1 **Title:** Climate warming increases spring phenological differences among temperate
2 trees

3 **Running Title:** Warming increases spring phenology difference

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33   **Abstract**

34   Climate warming has substantially advanced spring leaf flushing, but winter chilling

35   and photoperiod co-determine the leaf flushing process in ways that vary among

36   species. As a result, the interspecific differences in spring phenology (IDSP) are

37   expected to change with climate warming, which may in turn induce negative or

38   positive ecological consequences. However, the temporal change of IDSP at large

39   spatio-temporal scales remains unclear. In this study, we analyzed long-term in-situ

40   observations (1951−2016) of six, co-existing temperate tree species from 305 sites

41   across central Europe and found that phenological ranking did not change when

42   comparing the rapidly warming period 1984−2016 to the marginally warming period

43   1951−1983. However, the advance of leaf flushing was significantly larger in early-

44   flushing-species EFS (6.7 ± 0.3 d) than in late-flushing-species LFS (5.9 ± 0.2 d)

45   between the two periods, indicating extended IDSP. This IDSP extension could not be

46   explained by differences in temperature sensitivity between EFS and LFS; however,

47   climatic warming-induced heat accumulation effects on leaf flushing, which were

48   linked to a greater heat requirement and higher photoperiod sensitivity in LFS, drove

49   the shifts in IDSP. Continued climate warming is expected to further extend IDSP

50   across temperate trees, with associated implications for ecosystem function.

51

52   **Keywords:** climate change, phenological shift, interspecific differences in spring

53   phenology, temperature sensitivity, photoperiod

Introduction

Climate warming impacts terrestrial ecosystem carbon and water cycles (Cannell & Smith, 1986; Chuine, 2010; Bradley, Leopold, Ross & Huffaker, 1999; Snyder & Spano, 2013) over the long term, partly due to earlier spring leaf flushing in temperate and boreal deciduous forests (Basler & Körner, 2014; Chuine, 2010; Fu et al., 2019a; Fu et al., 2019b; Laube et al., 2014). The timing of spring leaf flushing is one of the most sensitive and visible bio-indicators of ongoing climate change (Kharouba et al., 2018; Van Asch & Visser, 2007; Zohner, Benito, Svenning & Renner, 2016) because it is principally controlled by temperature (Peñuelas, Rutishauser & Filella, 2009; Zohner, Mo & Renner, 2018). However, other factors, such as winter low temperature (or chilling accumulation) (Keenan et al., 2014; Piao et al., 2019), and photoperiod (day length) (Chuine, 2010; Körner & Basler, 2010), also affect the timing of leaf flushing and their importance may increase under further warming (Menzel et al., 2006). Species differences in forcing, chilling and photoperiodic requirements (Chuine et al., 2016; Fu et al., 2014; Keenan et al., 2014) may result in altered interspecific time differences in leaf flushing phenology (IDSP), which may ultimately alter the sequence in time of leaf flushing ("ranking", previously also known as interception (Peñuelas et al., 2009)) among the different species. There are three theoretical shifts in IDSP between early and late flushing species (Vitasse, Lenz, Hoch & Körner,2014) (called hereafter EFS and LFS, respectively, ranking based on the timing of leaf-out) from current to future climatic conditions (Fig. S1a): stable IDSP, where leaf flushing advance is similar between EFS and LFS (Fig. S1b); reduced IDSP between EFS and

76   LFS, due to greater leaf flushing advance for LFS than EFS (Fig. S1c); and extended

77   IDSP between EFS and LFS, due to greater leaf flushing advance for EFS than LFS

78   (Fig. S1d).

79

80   Changes in IDSP may elicit ecological perturbations. For example, plant competition

81   may change, as species with greater advance in leaf flushing may profit from a longer

82   growing season, shade competitors with later flushing and thus gain a competitive

83   advantage providing that they can still avoid damaging late spring frost events.

84   Changes in competitive relationships or trophic mismatches could further influence

85   resource allocation and structural adjustment of the ecosystem, eventually altering

86   terrestrial carbon and water cycling. For example, leaf phenology directly affects the

87   light and water requirements in the forest canopy and understory, which further

88   determines the photosynthetic efficiency and carbon uptake and metabolism (Cleland,

89   Chuine, Menzel, Mooney & Schwartz, 2007; Peñuelas, Rutisshauser & Filella, 2009;

90   Schwartz, 1998). Reductions in spatial variation of leaf flushing have been reported

91   across central Europe within species both across elevations (Vitasse, Signarbieux & Fu,

92   2018) and latitudes (Ma, Huang, Hänninen & Berninger, 2018), which was also

93   confirmed by remote sensing analyses associated with climatic warming across the

94   Northern hemisphere (Liu et al., 2019). However, temporal changes in IDSP among

95   species have been little studied (but see Peñuelas & Filella, 2001; Roberts, Tansey,

96   Smithers & Phillimore, 2015) despite their importance in understanding ecosystem

97   responses to ongoing climate change.

