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4
5 **The within-population variability of leaf spring and autumn**
6 **phenology is influenced by temperature in temperate deciduous**
7 **trees.**

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41
42 **Key words:** Leaf phenology, budburst, leaf senescence, temperate forest, within-population
43 variability, uncertainty quantification.

44 **Abstract**

45
46 Leaf phenology is a major driver of ecosystem functioning in temperate forests, and a robust
47 indicator of climate change. Both the inter-annual and inter-population variability of leaf
48 phenology have received much attention in the literature; in contrast, the within-population
49 variability of leaf phenology has been far less studied. Beyond its impact on individual tree
50 physiological processes, the within-population variability of leaf phenology can affect the
51 estimation of the average budburst or leaf senescence dates at the population scale. Here, we
52 monitored the progress of spring and autumn leaf phenology over 14 tree populations (9 tree
53 species) in six European forests over the period of 2011 to 2018 (yielding 16 site-years of data
54 for spring, 14 for autumn). We monitored 27 to 512 (with a median of 62) individuals per
55 population. We quantified the within-population variability of leaf phenology as the standard
56 deviation of the distribution of individual dates of budburst or leaf senescence (SD_{BBi} and SD_{LSi} ,
57 respectively). Given the natural variability of phenological dates occurring in our tree
58 populations, we estimated from the data that a minimum sample size of 28 (resp. 23)
59 individuals, are required to estimate SD_{BBi} (resp. SD_{LSi}) with a precision of 3 (resp. 7) days.
60 The within-population of leaf senescence (average $SD_{LSi}=8.5$ days) was on average two times
61 larger than for budburst (average $SD_{BBi}=4.0$ days). We evidenced that warmer temperature
62 during the budburst period and a late average budburst date were associated with a lower SD_{BBi} ,
63 as a result of a quicker spread of budburst in tree populations, with a strong species effect.
64 Regarding autumn phenology, we observed that later senescence and warm temperatures during
65 the senescence period were linked with a high SD_{LSi} , with a strong species effect. The shares of
66 variance explained by our models were modest suggesting that other factors likely influence
67 the within-population variation in leaf phenology. For instance, a detailed analysis revealed that
68 summer temperatures were negatively correlated with a lower SD_{LSi} .

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78 **Introduction**

79
80 Phenology was defined by the International Biological Program (IBP) as “the study of
81 the timing of recurring biological events, the causes of their timing with regard to biotic and
82 abiotic forces, and the interrelation among phases of the same or different species” (Lieth,
83 1974). Leaf phenology has received substantial attention in the last decades mainly because it
84 is a robust indicator of current climate change (Badeck et al., 2004; Donnelly and Yu, 2017;
85 Donnelly et al., 2004). Observations, experiments and modelling have shown that the
86 occurrence of leaf phenological events such as budburst and leaf senescence is mainly driven
87 by both temperature (Delpierre et al., 2009a; Lim et al., 2007; Menzel et al., 2006; Vitasse et
88 al., 2009; Walther et al., 2002) and photoperiod (Delpierre et al., 2016; Fu et al., 2019; Singh
89 et al., 2017; Thakur et al., 2016; Vitasse and Basler, 2013; Way and Montgomery, 2015). In the
90 Northern Hemisphere there is strong evidence that the global warming hastens the occurrence
91 of spring phenological events (Menzel et al., 2006; Walther et al., 2002) and delays the
92 occurrence of leaf senescence (Estrella and Menzel, 2006). The timing of spring and autumn
93 phenological transitions could affect the ecosystem functioning. Indeed, the timing and duration
94 of the leafy period impact the ecosystem carbon uptake (Delpierre et al., 2009b; Richardson et
95 al., 2010; White et al., 1999). Moreover, leaf phenology, especially budburst, is strongly
96 correlated with insect and insectivore phenology (Harrington et al., 1999) and could affect food
97 webs within ecosystems.

