

1 **Greater capacity to exploit warming temperatures in northern**  
2 **populations of European beech is partly driven by delayed leaf**  
3 **senescence**

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22 **Abstract**

23 One of the most widespread consequences of climate change is the disruption of trees'  
24 phenological cycles. The extent to which tree phenology varies with local climate is largely  
25 genetically determined, and while a combination of temperature and photoperiodic cues are  
26 typically found to trigger bud burst (BB) in spring, it has proven harder to identify the main cues  
27 driving leaf senescence (LS) in autumn. We used 905 individual field-observations of BB and LS  
28 from six *Fagus sylvatica* populations, covering the range of environmental conditions found across  
29 the species distribution, to: (i) estimate the dates of BB and LS of these populations; (ii) assess the  
30 main drivers of LS; and (iii) predict the likely variation in growing season length (GSL; defined  
31 as the period from BB to LS timing) across populations under current and future climate scenarios.  
32 To this end, we first calibrated linear mixed-effects models for LS as a function of temperature,  
33 insolation and BB date. Secondly, we calculated GSL for each population as the number of days  
34 between BB and LS. We found that: i) there were larger differences among populations in the date  
35 of BB than in the date of LS; ii) the temperature through September, October and November was  
36 the main determinant of LS, although covariation of temperature with daily insolation and  
37 precipitation-related variables suggests that all three variables may affect LS timing; and iii) GSL  
38 was predicted to increase in northern populations and to shrink in central and southern populations  
39 under climate change. Consequently, the large present-day differences in GSL across the range of  
40 beech are likely to decrease under future climates where rising temperatures will alter the  
41 relationship between BB and LS. Northern populations are likely to increase their productivity as  
42 warmer conditions will enable them to extend their growing season.

43 Key words (4-6): *Fagus sylvatica*, spring phenology, autumn phenology, environmental factors,  
44 provenance effect, climate change

45

## 46 **1 Introduction**

47 Plants are changing their phenological cycles in response to current climate change (Chmura et al.  
48 2018). Generally, these changes involve a combination of advances in spring leaf phenology and  
49 delays in autumn leaf phenology (Gallinat et al. 2015; Piao et al. 2015; Yang et al. 2017), resulting  
50 in a longer growing season (Walther et al. 2002; Estiarte and Peñuelas 2015) and potentially  
51 increasing forest net ecosystem productivity (NEP) (Way and Montgomery 2015). Phenological  
52 responses to environmental cues are to a large extent genetically determined in trees (Liang 2019).  
53 Numerous studies along elevational gradients and experiments in common-gardens have found  
54 bud burst (BB) in populations of different origin to occur at different dates in many tree species  
55 (Vitasse et al. 2013; Dantec et al. 2015; Sampaio et al. 2016; Kramer et al. 2017; Cooper et al.  
56 2018). Leaf senescence (LS) has been less widely studied in such settings, but it also differs  
57 inherently among populations of *Betula pubescens* (Pudas et al. 2008), *Fraxinus americana* (Liang  
58 2015), *Populus balsamifera* (Soolanayakanahally et al. 2013), *Populus deltoides* (Friedman et al.  
59 2011), *Populus tremula* (Michelson et al. 2018; Wang et al. 2018) and *Populus trichocarpa* (Porth  
60 et al. 2015). However, it is not yet clear to what extent the genetic determinism and the  
61 environmental cues of BB match those for LS, and how the interplay of BB and LS drives among-  
62 population variation in growing-season length (GSL) (Signarbieux et al. 2017).