98   Therefore, we investigated the IDSP among six common, co-existing tree species, three

99   of them EFS and three LFS, across 305 central European sites with temperate forest

100   tree species (Fig. S2). The aim of our study was to determine and quantify temporal

101   changes and associated physiological and climatic drivers in leaf flushing IDSP among

102   the six species during the period 1951−2016.

103

104   **Material and methods**

105   **Datasets.** Leaf flushing data for EFS *Betula pendula* (BP, European silver birch),

106   *Aesculus hippocastanum* (AH, horse chestnut), and *Alnus glutinosa* (AG, European

107   alder), and LFS *Fagus sylvatica* (FS, European beech), *Quercus robur* (QR, Pedunculate

108   oak), and *Fraxinus excelsior* (FE, European ash) co-occurring in central European sites

109   during the period 1951–2016 were obtained from the open access Pan European

110   Phenology network (www.pep725.eu). It is one specimen per site for each species, and

111   a specimen presents a group of individuals (2-3) at each site, and then the averaged dates

112   were defined at the phenological dates (DWD, 2018). Datasets comprised a minimum

113   of 30 years over the period 1951-2016, representing 15 years in each of two 33-year

114   periods (mild warming period of 1951−1983 and pronounced warming period of

115   1984−2016, Fig. S3), for all six species at each site. Data >2×SD (standard deviation of

116   the mean leaf flushing date) were excluded to discard possible errors, which account for

117   3.8% in EFS and 4.0% in LFS during 1951-2016, distributed randomly. Similar results

118   without data reduction were found (Fig. S4). In total, we selected data for 305 sites (Fig.

119   S2), to which a gridded climatic dataset was applied, with a spatial resolution of 0.25°

120 (approximately 25 km, Beer et al., 2014), comprising daily mean air temperature,

121 precipitation, and radiation measurements (Fu et al., 2015). We further tested the

122 reliability of the results using the well-known Princeton climatic dataset, at 0.25°

123 spatial resolution, (http://hydrology.princeton.edu/data/pgf/v3/0.25deg /daily/), and

124 very similar results were found (Fig. S5).

125

126 **Analysis.** We analyzed spring warming as the mean value and the corresponding SD

127 of the air temperature during the temperature relevant period (TRP). TRP was

128 calculated as the period before leaf flushing with the highest absolute partial correlation

129 between leaf flushing date and mean air temperature. Considering the differences

130 among species and sites in responding to climate change, different TRPs were used for

131 each species and site (Fig. S6), like in earlier analyses (Fu et al., 2015), ranging from

132 15 to 120 d, with 15-d steps. We investigated the TRP variation with latitudes (Fig. S6).

133 The mean length of TRP was 59 days prior to the day of leaf flushing, but a large

134 variation was found among sites and species, with TRP decreasing with increasing

135 latitudes (Fig. S6), thus showing the robustness of the location-specific application of

136 the TRP in the present study.

137

138 Apparent temperature sensitivity (S_T) was defined as the number of advanced days per

139 1 □ of warming, which has been widely used to evaluate the long-term implications of

140 temperature changes for plant phenology. The S_T was determined by reduced major-

141 axis regression (RMA) between leaf flushing date and mean air temperature during the

142   TRP (Keenan, Richardson & Hufkens, 2019). To validate the results, we also used daily

143   maximum temperatures to analyze TRP and apparent sensitivities of leaf flushing to

144   maximum temperature during TRP (S_{Tmax}). Similar results were found (Fig. S7).

145

146   Chilling accumulation breaks dormancy in deciduous tree species and heat

147   accumulation leads to leaf flushing, so their metrics have been widely used to estimate

148   the physiological requirement of spring leaf flushing in temperate woody species.

149   Chilling requirement (CD_{req}) was defined as the number of days with non-freezing

150   mean air temperature (generally between 0 and 5 °C) during the period 1st November

151   to the mean leaf flushing date:

152
$$CD_{req}(t) = \sum_{t_0}^{LO} 1 \qquad \text{if} \quad 0 \leq T_t \leq T_{high}$$

153   where t_0 is the start date of chilling accumulation (fixed at 1st November before the year

154   of leaf flushing), LO is the mean leaf flushing date, T_t is mean daily air temperature,

155   and T_{high} is the upper limit of the temperature threshold (generally 5 or 8 °C). We tested

156   the same calculation by setting the temperature threshold within 0 to 8 °C and tested

157   1st September as start date (Fig. S8); In addition, because the correlation between

158   chilling and forcing is still unclear, to test the robustness of the chilling estimation, we

159   also calculated the chilling accumulation by fixing the time period from 1st November

160   to 31th December (Fig. S8d). This led to very similar results, so we reported the results

161   using the threshold of 5 °C and 1st November until the start date of leaf flushing.