98
99 To date, most phenological studies have addressed questions related to the inter-specific
100 and the inter-annual variability of phenological events (see Ma et al., 2018 and Xie et al., 2018
101 for recent examples). However, the within-population variability of leaf phenology has received
102 little attention in the literature (Cole and Sheldon, 2017; Crawley and Akhteruzzaman, 1988;
103 Delpierre et al., 2017; Wesołowski and Rowiński, 2006). This is rather surprising since the
104 within-population variability of leaf phenology can be large, averaging 19 days from the earliest
105 to the latest tree leafing out, and 26 days from the earliest to the latest tree showing leaf
106 senescence in a given population (as reviewed by Delpierre et al. (2017)). This is about 30% of
107 the amplitude of the continental gradient of budburst or leaf senescence (Delpierre et al. 2017).
108 Phenological studies conducted at the population scale have shown that individual trees can
109 usually be grouped according to their phenological rank for both spring (Chesnoiu et al. 2009;
110 Delpierre et al. 2017; Crawley and Akhteruzzaman, 1988) and autumn (Delpierre et al. 2017)
111 phases: some are identified as “early-trees”, others as “late-trees” and the majority are grouped

112 around the average (Chesnoiu et al., 2009). Moreover, individual tree phenology is often highly
113 repeatable between years, suggesting that genetic factors and/or local micro-climatic variations
114 would play a predominant role (Delpierre et al., 2017). Since the duration of the leafy period
115 impacts the potential of resource acquisition of trees, one may assume that the phenological
116 ranks of individual trees within a population affect their competitive status. For instance,
117 individual European beeches (*Fagus sylvatica* L.) and deciduous oaks (*Quercus petraea* Matt.
118 (Liebl) and *Quercus robur* L.) characterised by an earlier budburst or a later senescence than
119 the population average, respectively, also showed a higher girth increment (Delpierre et al.,
120 2017).

121
122 In this study, we explored how the within-population variability of leaf phenology varies
123 with environmental predictors. Process-based models of leaf phenology (Chuine, 2000;
124 Delpierre et al., 2009b, 2016; Vitasse et al., 2011) postulate that budburst or leaf senescence
125 occur when a given accumulation of “warm” temperatures (i.e. above a temperature threshold,
126 for spring phases) or “cold” temperatures (i.e. below a temperature threshold, for autumn) has
127 been reached. Such models have been developed to predict the average date of occurrence of
128 the phenophase of interest among trees in a population. We can go a step further and assume
129 that the within-population variability of leaf phenology proceeds from the variability of an
130 individual trait, such as the temperature sum required for triggering budburst (Kramer et al.,
131 2008; Oddou-Muratorio and Davi, 2014) or leaf senescence. For example, as the accumulation
132 of degree-days occurs faster during a warm spring, the time interval from the first to the last
133 tree bursting buds in the population would be reduced as compared to a colder spring (see Suppl.
134 Mat. 1). The same argument holds with the accumulation of cold temperature for the leaf
135 senescence period. It follows that a warmer spring or a colder autumn would shorten the spread
136 of budburst or leaf senescence dates in a tree population. On that basis, we hypothesize that
137 warm temperatures during the budburst or cold temperatures during the senescence period
138 would decrease the within-population variability of budburst or leaf senescence, respectively
139 (hypothesis n°1). In addition to the impact of temperatures, photoperiod may act as a threshold
140 signal triggering trees to burst buds in late spring (Vitasse and Basler, 2013) or to enter leaf
141 senescence in late autumn (White et al., 1997). Hence, we formulate a second hypothesis stating
142 that a late population-average date of budburst or leaf senescence would be associated with a
143 reduced within-population variability of leaf phenology both for spring and autumn (hypothesis
144 n°2).

145

146 **Material and methods**

147

148 **Description of the phenological database**

149

150 This study is based on phenological data collected from tree communities located across a
151 longitudinal gradient spanning 2100 km in Europe (Table 1 and Suppl. Mat. 2). Budburst and
152 leaf senescence observations were conducted at the individual tree scale for nine species: *Acer*
153 *pseudoplatanus* L., *Betula pendula* Roth., *Carpinus betulus* L., *Castanea sativa* Mill., *Corylus*
154 *avellana* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Quercus petraea* (Matt.) Liebl and
155 *Quercus robur* L. These species are distributed in 12 populations representing 37 populations-
156 years¹ for the budburst, and in 15 populations representing 46 populations-years for the leaf
157 senescence (Suppl. Mat. 3). The tree populations were observed in their natural habitat, with
158 the notable exception of the *Quercus petraea* populations observed in Toulence (Table 1) which
159 is a *common garden* experiment into which 10 populations from two altitudinal gradients are
160 grown. This study took advantage of a high number of individual trees observed for each
161 population-year: spring and autumn phenological observations were conducted over
162 populations ranging from 27 to 249 (with a median of 62) individuals, and 27 to 512 (with a
163 median of 61) individuals, respectively (Suppl. Mat. 3). Phenological observations were
164 conducted at the individual-tree scale by local observers using binoculars at an interval of 3.7
165 days on average (from 2 to 7 days) from March to May for budburst (*BB*) and of 7.1 days on
166 average (from 3 to 14 days) from September to November for leaf senescence (*LS*). The number
167 of observers varies from one (Orsay) to five (Wytham Woods) for spring phenology. All
168 autumn phenological observations were systematically conducted by the same local observers.
169 Temperature data were in most cases acquired in the vicinity of the study sites, except for the
170 Fundeanu site for which gridded meteorological data at a 0.5° spatial resolution were used
171 (Haylock et al., 2008) (Table 1).