63         Extensive research has identified cold winter temperatures (i.e., chilling requirements) and  
64 accumulated spring temperatures (i.e., forcing requirements) as the main drivers of BB; sometimes  
65 coupled with photoperiod (Basler and Körner 2014; Fu et al. 2015) (Fig. 1). The major drivers of  
66 LS have been more difficult to identify (Gallinat et al. 2015; Brelsford et al. 2019). A recent meta-  
67 analysis showed that summer and autumn temperatures, precipitation and long photoperiod can all

68 affect LS (Gill et al. 2015). Generally, temperature tends to be predominant at lower latitudes  
 69 (Pudas et al. 2008; Lang et al. 2019), whereas photoperiod is more important at higher latitudes  
 70 (Soolanayakanahally et al. 2013; Lang et al. 2019) (Fig. 1). Yet temperature effects on LS are not  
 71 straightforward: increasing summer and autumn temperatures and even moderate drought can  
 72 delay LS (Xie et al. 2015), whereas severe drought tends to promote earlier LS (Chen et al. 2015;  
 73 Estiarte and Peñuelas 2015), (Fig. 1). Finally, high insolation and high photoperiod may also delay  
 74 LS (Liu et al. 2016a) (Fig. 1). The complex nature of the environmental triggers of LS has to-date  
 75 hampered attempts to understand the causes of its variation across large geographical scales  
 76 (Chmura et al. 2018). This uncertainty makes it very difficult to estimate GSL across species  
 77 ranges. Recent studies based on *in-situ* records and satellite data have shown positive correlations  
 78 between the timing of BB and LS that tend to stabilize GSL across populations (Keenan and  
 79 Richardson 2015; Liu et al. 2016b). But this is not a universal finding and the extent to which GSL  
 80 can change depends on the combination of many factors, as explained in Fig. 1.

GSL					
Reference	EV	BB <sub>R</sub>	LS <sub>R</sub>	EV	Reference
(Gárate-Escamilla <i>et al.</i> , 2019; Ibáñez <i>et al.</i> , 2010; Signarbieux <i>et al.</i> , 2017; Yang <i>et al.</i> , 2017)	↑ Twin/spr			↑ Tsum/aut	(Ibáñez <i>et al.</i> , 2010; Yang <i>et al.</i> , 2017; Fu <i>et al.</i> , 2018)
	↓ Twin/spr			↓ Tsum/aut	
(Basler & Körner, 2012; Gauzere <i>et al.</i> , 2017; Malyshev <i>et al.</i> , 2018)	↑ Phot			↑ Phot/ln	(Liu <i>et al.</i> , 2016a)
	↓ Phot			↓ Phot/ln	(Cooke <i>et al.</i> , 2012)
(Basler & Körner, 2014; Vitasse <i>et al.</i> , 2017; Malyshev <i>et al.</i> , 2018)	↑ Chill			↑ Psum	(Zu <i>et al.</i> , 2018)
	↓ Chill			↑ Drou	(Wu <i>et al.</i> , 2018)

82 **Figure 1.** Environmental drivers of growing season length through their effects on bud burst and  
83 leaf senescence. GSL: growing season length; EV: environmental variables; BB<sub>R</sub>: bud burst  
84 response; LS<sub>R</sub>: leaf senescence response; Twin/spr: winter and spring temperatures; Tsum/aut:  
85 summer and autumn temperatures; Phot: photoperiod; In: insolation; Chill: chilling requirements;  
86 Psum: summer precipitation; Drou: drought; Columns EV: up arrow: increase in the environmental  
87 variable; down arrow: decrease in the environmental variable; Columns BB<sub>R</sub> and LS<sub>R</sub>: left arrow:  
88 early bud burst/leaf senescence; right arrow: delayed bud burst/leaf senescence; Green colour and  
89 green leaf: Reference, EV related to bud burst and BB<sub>R</sub>; Orange colour and orange leaf: Reference,  
90 EV related to leaf senescence and LS<sub>R</sub>. All the combinations of bud burst and leaf senescence  
91 responses defining the growing season length are possible.