162

163   The heat requirement for leaf flushing was defined as the growing degree days (GDD),

164   calculated as the sum of mean air temperature above a temperature threshold from 1st

165   January to leaf flushing date. We used three common methods as follows:

166   (1) Linear function, by using a base temperature of 5 °C:

167
$$GDD = \sum_{t_0}^{LO} (T_t - 5) \qquad if \quad T_t \geq 5$$

168   (2) Piecewise function, by using a temperature threshold of 5 and 15 °C, and fixed

169   units when temperature was above 15 °C:

170
$$GDD = \sum_{t_0}^{LO} \begin{cases} 0 & if \quad T_t < 5 \\ T_t - 5 & if \quad 5 \leq T_t \leq 15 \\ 10 & if \quad T_t > 15 \end{cases}$$

171   (3) Sigmoidal function, by using a base temperature of 0 °C:

172
$$GDD = \sum_{t_0}^{LO} \begin{cases} 0 & if \quad T_t < 0 \\ \dfrac{28.4}{1 + e^{-0.185(T_t - 18.4)}} & if \quad T_t \geq 0 \end{cases}$$

173   where t_0 is the start date of GDD calculation, fixed at 1st January, *LO* is the leaf flushing

174   date, and T_t is daily mean air temperature. The three methods produced similar results,

175   so we only reported the results of the linear function in the main text and reported the

176   results of the other two functions in the appendix (Fig. S9).

177

178   **Statistical analysis.** We then determined the frequency distributions of main variables

179   (difference in leaf flushing dates / temperature sensitivity / chilling accumulation /

180   GDD requirements between EFS and LFS or between 1951-1983 and 1984-2016), and

181   plotted in histograms. For each species, we applied paired t-tests to detect whether the

182   average flushing date and its variance changed significantly between time periods. To

183   adequately model the structure in the data (e.g. site locations, species, years), we

184   adopted the mixed effect models using lmerTest package in R3.5.2 (Phillimore, Leech,

185   Pearce-Higgins & Hadfield, 2016), by setting leaf flushing dates, temperature

186   sensitivity, chilling accumulation and GDD requirements as response variables, setting

187   time period (1951-1983 versus 1984-2016) and grouping of species (EFS versus LFS)

188   as fixed effects, and setting sites (including latitude, longitude and elevation), species

189   and years as random effects (Table S1). We also analyzed the number of sites in which

190   species phenological shift occurred and the direction of change, and presented the

191   results through CIRCOS figures (Fig. 1c) by http://mkweb.bcgsc.ca/tableviewer/.

192

193   **Results and discussion**

194   The mean leaf flushing date over the period 1951−2016 was 21 April (Day of year: 111

195   ± 6, mean ± SD across sites and species) for the EFS *Betula pendula* (BP), *Aesculus*

196   *hippocastanum* (AH), and *Alnus glutinosa,* (AG), and 4 May (Day of year: 124 ± 5 d)

197   for the LFS *Fagus sylvatica* (FS), *Quercus robur* (QR), and *Fraxinus excelsior* (FE)

198   (Fig. 1a). Thus, there was a difference of 13 d in mean leaf flushing dates between EFS

199   and LFS. Variation in mean leaf flushing date (measured as the standard deviation of

200   leaf flushing date over the study period, 1×SD) tended to be greater for EFS (9.4 ± 2.5

201   d) than for LFS (7.8 ± 2.0 d) ($P < 0.05$, Fig. 1a). We found that the advance in leaf

202   flushing date across the six temperate tree species increased from 0.9 ± 0.7 d (mean ±

203   s.e.) during the period 1951−1983 to 13.5 ± 0.7 d during the period 1984−2016 , when

204   climate warming accelerated (the species-specific temporal changes in leaf flushing

205   dates across all sites between the two time period can be found in Table S2 and Fig.

206   S10), supporting previous reports (Fu et al., 2019b; Menzel, 2013). Although the

207   magnitude of advance differed among the six species, the overall phenological ranking

208   remained stable over the period 1951-2016 (Fig. S10) while site-specific shifts in

209   ranking occurred at 49.2-52.8% of sites for EFS and 16.1-33.1% of sites for LFS (Fig.

210   1c). When compared the leaf flushing dates between 1951−1983 and 1984−2016, we

211   found a greater magnitude of advancement in the EFS (mean ± s.e.: 6.7 ± 0.3 d) than

212   in the LFS (5.9 ± 0.2 d) (Fig. 1b, mixed effect model was applied including sites and

213   species as random effects: P < 0.001), confirming an enlarged IDSP between

214   1951−1983 and 1984−2016.