172

173 <Expected location of Table 1>

174

175 **Individual estimation of budburst and leaf senescence date.**

176

¹A « population-year » refers to one tree population being observed during one year. Thus, e.g. four population-years may refer to one population observed for four years, or two populations observed both for two years, or two populations observed for three and one year, respectively etc.

177 We considered as target phenological events the occurrence of 50% of leaf buds opened (for
178 spring, Fig.1) or 50% of senesced (coloured or fallen) leaves (for autumn) in individual tree
179 crowns. A leaf bud is considered open “once a green leaf tip is visible at the end of the bud, but
180 before the first leaf from the bud has unfolded to expose the leaf stalk (petiole) or leaf base”
181 (Denny et al., 2014). For leaf senescence, observations of both the individual tree crown
182 percentages of coloured (i.e. yellow for the study species) and fallen leaves were combined in
183 a single senescence metric (Vitasse et al., 2009). Continuous bud development and leaf
184 senescence stages were calculated for each tree by linear interpolation of visual observations,
185 assuming that bud development and leaf senescence trajectories are linear around 50% opened
186 buds or 50% senesced leaves, respectively. For each individual tree, the date of the target stage
187 (hereafter BB_i for spring and LS_i for autumn, expressed as a day of year, DoY) was estimated
188 by the intersection between the phenological stages and the straight line passing through the
189 two phenological observations bounding the stage (Fig. 1).

190

191 **Quantification of the within-population variability of leaf phenology.**

192

193 We used the standard deviation of BB_i and LS_i (SD_{BB_i} and SD_{LS_i} , respectively, expressed as a
194 number of days) as a measurement of the within-population variability of spring and autumn
195 phenology for a population-year. Standard deviation is a measure of the average duration
196 between each individual BB_i or LS_i date and the average date established over all individuals.
197 In other words, it is a metric of the dispersion of data values in a distribution. A low standard
198 deviation indicates that individual phenological dates are close to each other, while a high
199 standard deviation indicates that phenological dates are spread out.

200

201 <Expected location of Figure 1>

202

203 **Quantification of the speed of phenological events.**

204

205 In order to further describe the spread of phenological events among individuals, we calculated
206 the speed of the budburst or leaf senescence sequence within population-years. The
207 phenological development speed for each population-year is as follows:

$$208 \quad \text{Speed}_{py} = \frac{\Delta_{\text{stage}}}{\Delta_{t_{py}}} \quad (\text{eq. 1})$$

209 where Speed_{py} is the speed of the phenological sequence for the population-year py of interest,
210 expressed in percentage of phenological development per day; Δ_{stage} is the difference (in
211 percentage points of phenological development) between the occurrence of two stages of the

212 within-population phenological sequence (e.g. from 10% to 90% trees reaching BB_i, we
 213 calculate $\Delta_{\text{stage}} = 90 - 10 = 80$ points); and $\Delta_{t_{py}}$ is the duration in day between the two stages of
 214 interest for the population-year considered. We calculated the speed of spring and autumn
 215 phenological sequences over the intervals from 10% to 90% trees reaching BB_i (resp. LS_i) in a
 216 given population-year, as we observed that this stage interval resulted in the highest Pearson
 217 correlation coefficient with SD_{BB_i} (resp. SD_{LS_i}) (Suppl. Mat. 4).