92 *Fagus sylvatica* L. (European beech, henceforth “beech”) is one of the most dominant and  
93 widespread broadleaf forest trees in Europe (Preston and Hill 1997), and it is of high ecological  
94 and economic importance (Packham et al. 2012). In beech, BB responds to a combination of  
95 chilling and forcing temperature requirements (Heide 1993; Falusi and Calamassi 2012; Kramer  
96 et al. 2017) as well as to photoperiod (Heide 1993; Caffarra and Donnelly 2011; Basler and Körner  
97 2012), with the strength of these drivers changing along environmental gradients. For instance, BB  
98 is more affected by photoperiod in colder climates, and by chilling requirements in warmer  
99 climates (Gárate-Escamilla et al. 2019). Studies of LS in beech suggest that: (i) temperature may  
100 be a more important cue than photoperiod when nutrients and water are not limiting (Fu et al.  
101 2018); (ii) non-senescent green leaves are prematurely lost as a result of severe drought conditions  
102 (Bréda et al. 2006); (iv) early BB correlates with early LS (Fu et al. 2014; Chen et al. 2018; Zohner  
103 et al. 2018); (v) leaves first start to change colour in autumn from the upper part of the canopy,  
104 suggesting that hydraulic conductance or the amount of solar radiation received over the growing

105 season may play a role in triggering LS (Gressler et al. 2015; Lukasová et al. 2019), although this  
106 could also be related to an hormonal effect (Zhang et al. 2011).

107 Here, we investigate BB and LS in six different beech provenances (905 trees) planted in  
108 two common gardens in central Europe (Robson et al. 2018), and use this information to infer how  
109 range-wide patterns of beech GSL might evolve under future climate warming. Specifically, we  
110 attempt to: (i) estimate the dates of BB and LS, and how they differ among provenances; (ii) assess  
111 the main environmental drivers of LS; and (iii) predict GSL and how it would vary across  
112 populations under current and future climate.

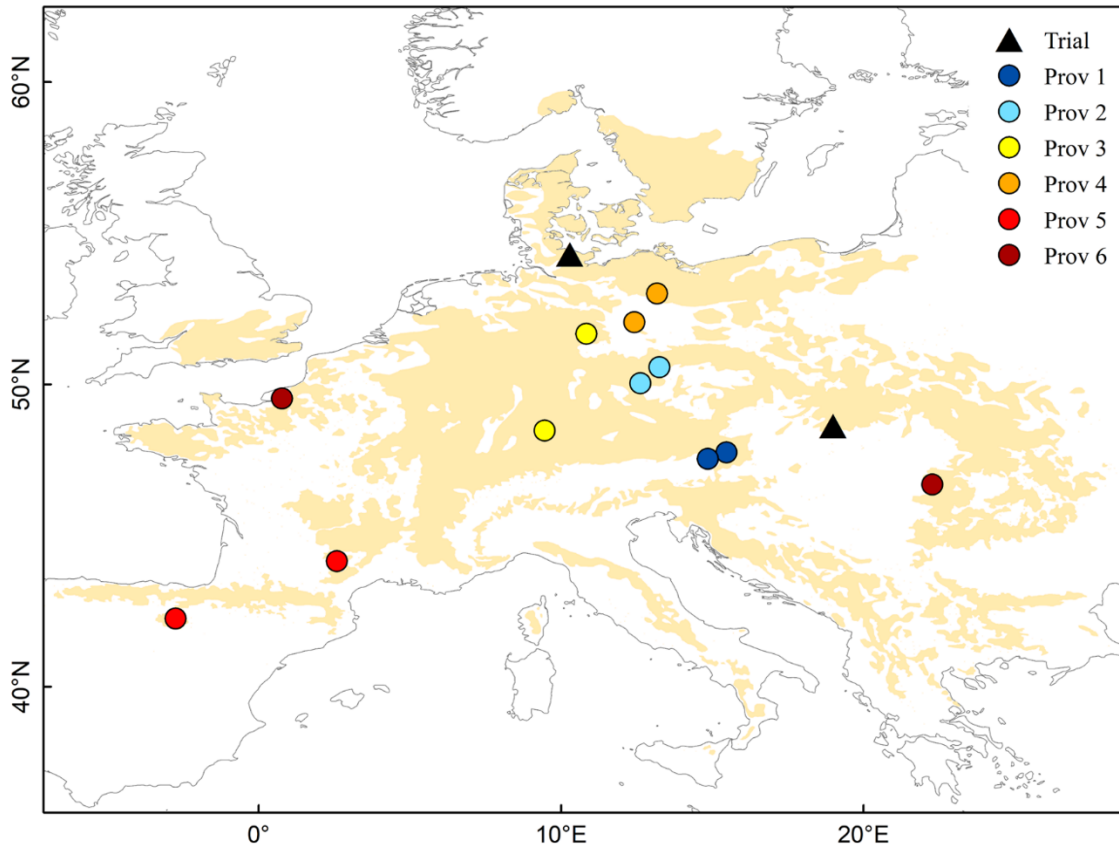
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## 114 **2 Materials and Methods**