215

216   To explain our finding of extended IDSP, but general stability in rank order of leaf

217   flushing among the six species, we propose four mutually non-exclusive hypotheses:

218   (1) difference in seasonal warming, since warming may be stronger during earlier

219   spring than in later spring; (2) difference in temperature sensitivity, where temperature

220   sensitivity to leaf flushing may be greater in EFS than LFS (Menzel, Estrella & Fabian,

221   2001; Menzel, Sparks, Estrella & Roy, 2006); (3) interaction between chilling effects

222   and heat requirements among species, where chilling effects are similar due to identical

223   winter conditions, but LFS may have greater heat requirement than EFS (Fu et al.,

224   2015); and (4) differences in photoperiod and water limitation among species, where

225   sensitivity to photoperiod and water shortage may be greater in LFS than EFS (Chuine,

226   2010; Cleland et al., 2007), leading to a smaller advance in LFS under climate warming.

227

228   To test the first hypothesis, we analyzed monthly warming trends over the study period,

229   but did not find early spring (February and March) significantly more strongly warming

230   ($P > 0.05$) than later spring (April and May); in contrast, climate warming in May was

231   greater than in February and March (Fig. 2a). Next, we estimated mean temperature

232   and its variability (1×SD) during the most temperature relevant period (TRP, see

233   Methods) for leaf flushing during the periods 1984−2016 and 1951−1983, and found

234   increased temperatures during the TRP for both groups of tree species (EFS and LFS),

235   but in contrast to the hypothesis, because the increase was greater in LFS (mean

236   increase: 0.9 °C) than in EFS (mean increase: 0.7°C) (Fig. 2b). Variation in temperature

237   during the most relevant period remained stable for EFS, but increased for LFS (Fig.

238   2c). A higher fluctuated temperature may constrain advances of leaf flushing of LFS to

239   avoid frost damages (Zohner et al., 2017). These results indicate that the climate

240   variation, more than warming, may drive the extended time difference in leaf flushing

241   between EFS and LFS, assuming that the temperature sensitivity of EFS and LFS was

242   identical.

243

244   It is more likely that sensitivity to temperature changes is greater in EFS than in LFS

245   in order to enable competitive advantages, although earlier leaf flushing may also

246 increase the risk of late frost damage (Inouye, 2008; Richardson et al., 2018). Therefore,

247 a greater advancement in leaf flushing may be expected in EFS, given stable warming

248 trends. Indeed, we found significantly larger S_T (apparent temperature sensitivity) of

249 leaf flushing in EFS than in LFS (3.8 ± 0.1 and 2.9 ± 0.1 d $^{\circ}C^{-1}$, respectively) during

250 the period 1951−1983 ($P < 0.05$, mixed effect model was applied including sites and

251 species as random effects); however, S_T was significantly reduced to 2.9 ± 0.1 d $^{\circ}C^{-1}$ in

252 EFS during the period 1984−2016, but remained stable in LFS. As a result, there was

253 no overall difference in S_T between EFS and LFS during the recent period 1984−2016

254 (Fig. 3d, mixed effect model: $P = 0.14$). Reduced S_T in EFS and a trend towards higher

255 temperatures at leaf flushing in LFS rather than in EFS (Fig. 2b) did not explain the

256 extended time difference in leaf flushing between the two groups, because a warmer

257 late spring and similar S_T for EFS and LFS during the period 1984−2016 should have

258 led to the greater advancement in leaf flushing for LFS.

259

260 The third hypothesis relates to physiological processes associated with chilling and

261 subsequent heat requirements for spring leaf flushing. Climate warming may reduce

262 the plants' ability to fulfill the amount of chilling that is required to break dormancy in

263 many temperate tree species (Hänninen, 2016; Piao et al., 2019), with the consequence

264 that greater heat is required to trigger leaf flushing (Cannell & Smith,1983; Fu et al.,

265 2015). EFS and LFS experience the same length of chilling days during the winter, but

266 EFS and LFS experience different amounts of chilling accumulation during the spring.

267 Our data support this hypothesis, because the difference in chill days between EFS and

268 LFS during the period 1951−1983 (2.0 ± 0.1 d) was not significantly different from the

269 period 1984−2016 (1.8 ± 0.1 d) (Fig. 3a, P = 0.62, mixed effect model was applied

270 including sites and species as random effects), but species' heat requirements, defined

271 as growing degree days (GDD, see Methods), were negatively related to chilling

272 accumulation and significantly increased in both EFS (1951−1983: 113.1 ± 1.9 °C;

273 1984−2016: 118.2 ± 2.0 °C) and LFS (1951−1983: 173.2 ± 2.5 °C; 1984−2016: 183.4

274 ± 2.7 °C) (Fig. 3b). This larger increase in GDD in LFS led to increased differences in