218
 219
 220

219 **Statistical methods**

221 Before conducting a detailed statistical analyses, and because we know of no paper describing
 222 such data, we plotted for illustrative purposes the SD_{BB_i} and SD_{LS_i} data against the absolute
 223 minimum and average temperature calculated over the spring / autumn phenological sequences
 224 (from the first to the last tree reaching budburst / leaf senescence) of each population-year (in
 225 relation with our hypothesis n°1) and against the species-specific site-year average date of the
 226 considered phenological event (in relation with our hypothesis n°2). We further computed the
 227 rank (Spearman's) correlation between SD_{BB_i} or SD_{LS_i} and these variables. Then, in order to
 228 test our hypotheses (i.e. hypothesis n°1: warm springs or cold autumns would decrease SD_{BB_i}
 229 or SD_{LS_i}, respectively; hypothesis n°2: a late budburst or senescence date would also decrease
 230 SD_{BB_i} or SD_{LS_i}, respectively) we fitted our data with a linear model of the form (in the case of
 231 spring phenology):

$$232 \quad \log (SD_{BB_{j,k}}) \sim Tav_{g_{BB_{j,k}}} + Date_{BB_{j,k}} + Species_k \quad (\text{eq. 2})$$

233 Where $SD_{BB_{j,k}}$ (days) is the standard deviation of budburst dates among individuals of
 234 population-year j of species k ; $Tav_{g_{BB_{j,k}}}$ (°C) is the temperature averaged throughout the BB
 235 sequence of population-year j of species k ; $Date_{BB_{j,k}}$ (DoY) is the observed average BB date for
 236 population-year j of species k ; and $Species_k$ accounts for a possible *species* effect on the
 237 intercept of the relation (i.e. the average SD_{BB_i} may differ among species). For autumn
 238 phenology, we expressed $SD_{LS_{j,k}}$ under (eq. 2) as a function of $Tav_{g_{LS_{j,k}}}$ (°C), $Date_{LS_{j,k}}$ (DoY),
 239 and $Species_k$. More complex model forms (including interaction terms temperature*species,
 240 date*species and date*species*temperature) were tested for both BB and LS but were not
 241 significantly different from zero and are consequently not reported. SD_{BB_i} and SD_{LS_i} data were
 242 log-transformed (eq. 2) for satisfying the linear model hypothesis of residuals homoscedasticity.
 243 In order to compare the average values of SD_{BB_i} or SD_{LS_i} we used Wilcoxon's rank sum test.

244 All statistical analyses were conducted with R 3.4.0. Because the experimental plan was
245 unbalanced, we used the “Anova” function from the “car” library to test model parameters.

246

247 **Quantification of the uncertainty of the within-population variability metric**

248

249 Determining the average date or quantifying the within-population variance of a phenological
250 event is subject to a population sampling effect, for obvious statistical reasons (see Sokal &
251 Rohlf, 1995, p. 136). We used the standard deviation from the average (SD) as a metric to
252 quantify the within-population variability of spring and autumn phenology (see above). Since
253 SD is sensitive to the size of the sample for which it is established, we quantified its uncertainty
254 due to population subsampling.

255 In a given population, phenological observations were conducted over N individuals
256 (Suppl. Mat. 3) leading to standard deviation values of budburst (SD_{BBi}). When subsampling n
257 individuals within the population ($n < N$), we decrease the precision of our SD_{BBi} estimate. To
258 quantify this loss of precision, we calculated the SD of phenological event dates (i.e. SD_{BBi} and
259 SD_{LSi}) for subsample sizes n taking values from 2 to N individuals. For each n , we randomly
260 picked individuals in the population sample and calculated the associated SD. We repeated the
261 sub-sampling 5000 times for each n to obtain a robust estimate of the range of possible standard
262 deviation values associated with a subsample size of n individuals (SD_n) (Fig. 2). We used the
263 distribution of SD_n values to quantify the uncertainty of the within-population variability of the
264 considered phenological event (e.g. uncertainty of SD_{BBi}) at a given sample size n (e.g. $SD_{BBi,n}$).
265 By repeating this process over all the populations sampled, we created a conservative
266 uncertainty scale by reporting for each possible sample size n the largest uncertainty of SD_{BBi}
267 or SD_{LSi} calculated among all populations (i.e. maximum value of $SD_{BBi,n}$ or $SD_{LSi,n}$). In
268 subsequent analyses, we assigned to each SD_{BBi} or SD_{LSi} value its worst uncertainty estimate
269 for the sample size of the population-year considered, according to this scale.

270 We determined that a minimum sample size of 28 individuals is required to estimate
271 SD_{BBi} with an uncertainty of 3 days (compared with the time resolution of BB observations
272 which is 3.7 days), and a minimum sample size of 23 individuals is required to estimate SD_{LSi}
273 with an uncertainty of 7 days (compared with the time resolution of LS observations which is
274 7.1 days) (Suppl. Mat. 5).