### 115 **2.1 Field trials and provenances**

116 Spring and autumn leaf phenological observations came from two common-gardens (i.e.  
117 provenance tests, genetic trials; hereafter “trials”) located in Schädtbek (54.30°N, 10.28°E),  
118 Germany, and Tále, Mláčik, Slovakia (48.62°N, 18.98°E) (henceforth termed “Germany” and  
119 “Slovakia” trials, respectively). These two tests belong to a large network of beech common-  
120 gardens planted to understand the population (i.e. provenance effect including genetics) effects of  
121 climate change on fitness-related traits across the distribution range (details given in Robson et al.  
122 2018). These trials were planted with seeds collected from 38 provenances (32 provenances in  
123 Slovakia and six provenances in Germany) that roughly span the entire environmental range of  
124 beech (Fig. 2, Map). Seeds were germinated in the greenhouse and planted in the trials when two  
125 years old, in 1995 (Germany) and 1998 (Slovakia). To maintain a balanced design (same number  
126 of provenances per trial), we used only six provenances from each of the two trials (Fig. 2, Map &

127 Table). The six provenances from the Slovakian trial were chosen based on their similar climatic  
128 origin to those planted in the German trial (Pearson correlation  $r \geq 0.98$ ). The provenances were  
129 ranked from colder (1) to warmer (6) origins (Fig. 2, Map & Table). Trees growing in Germany  
130 were measured at an age of 12 and 13 years, those in Slovakia at 11 and 12 years (Fig. 2, Table).



### Provenance Information

T	P	Lon	Lat	Elev	N	NT	Age	BIO 14	Ppet Min	P JJA	Tm JJA	Tm SON	DIM JJA	DIM SON	<i>r</i>
G	1	15.47	47.75	1171	99	76	12, 13	62.74	39.08	145.31	10.96	2.94	4.77	2.34	0.99
S		14.85	47.53	1223	199	124	11, 12	66.97	45.39	159.62	11.37	3.32	4.77	2.34	
G	2	12.62	50.03	909	97	55	12, 13	53.93	-15.57	96.22	13.09	5.00	4.44	1.87	0.99
S		13.25	50.57	795	94	66	11, 12	50.19	-5.59	91.98	13.22	5.23	4.44	1.87	
G	3	10.83	51.67	411	109	94	12, 13	55.73	-23.51	86.16	14.72	7.14	4.31	1.77	0.99
S		9.45	48.47	740	180	109	11, 12	50.58	-20.54	105.49	15.42	7.56	5.00	2.21	
G	4	13.17	53.00	57	78	58	12, 13	30.00	-58.73	64.89	16.96	8.67	4.29	1.67	0.99
S		12.42	52.05	154	116	81	11, 12	31.85	-69.49	64.42	17.08	8.77	4.36	1.71	
G	5	-2.75	42.25	943	80	66	12, 13	42.96	-140.38	47.96	16.83	9.56	5.83	3.02	0.99
S		2.58	44.15	698	79	52	11, 12	52.14	-111.58	65.79	18.05	11.35	5.79	2.88	
G	6	22.27	46.68	161	73	57	12, 13	39.27	-104.09	69.63	20.76	11.45	5.14	2.52	0.98
S		0.77	49.53	14	104	67	11, 12	44.52	-86.53	50.84	16.97	11.04	5.04	2.09	