275 GDD requirements between the two groups (1951−1983: 60.1 ± 1.0 °C; 1984−2016:

276 65.3 ± 1.1 °C) (Fig. 3b, P < 0.01). The time required to accumulate an increased GDD

277 in LFS may subsequently result in a smaller advance in leaf flushing in LFS and extend

278 the time difference in leaf flushing between the two groups. Thus, the extended IDSP

279 is likely to occur due to the asymmetric increase in heat requirements between EFS and

280 LFS.

281

282 Our fourth hypothesis relates to effects of photoperiod on the leaf flushing process that

283 may vary with species due to genotype and ontogeny (Chuine et al., 2016; Flynn &

284 Wolkovich, 2018; Richardson, Hufkens, Li & Ault, 2019; Yang & Rudolf, 2010); for

285 example, it has been suggested that LFS rely on photoperiod to a greater extent than

286 EFS (Van Asch & Visser, 2007). We found that climate warming advanced leaf

287 flushing, so the effects of a resulting shorter photoperiod on the leaf flushing process

288 may have increased in both EFS and LFS, but larger in LFS, and thus led to a relatively

289 shorter advancement in leaf flushing date. Since it was not possible to assess direct

290   effects of photoperiod in this study, we estimated changes in variation of leaf flushing

291   dates for both EFS and LFS between the two study periods as a surrogate measure,

292   because a higher photoperiod effect is likely to be associated with a lower variation in

293   flushing dates (the variation of flushing dates was defined as one standard deviation:

294    $1 \times SD$, LO_{SD}). We found that the LO_{SD} tended to be lower during the period 1984−2016

295   (EFS: 7.4 ± 1.8 d; LFS: 5.9 ± 1.6 d) than during 1951−1983 (EFS: 8.1 ± 1.7 d; LFS:

296   6.1 ± 1.5 d) (Fig. 3c) for both EFS and LFS, but the reduction was significantly lower

297   in LFS (0.2 ± 0.1 d) than in EFS (0.7 ± 0.1 d), suggesting a larger photoperiod effect

298   in LFS. To further test the photoperiod limitation hypothesis, we investigated the

299   correlation between latitudes and IDSP comparing EFS and LFS, as well as the species-

300   specific variation of advanced leaf flushing date along latitude. Interestingly, we found

301   the IDSP was significantly reduced at lower latitudes across all species (Fig. 4), and

302   the advancement increased at higher latitudes for each species ($P < 0.05$, Fig. S11). The

303   significant reduction in advancement at low latitudes suggested that photoperiod likely

304   limits the advancement at the low latitudes, rather than at high latitudes, to constrain

305   too early leaf flushing. Furthermore, a relatively smaller advancement in leaf flushing

306   was found at higher latitudes for LFS than EFS, which may be because LFS is more

307   sensitive to photoperiod than EFS at higher latitudes. These results suggest that the

308   extended IDSP difference between EFS and LFS may partially explained by the

309   photoperiod. In addition, within forests, earlier flushing of EFS may increase the water

310   stress for LFS (Bradley et al., 1999; Spano, Snyder & Cesaraccio, 2013), and thus

311   postpone the date of leaf flushing of LFS (Spano, Snyder & Cesaraccio, 2013).

312   However, annual precipitation over the study area is larger than 700 mm (EEA, 2012),

313   and the difference in precipitation sum over the TRP between EFS and LFS was

314   insignificant (Fig. S12). This suggests that water shortage limitations on spring leaf-

315   out for LFS were unlikely, rendering a contribution to the extended IDSP between EFS

316   and LFS improbable.

317

318   Phenological sensitivity to environmental changes is a strategy of temperate trees to

319   optimize growth in regards to climatic fluctuations. Our results provide empirical

320   evidence for an overall stability in phenological ranking among temperate tree species

321   in central Europe over the past six decades. Interestingly, we found that differences in

322   phenological responses between EFS and LFS under rapid warming resulted in a

323   significantly extended IDSP. Plant phenology plays a key role in ecosystem structure

324   and function, and changes in IDSP are likely to elicit ecological consequences (Cleland

325   et al., 2007; Van Asch & Visser, 2007; Vitasse et al., 2018). The advancement in leaf

326   flushing in EFS may be exacerbated under future climate warming conditions to a

327   greater extent than in LFS, so that EFS may benefit from a longer growing season and

328   gain a competitive advantage over LFS in light and water accessibility. Shifts in IDSP

329   may also affect trophic interactions, because of the reliance of many vertebrates on

330   leaf-feeding insects for food. However, great variation exists in the speed of

331   phenological adjustments of insects, possibly leading to trophic synchrony disruption

332   (Gaudry et al., 2015; Renner & Zohner., 2018). Further studies are warranted to

333   confirm these results for different tree species and in different climate zones, especially

15

334   in regions with larger climatic ranges, such as North America and Alpine ecosystems.