275

276 <Expected location of Figure 2>

277

278 **Results**

279

280 **Within-population variability of spring phenology**

281

282 The average duration between each individual budburst date (BB_i) and the population-year
283 average date, quantified as SD_{BB_i} , was 4.0 days (ranging from 1.7 to 9.7 days). Considering all
284 species and populations together, SD_{BB_i} was not correlated with the average date of budburst
285 (Fig. 3a). SD_{BB_i} was significantly and negatively correlated with both the average and the
286 absolute minimum temperatures during the budburst period (Fig. 3b,c). The relation of SD_{BB_i}
287 with average temperatures during the budburst period decreased from around 10 days at 9°C to
288 2.5 days at 12°C and then levelled off (Fig. 3b). The relation between SD_{BB_i} and minimum
289 temperatures during the budburst period decreased from 10 days at -1.8°C to 1.8 days at 3.7°C
290 degrees (Fig. 3c).

291

292 <Expected location of Figure 3>

293

294

295

296 A linear model considering simultaneously the influence of temperatures, of the
297 budburst date, and of the species described a good share of the variability of $\log(SD_{BB_i})$
298 (Adjusted $R^2=0.59$, $F=6.11$, $p<10^{-4}$). In this model, both T_{avg} and the budburst date decreased
299 SD_{BB_i} (Table 2). We observed a significant influence of the “species” factor on the intercept of
300 the relation, meaning that the general trend to a decrease of $\log(SD_{BB_i})$ with increasing T_{avg} and
301 budburst date was translated upward or downward depending on the species considered.

301

302 <Expected location of Table 2>

303

304

305 The speed of budburst was positively correlated with the average temperature during
306 phenological development period (Fig. 4a). Moreover, the speed of budburst was related with
307 the individual variability of budburst dates (Fig. 4b). Thus, the faster the bud development in
308 the population, the lower the within-population variability of budburst.

308

309 <Expected location of Figure 4>

310

311 **Within-population variability of leaf senescence**

312

313 The average duration between each individual leaf senescence date (LS_i) and the population-
314 year average date, quantified as SD_{LS_i} , was 8.5 days (ranging from 4.2 to 15.7 days). This is

315 significantly higher than SD_{BBi} (Wilcoxon rank sum test, $p < 1e-11$). When considered
316 independently, neither the average date of senescence (Fig. 5a), nor the average temperatures
317 (Fig. 5b), nor the minimum temperatures during the senescence period (Fig. 5c), were
318 significantly correlated with SD_{LSi} .

319

320 *<Expected location of Figure 5>*

321

322 A linear model considering simultaneously the influence of temperatures, of the leaf
323 senescence date, and of the species described a fair amount of the variability of $\log(SD_{LSi})$
324 (Adjusted $R^2=0.36$, $F=5.96$, $p < 0.0003$). In this model, both T_{avg} and the leaf senescence date
325 increased SD_{LSi} (Table 3). We observed a significant influence of the “species” factor on the
326 intercept of the relation, meaning that the general trend to an increase of $\log(SD_{LSi})$ with
327 increasing T_{avg} and senescence date was translated upward or downward depending on the
328 species considered.

329

330 *<Expected location of Table 3>*

331

332 The speed of leaf senescence was not related with the average temperatures during the
333 LS period (Fig. 6a). The within-population variability of LS was strongly negatively correlated
334 with the speed of leaf senescence (Fig. 6b).

335

336 *<Expected location of Figure 6>*

337

338

339

340 **Discussion**

341

342 **Determining robust estimates of the within-population variability of leaf phenology**

343

344 The within-population variability of leaf phenology affects the estimation of the statistical
345 parameters of a tree population (e.g. average date, within-population variability calculated as
346 the SD of the distribution etc.). This is all the more true that population sample sizes used in
347 most phenological studies are usually low (the median number of observed individuals is 15,
348 established across 132 tree populations reported in 22 papers; Liu et al., in prep.). Our study
349 revealed that given the natural variability of phenological traits within tree populations, 28 and
350 23 individuals are required to estimate the standard deviation of spring and leaf senescence
351 distribution with an accuracy of 3 and 7 days, respectively (Suppl. Mat. 5). Moreover, because

352 phenological observations are subjective, phenological parameter estimations are subject to an
353 “observer uncertainty”. Some protocols aim to reduce this uncertainty. For instance, Cole and
354 Sheldon (2017) collected phenological observations using five observers, covering the same
355 proportion of habitats and elevation. No quantification of the “observer effect” has been done
356 yet (Liu et al., in prep).