132

133 **Figure 2. Map:** Geographical distribution of beech provenances (coloured circles) and trials  
134 (triangles) underlying this study. Beige shading indicates the distribution range of beech. Each  
135 circle colour indicates a pair of similar provenances from each trial (the colour gradient depicts the  
136 clinal variation from cold [blue] to warm [red] provenances, as defined in Table S1). Table:  
137 Climatic and geographic data that were used for merging provenances of similar climatic origin  
138 for modeling purposes. As the provenances were not shared between the two sites, we selected  
139 provenances of similar climatic characteristics. T: trial where the trees were measured  
140 (G=Germany, S=Slovakia); P: number of the provenances as shown in Figure 1; Lon: longitude;  
141 Lat: latitude; Elev: elevation (m); N: total number of trait measurements (including repeated  
142 measurements over years); NT: total number of individual trees; Age: age of the trees when  
143 measured; BIO14: precipitation of driest month; Ppet Min: minimal annual water balance; P JJA:  
144 precipitation of January, July and August; Tm JJA: mean temperature of January, July and August;  
145 Tm SON: mean temperature of September, October and November; DIM JJA: mean daily  
146 insolation of June, July and August; DIM SON: mean daily insolation of September, October and  
147 November;  $r$ : Pearson correlations per pair of provenances accommodated under the same number.

148

## 149 **2.2 Estimation of bud burst, leaf senescence and growing season length**

150 We transformed the observational stages (phenophases), and score data (qualitative measurements)  
151 for BB and LS to Julian days by fitting the phenophases (Fig. 3 and S1; Table S1 and S2) for each  
152 tree in every trial using the Weibull function (Robson et al. 2011; Gárate-Escamilla et al. 2019).  
153 The Weibull function is non-linear and asymptotic in the upper and lower limits, hence it requires

154 at least two censuses to obtain a fit of the data: the day of the year (DOY) when BB is attained in  
155 spring (stage 2.5; Fig.3 and S1; Robson et al. 2013) and at the stage at which 50% of the trees'  
156 leaves have changed colour from green to yellow (stage 3; Fig. 3 and S1; (Lang et al. 2019)). We  
157 calculated GSL for each tree as the number of days between the estimated dates of BB and LS  
158 (Estiarte and Peñuelas 2015).

159

### 160 **2.3 Environmental data**

161 To separate the effects of the provenance (genetic effects) from those of the trial (environmental  
162 effects), we used the average climate from 1901 to 1990 for each provenance and the average  
163 climate during the years of measurement for the trials (Leites et al. 2012) in our models. We used  
164 the following precipitation- and temperature-related variables from EuMedClim (Fréjaville and  
165 Benito Garzón 2018): precipitation in the driest month (BIO14, mm), precipitation (P, mm) in  
166 June, July and August (JJA), minimal (Min) monthly water balance (PPET, mm), and mean  
167 temperature (Tm, °C) in June, July and August (JJA) and September, October and November  
168 (SON). In addition, we used latitude as a proxy of photoperiod as well as daily insolation, a  
169 function of day length and solar irradiance (Yeang 2007). We downloaded daily insolation data  
170 from the NASA Atmospheric Science Data Center ([https://power.larc.nasa.gov/data-access-  
171 viewer/](https://power.larc.nasa.gov/data-access-viewer/)), and we calculated solar radiation (direct and diffuse) over the wavelength range 400-  
172 2700 nm incoming on a horizontal surface for a given location. We used insolation including NIR  
173 and SWIR, as well as PAR, because the mode of action is still unknown, so a direct heating effect  
174 from NIR and SWIR may be important. We calculated the mean daily insolation (DIM, kWh m<sup>-2</sup>  
175 d<sup>-1</sup>) between the months of June, July and August (JJA) and September, October and November  
176 (SON), respectively. As with the climatic variables, we characterized the DIM of the trial as the

177 average between the planting year and the year of measurement. Because the insolation data series  
178 from the NASA Atmospheric Science Data Center begins in July 1983, we characterized the DIM  
179 of the population as the average between 1984 and 1990 for JJA, and between 1983 and 1990 for  
180 SON.