335

336   Under future climate warming conditions, differences in timing of spring leaf flushing

337   among species may continue to increase, and may result in a change in the order of

338   spring phenology in temperate forests, especially due to species-specific chilling

339   requirement, as argued by Roberts et al. (2015) using modeling approaches.

340   Furthermore, as extreme weather events become more frequent, it is also worth noting

341   that chilling and GDD requirements for some tree species would also be altered, which

342   will further complicate the model development. However, accurate prediction of the

343   development of phenological difference under future climate change remains a

344   challenge and requires additional investigation, because chilling and GDD

345   requirements, and the temperature thresholds in chilling and GDD estimation, differed

346   at species- and site-scales, and their correlations with photoperiod effects are still

347   uncertain. Ecosystem-scale impacts of enlarged IDSP, for example, effects of extended

348   phenological differences on the carbon and water balance and on nutrient losses, are

349   largely unknown. In LFS-dominated forests, like in our study area (EEA, 2017), the

350   extended IDSP would likely hamper increases in the forests' carbon sink strength

351   because the LFS would not be able to extend their leaf season to the same extent than

352   EFS. In addition, the extended IDSP may increase uncertainty in spring phenology

353   estimation from satellite images, as remote sensing approaches mainly trace the

354   phenology of EFS (Fu et al., 2019a), and are subsequently prone to overestimation of

355   ecosystem carbon uptake (Piao, Friedlingstein, Ciais, Viovy & Demarty, 2007). In

356   addition, previous studies have estimated that earlier start of growing season will

357   increase the vegetation productivity (Zohner, Mo, Pugh, Bastin & Crowther, 2020).

358   However, when considering the spatial variability of phenology shifts and the possible

359   mutual constrains caused by interspecific differences in leaf flushing, the prediction of

360   ecosystem productivity becomes more uncertain. Therefore, we encourage further

361   research that focuses on potential implications of shifted IDSP for ecosystem carbon

362   and water balance, as well as for plant−animal interactions, where experimental studies

363   would be particularly insightful to improve our understanding of shifted IDSP

364   consequences for ecosystems.

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Figure legends

Fig. 1 Distribution of mean leaf flushing dates in early and late flushing species

(EFS and LFS, respectively) and changes in leaf flushing orders. (a) Distribution

of leaf flushing for each species during the period 1951−2016. **(b)** Direction and

magnitude of phenological shift (indicated by arrow direction and length) in leaf

flushing dates of EFS and LFS. **(c)** Direction and proportion of changes in leaf flushing

orders across 305 sites within EFS and LFS. The arrow indicates the direction of

changes in leaf flushing orders among species within group. Each value in the tables

indicate the percentage of sites where the leaf flushing order of the two species in the

corresponding row and column is interchanged. BP: *Betula pendula*; AH: *Aesculus*

hippocastanum; AG: *Alnus glutinosa;* FS: *Fagus sylvatica;* QR: *Quercus robur;* and,

FE: *Fraxinus excelsior*.

Fig. 2 Temporal changes of temperature and leaf flushing sensitivity to

temperature (S_T). (a) Mean monthly warming rates across all sites during the period

1951−2016. Mean monthly warming rate was calculated using linear regression

between mean monthly temperature and year. **(b)** Mean spring temperature during the

TRP (Spring Tmean) over the periods 1951−1983 and 1984−2016 for early and late

flushing species (EFS and LFS, respectively). **(c)** Changes of spring temperature

variance (T_{SD}) during the TRP over the periods 1951-1983 and 1984-2016 for EFS and