357

358 **Factors affecting the within-population variability of budburst**

359

360 Our hypothesis n°1, which predicted that warmer spring would decrease the within-population
361 variability, was validated (Fig. 3b,c; Table 2). Moreover, we observed positive correlations
362 between the speed of phenological development within populations and temperature (Fig. 4a).
363 The overall hastening of the budburst date by warm temperatures has been established for a
364 long time (e.g. Delpierre et al. 2016). More recently, warm temperatures were demonstrated to
365 affect the rate of bud development (Basler and Korner, 2014). Our results show that the impact
366 of warm temperatures extend at higher integration scales: that of the individual tree crown
367 (Suppl. Mat. 6), and that of the tree population (Fig. 4a). Overall, our results support the idea
368 of considering phenological traits such as the required temperature sum for reaching budburst
369 (Kramer et al., 2008; Oddou-Muratorio and Davi, 2014) as discriminant among tree individuals
370 in a population. However, the interplay between tree individual sensitivities to photoperiod and
371 exposure to chilling remains to be determined before being able to build robust models of the
372 within-population variability of budburst. Indeed, our results showed that beyond the influence
373 of average temperature conditions during budburst, the average date of budburst (or
374 photoperiod, since both are almost equivalent in spring on the latitudinal range of our study,
375 Table 1) influenced the within-population variability (Table 2). Later budburst dates are
376 associated with a lower within-population variability of budburst (see negative coefficient
377 associated to $Date_{BBi}$ in Table 2), and more generally with a faster development of leaves
378 (Klosterman et al., 2018). Contrary to the influence of temperatures, the influence of budburst
379 date on SD_{BBi} is probably of second order, since it is not significant (Fig. 3a) without
380 simultaneously considering an effect of both temperatures and the species (as appears in Table
381 2). We tested our hypotheses over a set of populations from different species and locations,
382 looking for general patterns. For some species (*Acer pseudoplatanus*, *Corylus avellana*, *Fagus*
383 *sylvatica*, *Fraxinus excelsior*), we could only gather data for two population-years, satisfying
384 our criteria as regards the number of trees sampled (a minimum of 28 tree per population, see
385 above) and the time resolution of phenological observations (twice a week for budburst). It is

386 clear that a detailed understanding of the within-population variability of budburst, and its
387 stratification among species, will require more data.

388

389 **Factors affecting the within-population variability of leaf senescence.**

390

391 Our first hypothesis, which predicted that cold autumn would decrease the within-population
392 variability of LS was partially validated. Individually, the three factors do not influence the
393 SD_{LSi} (Fig. 5). However, when considered together, the average temperatures, the date of LS
394 and the Species predict SD_{LSi} (Table 3). In agreement with our prediction, increasing
395 temperatures is linked with higher SD_{LSi} . However, contrary to our expectations later
396 senescence dates are linked with higher SD_{LSi} .

397 Overall, the linear model explains 36% of the variability of $\log(SD_{LSi})$, strongly
398 suggesting that other factors are probably acting here. When considered as a single predictor,
399 temperature is not related to SD_{LSi} (Fig. 5b,c), nor is it related with the speed of LS (Fig. 6a)
400 which is a powerful predictor of SD_{LSi} (Fig. 6b). More generally, the interplay of temperature
401 with photoperiod and other drivers likely to affect leaf senescence (e.g. soil water stress or the
402 date of budburst) remains unclear to date (Gill et al. 2014; Delpierre et al. 2016). Hence it is
403 not surprising that we are not able to identify clear drivers explaining the within-population
404 variability of leaf senescence. A recent study by Liu et al. (2018) revealed that temperature cues
405 are related to leaf senescence in a complex way, with antagonistic influences of autumn
406 (delaying) and summer (hastening) leaf senescence in several temperate trees species. In line
407 with their work, and contrary to our hypothesis, we observed that SD_{LSi} were more strongly
408 related with summer temperatures (Suppl. Mat. 7) than with autumn temperature (Fig. 5). The
409 correlation is negative, meaning that warm summer temperatures are related with a low SD_{LSi} ,
410 while cold summer temperatures are related with a high SD_{LSi} (Suppl. Mat. 7). Since warm
411 summer temperatures may reduce the cold-degree-days (CDD) requirement for leaf senescence
412 in some species (Liu et al., 2018, 2019), a logical link would be that a warmer summer reduces
413 the within-population variability of CDD requirement for leaf senescence, implying a narrower
414 distribution of leaf senescence dates in the following autumn.