181 We used the 2070 Representative Concentration Pathway (RCP) 8.5 GISS-E2-R  
182 ([http://www.worldclim.org/cmip5\\_30s](http://www.worldclim.org/cmip5_30s)) scenario for GSL predictions under future climate. We  
183 deliberately chose only this pessimistic scenario because, for long-lived organisms such as forest  
184 trees, it makes little difference whether the projected situation will be reached in 2070 or some  
185 decades later.

186

## 187 **2.4 Statistical analysis**

188 We used a model of BB already calibrated for the same set of trials and provenances (Gárate  
189 Escamilla et al. 2019). We then performed a linear mixed-effects model for LS as a function of the  
190 combination of environmental variables with BB date as a co-variate. Environmental variables  
191 were selected individually to account for separate trial and provenance effects. Our model allowed  
192 us to: (i) estimate the date of LS for each of the six pairs of provenances; (ii) compare the date of  
193 LS with the date of BB that was already modelled following a similar methodology (Gárate  
194 Escamilla et al. 2019); (iii) calculate GSL for each provenance; and (iv) perform spatial predictions  
195 of BB, LS and GSL under current and future climate scenarios.

196

### 197 **2.4.1 Environmental variable selection**

198 To avoid co-linearity and reduce the number of variables in our models, we only retained  
199 moderately correlated variables ( $-0.5 < r < 0.5$ ) for modelling purposes. The full correlation matrix  
200 between all variables is provided in Fig. S2.

201

#### 202 2.4.2 Linear mixed-effects model of leaf senescence

203 We performed a series of linear mixed-effects models of LS as a function of environmental  
204 variables from the trial and the provenances, with BB as a co-variable (Equation 1). Each model  
205 included one environmental variable from the provenance, one environmental variable from the  
206 trial site and BB as fixed effects. The trial, blocks nested within the trial, individual trees and  
207 provenances were included as random effects to control for differences among sites and for  
208 repeated measurements of the same tree. The general form of the LS model was:

$$\begin{aligned} 209 \quad \log(LS_{ijk}) = & \alpha_0 + \alpha_1(EP_{ij}) + \alpha_2(ET_{ik}) + \alpha_3(BB_{ik}) + \alpha_4(EP_{ij} \times ET_{ik}) + \alpha_5(EP_{ij} \times BB_{ik}) \\ 210 \quad & + \alpha_6(ET_{ik} \times BB_{ik}) + \beta + \varepsilon \end{aligned}$$

211 (Equation 1)

212 Where LS = leaf senescence of the  $i^{th}$  individual of the  $j^{th}$  provenance in the  $k^{th}$  trial; EP =  
213 environmental variable that characterizes the provenance site of the  $i^{th}$  individual of the  $j^{th}$   
214 provenance; ET = environmental variable that characterizes the trial site of the  $i^{th}$  individual in the  
215  $k^{th}$  trial; BB = bud burst of the  $i^{th}$  individual in the  $k^{th}$  trial;  $\beta$  = random effects and  $\varepsilon$  = residuals. In  
216 addition, the model included the following interaction terms: EP  $\times$  ET, EP  $\times$  BB, and ET  $\times$  BB.  
217 EP  $\times$  ET. Interactions represent differences in LS values that can be attributed to the interactions  
218 between genetic (provenance) and environmental (site) effects. EP  $\times$  BB and ET  $\times$  BB interactions

219 represent the effects of the provenance on LS related to BB and the effects of the site related to  
220 BB.