LFS. **(d)** Temperature sensitivity of leaf flushing (S_T) for EFS and LFS between
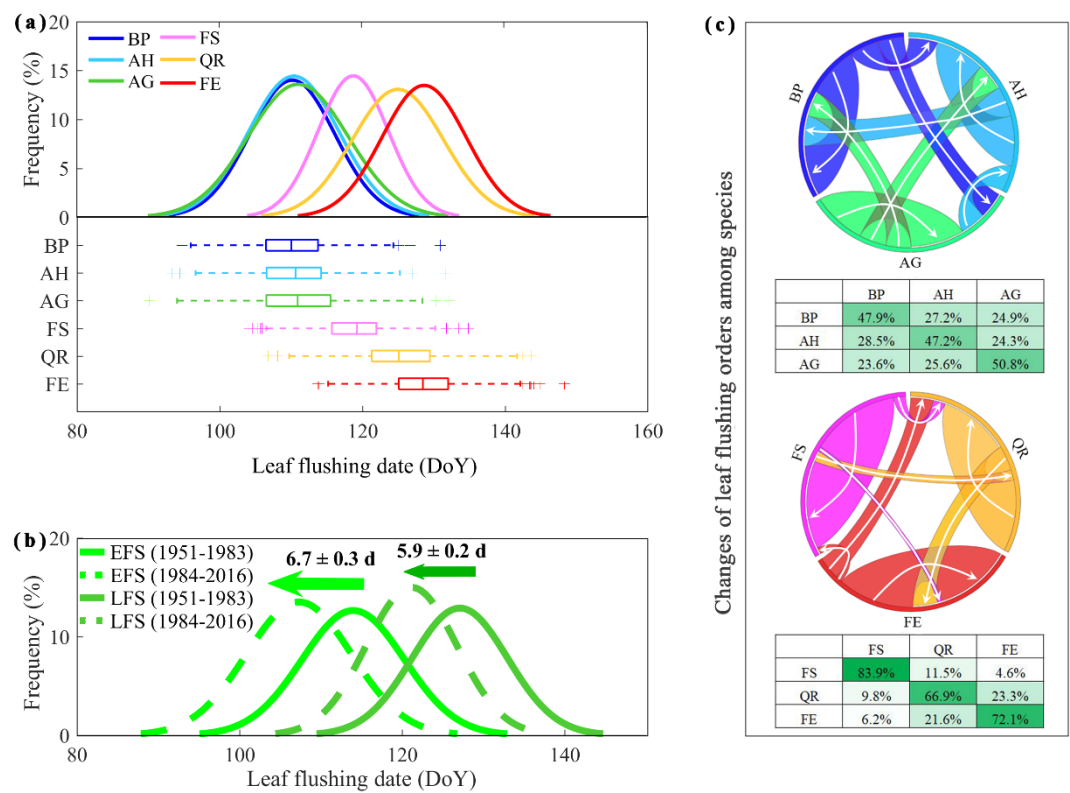
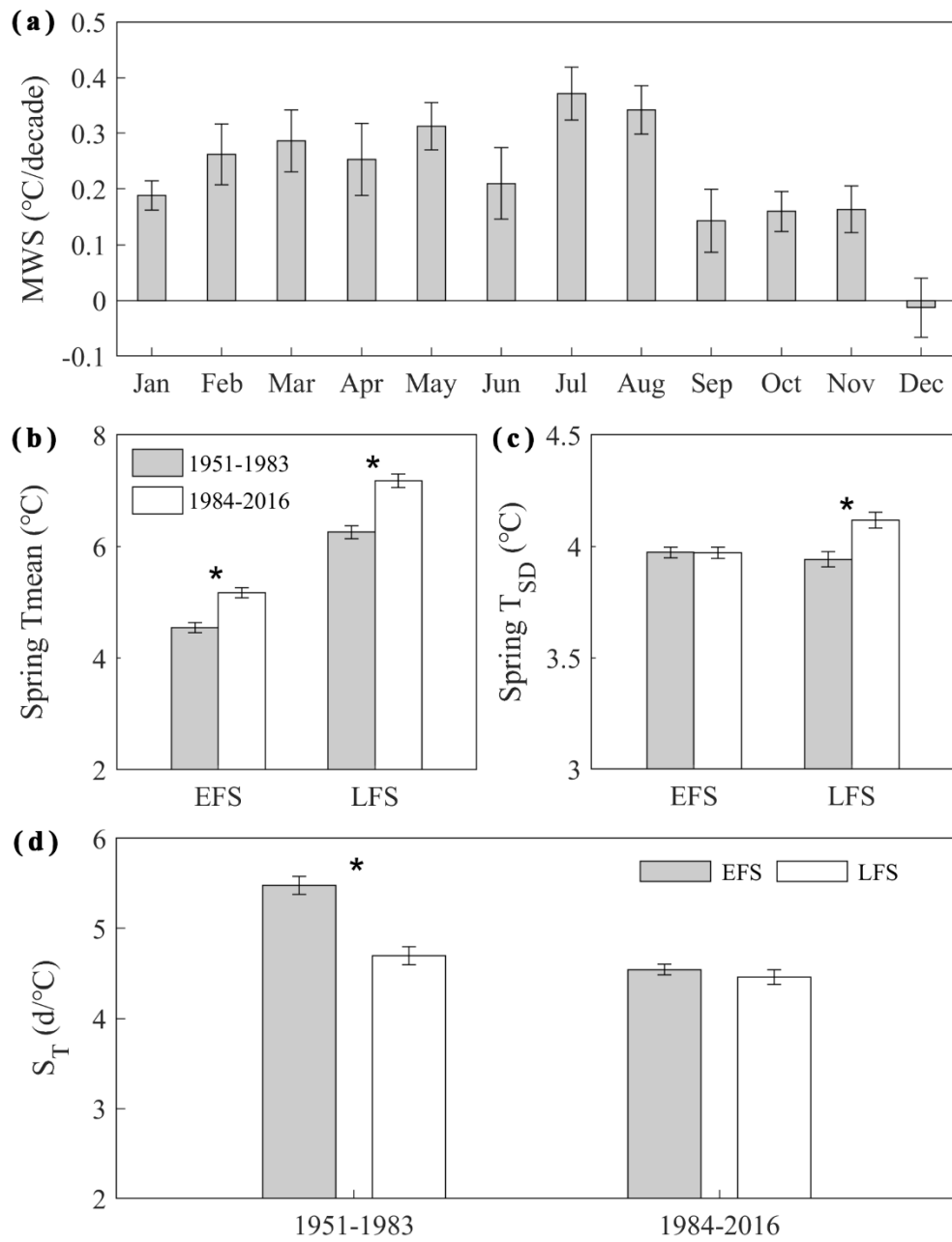1951−1983 and 1984−2016, determined by reduced major-axis regression. Asterisks