415

416 **Conclusion**

417

418 In this study, we took advantage of a high number of trees observed per population to evaluate
419 the uncertainty of phenological metrics caused by population subsampling. We calculated that
420 a minimum of 28 (23) trees is required to evaluate with an uncertainty of 3 (respectively 7) days

421 the within-population standard deviation of budburst (respectively leaf senescence). Most
422 phenological studies concern a lower number of individuals per population. If similar studies
423 are to be conducted in the future, this will require an increase in the population sampling effort.

424 We have demonstrated that the within-population individual variability of budburst
425 ($SD_{B_{Bi}}$) in temperate tree populations decreases with increasing temperature during budburst.
426 Beyond the single effect of temperature, we showed that the population average budburst date
427 and the species identity affect $SD_{B_{Bi}}$. The relation of the within-population individual variability
428 of leaf senescence ($SD_{L_{Si}}$) with autumn temperatures, the average date of leaf senescence and
429 species identity was weaker than the one established for spring. Contrary to our hypothesis, we
430 observed no strong link between $SD_{L_{Si}}$ and temperature conditions during leaf senescence.
431 However, in line with recent advances in the study of leaf senescence, we evidenced a clear
432 relation of $SD_{L_{Si}}$ with summer temperatures.

433

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439

440 **Author's contributions**

441

442 N.D. and R.D. designed the research. R.D. and N.D. performed the research and wrote the
443 manuscript. All authors contributed phenological data and commented on the manuscript.

444

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556

557 **Table 1. Characteristics of the phenological sites.** The sites were sorted according to longitude. Asl=
 558 above sea level.

Sites	Site locations	Species	Years of spring observation	Years of autumn observation	Temperature data acquisition	Reference
Wytham Woods	51.8°N, 1.3°W, 60 m asl, England	<i>Fraxinus excelsior</i> , <i>Quercus robur</i> , <i>Acer pseudoplatanus</i> , <i>Fagus sylvatica</i> , <i>Corylus avellana</i> , <i>Betula pendula</i>	2013-2014	none	Local (0 km), below tree canopy	(Cole and Sheldon, 2017)
Toulenne	44.5°N, 0.25°W, 20 m asl, France	<i>Quercus petraea</i>	none	2014, 2016, 2017	Meteorological station (0.3 km), measured at 2-m height over grassland	(Firmat et al., 2017)
Orsay	48.7°N 2.2°E, 150 m asl, France	<i>Quercus petraea</i> , <i>Castanea sativa</i> , <i>Carpinus betulus</i>	2012-2015, 2018	2011-2015	Meteorological station (4 km), measured at 2-m height over grassland	(Delpierre et al., 2017)
Barbeau	48.5°N, 2.8°E, 90 m asl, France	<i>Quercus petraea</i> , <i>Carpinus betulus</i>	2013, 2015-2017	2015-2017	Flux tower (0 km), above tree canopy	(Delpierre et al., 2017)
Freising	48.2°N, 11.4°E, 450 m asl, Germany	<i>Fagus sylvatica</i>	none	2012	Local (0 km), below tree canopy	(Gressler et al., 2015)
Fundeanu	46.0°N, 26.7°E, 230 m asl, Romania	<i>Quercus robur</i>	2008, 2009, 2015-2017	none	Regional circulation model (spatial resolution 0.5°)	(Chesnoiu et al., 2009)

559
 560

561 **Table 2. Outputs from a linear model testing the impact of average temperature, budburst average**
562 **date and species on $\log(SD_{BBi})$.** The model is described by eq. 2. Bold lines highlight significant
563 coefficients ($p < 0.05$). *Acer pseudoplatanus* was used as a reference for calculating the intercept, so all
564 other species effect are expressed as a difference to the *Acer* coefficient (illustrated with Δ).
565

Model parameter	Estimate	SE	t-value	Pr(> t)
Tavg_i	-0.10	0.03	-3.28	0.003
Date_{BBi}	-0.03	0.01	-4.86	<10⁻⁴
<i>Acer pseudoplatanus</i> (Intercept)	6.90	0.86	8.05	<10⁻⁷
Δ <i>Betula pendula</i>	-0.49	0.27	-1.79	0.085
Δ <i>Carpinus betulus</i>	-1.30	0.26	-4.94	<10⁻⁴
Δ <i>Castanea sativa</i>	-0.44	0.23	-1.92	0.067
Δ <i>Corylus avellana</i>	-0.84	0.28	-2.97	0.006
Δ <i>Fagus sylvatica</i>	-0.26	0.27	-0.96	0.347
Δ <i>Fraxinus excelsior</i>	0.42	0.30	1.43	0.165
Δ <i>Quercus petraea</i>	-0.68	0.23	-2.98	0.006
Δ <i>Quercus robur</i>	-0.59	0.22	-2.61	0.015