221 LS models were fitted with the ‘lmer’ function of the package ‘lme4’ (Bates et al. 2018),  
222 within R statistical framework version 3.2.0 (R Development Core Team 2015). To choose the  
223 best supported model, we followed a stepwise procedure: (i) to minimize model complexity and  
224 collinearity among environmental variables, we selected the most important variable related to the  
225 trial by comparing a series of models that included one environmental variable for the trial and  
226 BB, and then selected the best model using the Akaike information criterion (AIC) with criterion  
227  $\Delta < 2$  (Mazerolle 2006), and the variance explained by the fixed effects (marginal  $R^2$ )  
228 (Supplementary Table S3); (ii) we chose the optimal random component of the model by  
229 comparing the set of models that included different combinations of random effects, the previously  
230 selected environmental variable from the trial and BB using restricted maximum likelihood  
231 (REML), and selected the best model among them using the AIC criterion; (iii) we retained the  
232 best environmental variable related to the provenance comparing the models that included one  
233 environmental variable from the provenance, the selected variable from the trial, the BB, the  
234 interaction between the three variables and the random terms using maximum likelihood (ML)  
235 using the AIC criterion (Supplementary Table S4); (iv) we combined the best optimal random and  
236 fixed components (previously selected) and adjusted them using REML to obtain the best  
237 performing model.

238 The goodness of fit of the final models was assessed using two approaches. First, we  
239 quantified the percentage variance explained by the model attributed to the fixed effects (marginal  
240  $R^2$ ) and attributed to the fixed and random effects (conditional  $R^2$ ). Second, we measured the  
241 generalisation capacity of the model using cross-validation with independent data. To this end, we

242 calibrated the model with 66% of the data and performed an independent validation (using Pearson  
243 correlations) with the remaining 34% of the data.

244

#### 245 2.4.3 Interactions of leaf senescence with bud burst and environmental variables

246 For the best supported LS model, we analysed the significant interactions ( $EP \times ET$ ,  $EP \times BB$ , and  
247  $ET \times BB$  in Equation 1) between LS and the environment (ET; represented by the environmental  
248 variable from the trial selected by the best supported LS model) and according to provenances  
249 showing early, mean and late BB. We also inspected gradients of GSL for the six provenances by  
250 plotting GSL against the environmental variable of the trial selected in the model (ET) and  
251 population under current conditions. We predicted the date of LS for the future climate scenario  
252 RCP 8.5 using our LS model and the date of BB for the same provenances according to our BB  
253 model (Gárate-Escamilla et al. 2019), and plotted the predicted future GSL against ET for each of  
254 the provenances.

255

#### 256 2.4.4 Spatial predictions

257 Spatial projections of LS were calculated using our LS model for current and future climatic  
258 conditions with predictions of BB from Gárate Escamilla et al. (2019). Predictions of GSL were  
259 calculated by subtracting the predicted BB from LS for both current and future climatic conditions  
260 across the species range. For both current and future predictions, the climate for provenances was  
261 represented by the average of the period from 1900 to 1990. The climate of the trials was  
262 represented by the average of the period from 2000 to 2014 for current predictions, and by the  
263 mean value for the year 2070 according to RCP 8.5 for future predictions.