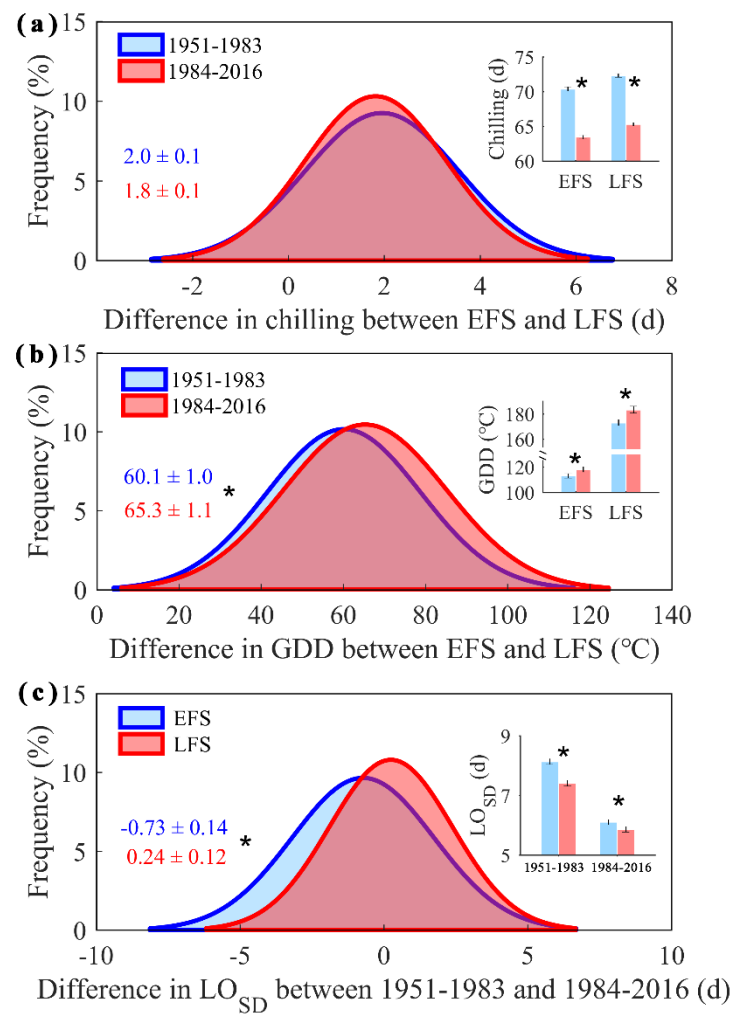indicate differences at $P < 0.05$.

549   **Fig. 3 Changes in chilling and heat accumulation, as well as standard deviation of**

550   **leaf flushing dates (LO$_{SD}$) between 1951−1983 and 1984−2016 in early and late**

551   **flushing species (EFS and LFS). (a)** Difference in chilling accumulation between EFS

552   and LFS, which was calculated as the number of days when mean air temperature was

553   <5 °C from 1st November until leaf flushing date. **(b)** Difference in growing degree

554   days (GDD) between EFS and LFS, which was calculated as the sum of mean air

555   temperatures >5 °C from 1st January until leaf flushing date. Numbers in blue and red

556   font are means ± SE for 1951−1983 and 1984−2016, respectively. **(c)** Difference in

557   LO$_{SD}$ between 1951-1983 and 1984-2016 for EFS and LFS. Asterisks indicate

558   differences at $P < 0.05$.

559   **Fig. 4 The interspecific differences in leaf flushing date (IDSP) between early and**

560   **late flushing species (EFS and LFS) varied along latitudes.** All the sites were

561   averaged every 0.5 degree along the latitude gradient.

Fig. 1

Fig. 2

564 **Fig. 3**

565 **Fig. 4**