Fig. 5). Our results showed that summer precipitation was related to
330 NEP_{max} in GRA and DBF, indicating that increases in annual NEP due to increases in CUP may be
331 offset by the influence of summer precipitation on NEP_{max}. These results suggest that CUP and
332 NEP_{max} may play different roles in regulating the variability of annual NEP, depending on their
333 interactions.

334

335 **4.4. Seasonal NEP contributions to annual NEP anomalies**

336 NEP anomalies in different seasons were related to annual NEP anomalies as expected (Fig. 6).
337 Spring phenology was more strongly related to spring NEP than to annual NEP, suggesting that
338 annual fluxes are much more variable because they are affected by weather events in other seasons.

339 For example, in grasslands, although early onset of BDOY led to an increase of spring NEP, annual
340 NEP showed no relationship with BDOY anomalies (Fig. 3). This is possibly due to the limitations
341 of summer precipitation, which led to lower summer NEP (Fig. 1E). The insignificant relationship
342 between spring NEP anomalies and NEP anomalies in other seasons in GRA (Fig. 6) also indicates
343 that the depression of NEP in other seasons may exceed the legacy effects of spring NEP on later
344 seasons. DBF and EF showed strong lag effects of spring NEP on the summer/autumn NEP (Fig. 6),
345 suggesting that spring phenology plays an important role in determining the seasonal and annual
346 NEP in these two biomes. Flux anomalies in other seasons may also partly contribute additional
347 variability to the annual NEP.

348 The various relationships between NEP anomalies in different seasons indicate that the
349 interannual variability of NEP can only be better understood by fully addressing the different
350 responses of seasonal NEP to climate and meteorological variability. If we connect annual NEP
351 anomalies to climate factors only at annual time scales, we might miss many significant relationships
352 between seasonal NEP and climate factors at the ecosystem scale. Temperature is the main factor
353 controlling the interannual variability of terrestrial NEP at the global scale (Jung et al., 2017; Wang
354 et al., 2013; Wang et al., 2014), as the ecosystem and regional effects of precipitation compensate
355 for each other (Ahlström et al., 2015; Poulter et al., 2014; Zeng et al., 2005). Understanding the links
356 between ecosystem and global scale responses to climate variability is an important avenue of future
357 research, and we must extend our understanding of the controls over NEP to tropical and subtropical
358 ecosystems to do so from the “bottom up” using ecosystem-scale observations.

359

360 **5. Conclusions**

361 By analyzing eddy covariance CO₂ fluxes from 24 flux tower sites, this study examined the
362 responses of CUP and NEP_{max} to climate factors in temperate and boreal ecosystems with
363 pronounced seasonality. Spring temperature was the primary controlling factor for BDOY, but the
364 controlling factors for EDOY were different among biomes. Summer precipitation was the main
365 factor effecting NEP_{max} for DBF and GRA. Because these critical phenology and physiology-
366 relevant variables were controlled by different seasonal environmental factors, there existed complex
367 relationships among NEP anomalies in different seasons. This study provides a fundamental
368 understanding of the role of ecosystem level phenology and physiology in regulating ecosystem
369 carbon sequestration across temperate and boreal ecosystems, and future studies should extend our
370 understanding to regions with less-pronounced seasonality to improve our understanding of the
371 relationship between climate and ecosystem carbon exchange.

372

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531

532 **Appendix A**

533 Table A1. Site characteristics, climatic index, and studied period of eddy covariance research sites in
 534 this analysis.