566
567

568 **Table 3. Outputs from a linear model testing the impact of average temperature, leaf senescence**
 569 **average date and species on $\log(SD_{LSi})$.** The model is described by eq. 2. Bold lines highlight
 570 significant ($p < 0.05$) coefficients. *Carpinus betulus* was used as a reference for calculating the intercept,
 571 so all other species effect are expressed as a difference to the *Carpinus* coefficient (illustrated with Δ).
 572

Model parameter	Estimate	SE	t-value	Pr(> t)
Tavg_i	0.17	0.04	3.998	0.0003
Date_{LSi}	0.04	0.01	4.128	0.0002
<i>Carpinus betulus</i> (Intercept)	-12.43	3.59	-3.47	0.001
Δ <i>Castanea sativa</i>	0.23	0.19	1.207	0.23
Δ <i>Quercus petraea</i>	-0.34	0.13	-2.579	0.014
Δ <i>Fagus sylvatica</i>	-0.002	0.31	-0.007	0.994

573
 574

575 Figure Captions

576

577 **Figure 1. Individual budburst development for *Quercus petraea* in Orsay, 2018.** Phenological
578 observations for a given tree are linked by gray lines. The within-population variability (red double
579 arrow, n= 58 trees) and the average date of budburst (blue vertical line) are presented. An example tree
580 (yellow line) has been artificially advanced in time to exemplify its estimated budburst date (green
581 vertical line).

582 **Figure 2. Example of the quantification of the SD_{BBi} uncertainty due to subsampling for the**
583 ***Quercus robur* population of Wytham Woods, 2014.** (A) The distribution of possible standard
584 deviation values of individual budburst dates for each sample size (196 individuals were observed for
585 this population in 2014). We considered that the minimum sample size required for estimating SD_{BBi}
586 accurately was reached when 90% of the standard deviation values were within 3 days (see text),
587 corresponding to 28 individuals in this case. (B) The distribution of the standard deviations values
588 (SD_{BBi}) estimated by randomly picking 28 trees among 196 (indicated by the blue vertical line in plot
589 A). The red lines in plots A and B indicate the best estimate of SD_{BBi} , calculated over 196 individuals.

590 **Figure 3. Relation of SD_{BBi} with the population average date of budburst, and temperature**
591 **conditions during budburst.** SD_{BBi} (in days) is related to (a) the average date of budburst, (b) the
592 average temperatures during the budburst period and (c) the absolute minimum temperature during the
593 budburst period. Rho = Spearman's rank correlation established across population-years, with its p-
594 value. Two values of Rho were calculated, including ("with Orsay 2012") or excluding ("without Orsay
595 2012") the maximum SD_{BBi} value of 9.7 days which was observed for the *Quercus petraea* population
596 located in Orsay in 2012. Error bars indicate the subsampling uncertainties of standard deviation values.

597

598 **Figure 4. The within-population speed of budburst depends on spring temperatures (a) and is**
599 **related with SD_{BBi} (b).** We calculated the speed of budburst over the interval stage of phenological
600 development (from 10 to 90 % of BB_i in the population) best correlated with SD_{BBi} . The average
601 temperatures were calculated between these two stages for each population-year.

602

603 **Figure 5. Relation of SD_{LSi} with the population average date of leaf senescence, and temperature**
604 **conditions during leaf senescence.** SD_{LSi} (in days) is related to (a) the average date of leaf senescence,
605 (b) the average temperatures during the leaf senescence period and (c) the lowest temperature during the
606 leaf senescence period. Rho = Spearman's rank correlation established across population-years, with its
607 p-value. The different species codes for *Quercus petraea* in the Toulonne common garden refer to the
608 different altitudes where trees were collected before planting.

609

610 **Figure 6. The within-population speed of leaf senescence does not depend on autumn temperatures**
611 **(a) but is related with SD_{LSi} (b).** We calculated the speed of leaf senescence over the interval stage of
612 phenological development (from 10 to 90 % of LS_i in the population) best correlated with SD_{LSi} . The
613 average temperatures were calculated between these two stages for each population-year. The different
614 species codes for *Quercus petraea* tree populations observed in the Toulonne common garden refer to
615 the different altitudes where trees were collected.

616