| Site name | Veg ¹ | Lat* | Lon** | PPT ² (mm) | Ta (°C) | Period | References |
|-----------|------------------|-------|---------|-----------------------|---------|-----------|--------------------------------|
| AT-Neu | GRA | 47.12 | 11.32 | 1040.4 | 6.3 | 2002-2009 | (Wohlfahrt et al., 2008) |
| BE-Bra | EF | 51.31 | 4.52 | 742.7 | 10.0 | 2000-2009 | (Gielen et al., 2010) |
| BE-Vie | EF | 50.31 | 6.00 | 1065.1 | 7.4 | 1996-2007 | (Aubinet et al., 2001) |
| CA-Ca1 | EF | 49.87 | -125.33 | 1369.2 | 9.9 | 1998-2005 | (Humphreys et al., 2006) |
| CA-Let | GRA | 49.71 | -112.94 | 349.9 | 6.2 | 1998-2005 | (Flanagan et al., 2002) |
| CA-Man | EF | 55.88 | -98.48 | 515 | -1.2 | 1995-2003 | (Dunn et al., 2007) |
| CA-Oas | DBF | 53.63 | -106.2 | 428.5 | 0.3 | 1997-2005 | (Black et al., 2000) |
| DE-Hai | DBF | 51.08 | 10.45 | 780.3 | 7.2 | 2000-2007 | (Knobl et al., 2003) |
| DE-Tha | EF | 50.96 | 13.57 | 643.1 | 8.1 | 1997-2008 | (Grunwald and Bernhofer, 2007) |
| DK-Sor | DBF | 55.49 | 11.65 | 952 | 8.7 | 1998-2009 | (Pilegaard et al., 2003) |
| FI-Hyy | EF | 61.85 | 24.29 | 620.2 | 2.2 | 1997-2008 | (Suni et al., 2003) |
| FR-Pue | EF | 43.74 | 3.59 | 734.5 | 12.9 | 2001-2008 | (Rambal et al., 2004) |
| FR-Hes | DBF | 48.67 | 7.06 | 793.3 | 9.2 | 1997-2008 | (Granier et al., 2000) |
| IT-Ren | EF | 46.59 | 11.43 | 964.7 | 6.2 | 2001-2009 | (Montagnani et al., 2009) |
| IT-Col | DBF | 41.85 | 13.59 | 970.9 | 7.3 | 1997-2007 | (Van Dijk and Dolman, 2004) |
| US-Blo | EF | 38.9 | -120.63 | 1630 | 12.5 | 1999-2006 | (Goldstein et al., 2000) |
| US-MMS | DBF | 39.32 | -86.41 | 1031.6 | 10.8 | 1999-2006 | (Schmid et al., 2000) |
| IT-Ro1 | DBF | 42.41 | 11.93 | 763.7 | 15.3 | 2001-2008 | (Rey et al., 2002) |
| NL-Loo | EF | 52.17 | 5.74 | 786.2 | 9.4 | 1997-2009 | (Dolman et al., 2002) |
| US-Ha1 | DBF | 43.54 | -72.17 | 1071 | 6.6 | 1993-2006 | (Urbanski et al., 2007) |
| US-Ho1 | EF | 45.2 | -68.74 | 1070.3 | 5.3 | 1996-2004 | (Hollinger et al., 2004) |
| US-UMB | DBF | 45.56 | -84.71 | 803.4 | 5.8 | 1999-2006 | (Gough et al., 2008) |
| US-NR1 | EF | 40.03 | -105.54 | 595.2 | 0.4 | 1999-2007 | (Monson et al., 2002) |
| US-Var | GRA | 38.41 | -120.95 | 543.9 | 15.9 | 2001-2008 | (Xu and Baldocchi, 2004) |

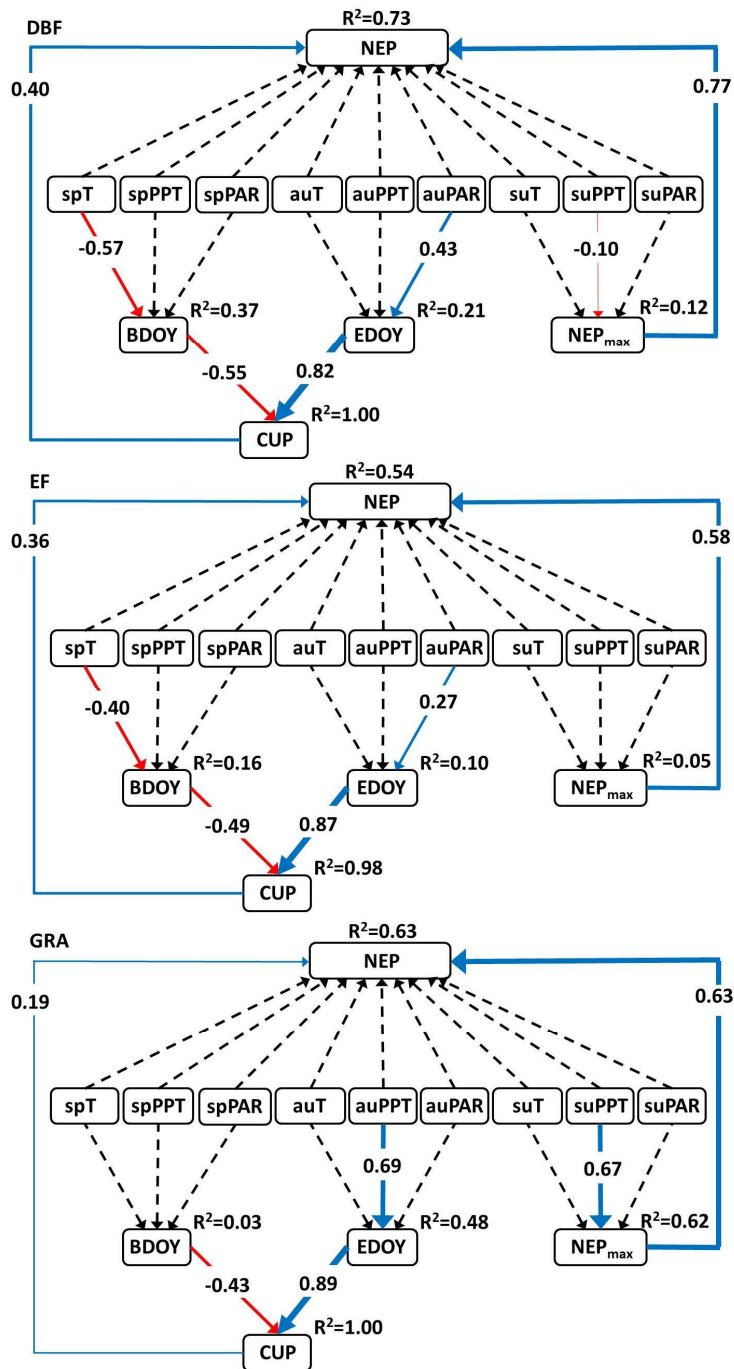
535 *Positive value indicates north latitude. **Negative value indicates west longitude. ¹vegetation, ²precipitation. DBF:

536 deciduous broadleaf forest; EF: evergreen forest; GRA: grassland.

537 Table A2. The mean and variability of the beginning date (BDOY) and ending date (EDOY) of net
 538 carbon uptake for each study site during the study period.

| Sites | Vegetation | BDOY | | EDOY | |
|--------|------------|-------|------|-------|------|
| | | Mean | SD | Mean | SD |
| CA-Oas | DBF | 135.6 | 10.8 | 251.4 | 4.2 |
| DE-Hai | DBF | 116.0 | 4.5 | 280.3 | 5.6 |
| DK-Sor | DBF | 108.7 | 6.4 | 262.8 | 8.3 |
| FR-Hes | DBF | 18.4 | 23.0 | 337.3 | 19.5 |
| IT-Col | DBF | 53.3 | 12.7 | 322.3 | 11.5 |
| US-MMS | DBF | 31.3 | 9.9 | 277.8 | 21.3 |
| IT-Ro1 | DBF | 30.7 | 21.6 | 306.4 | 31.7 |
| US-Ha1 | DBF | 77.2 | 5.1 | 294.0 | 18.9 |
| US-UMB | DBF | 110.0 | 8.1 | 285.9 | 5.1 |
| BE-Bra | EF | 91.3 | 16.2 | 267.7 | 7.7 |
| BE-Vie | EF | 45.9 | 16.3 | 292.6 | 10.9 |
| CA-Ca1 | EF | 12.9 | 6.4 | 290.8 | 54.1 |
| CA-Man | EF | 98.8 | 17.8 | 247.6 | 16.7 |
| DE-Tha | EF | 42.0 | 17.1 | 314.7 | 13.4 |
| FI-Hyy | EF | 85.8 | 10.1 | 260.8 | 11.4 |
| FR-Pue | EF | 108.1 | 4.3 | 277.9 | 16.0 |
| IT-Ren | EF | 111.4 | 12.7 | 278.9 | 12.8 |
| US-Blo | EF | 91.3 | 11.6 | 269.0 | 35.7 |
| NL-Loo | EF | 133.2 | 5.3 | 274.5 | 4.1 |
| US-Ho1 | EF | 109.6 | 3.7 | 279.0 | 5.9 |
| US-NR1 | EF | 132.3 | 7.5 | 267.4 | 5.3 |
| AT-Neu | GRA | 89.7 | 4.5 | 255.1 | 4.0 |
| CA-Let | GRA | 110.7 | 13.8 | 219.2 | 35.3 |
| US-Var | GRA | 16.7 | 15.8 | 134.4 | 7.1 |

539



540
 541 Fig. A1. The structure equation modeling results of the relationship between the anomalies in
 542 environmental factors and the anomalies in net carbon uptake period (CUP) and the maximum daily
 543 net ecosystem productivity (NEP_{max}) attributes of NEP in temperate and boreal deciduous broadleaf
 544 (DBF), evergreen forest (EF) and grassland (GRA) ecosystems. Blue arrows indicate significant
 545 positive relationships while red arrows indicate significant negative relationships ($P < 0.05$). Black

546 dashed arrows indicate insignificant relationships ($P>0.05$). Arrow width is proportional to the
547 strength of the relationship. Numbers adjacent to arrows are path coefficients and indicative of the
548 effect size of the relationship. The proportion of variance explained (R^2) appears alongside every
549 response variable in the model. BDOY and EDOY indicate the beginning and ending date of net
550 carbon uptake, respectively. T, PPT, and PAR indicate temperature, precipitation, and radiation,
551 respectively. Sp, su, and au indicate spring, summer, and autumn, respectively.
552

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