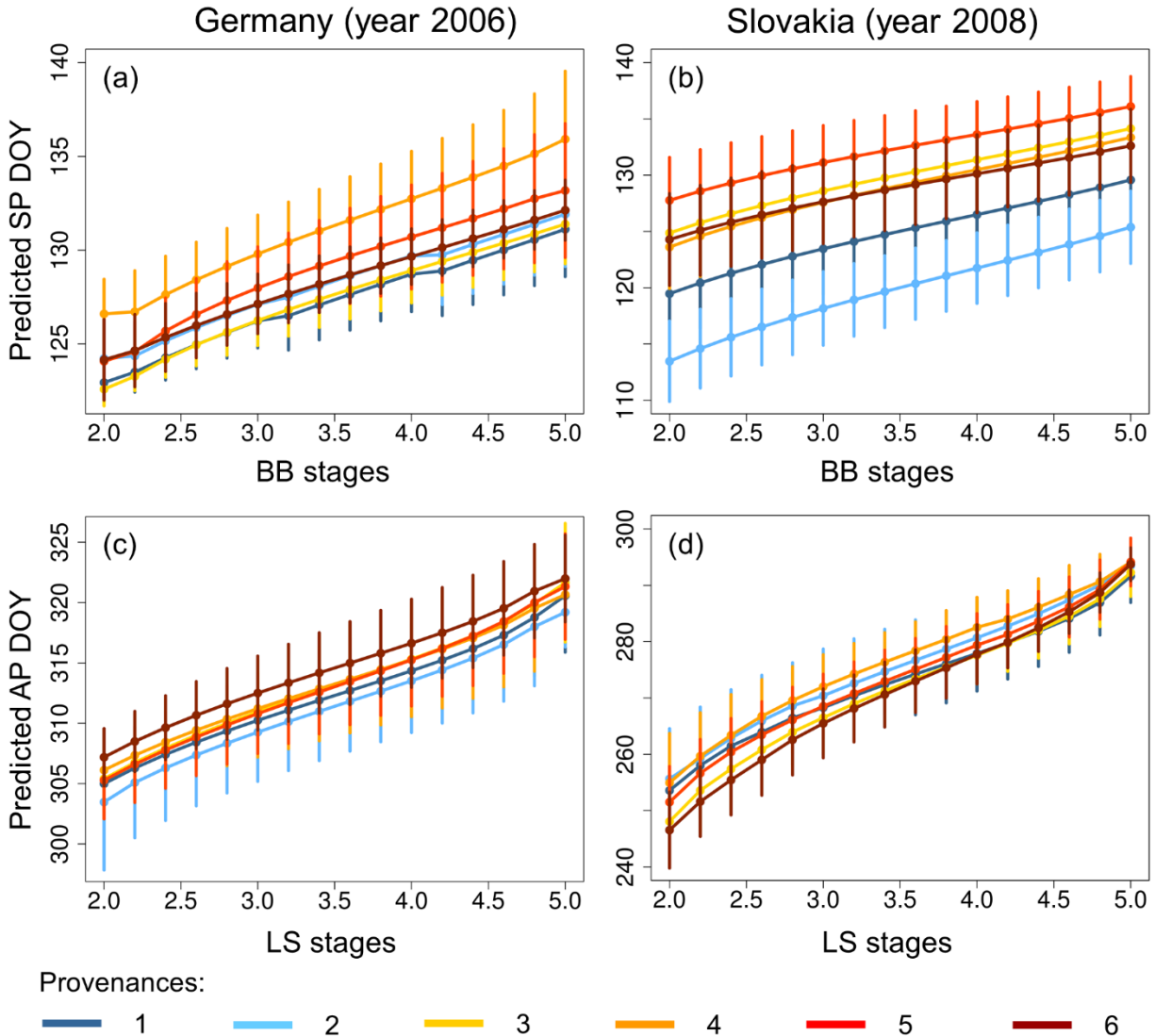
264 The current and future spatial predictions of BB and LS include a non-extrapolated area (i.e.,  
265 predictions including exclusively the climatic range of the two trials, 7.5 to 10°C) and an  
266 extrapolated area (i.e., predictions outside the climatic range of the trials) delimited within the  
267 distribution range of the species (EUFORGEN 2009). Spatial analyses were performed with the  
268 ‘raster’ package in R (Hijmans et al. 2017).

269

## 270 **3 Results**

### 271 **3.1 Estimation of bud burst and autumn leaf senescence dates from field observations**

272 In both trials, differences among provenances were larger for spring leaf flush stages (including  
273 bud burst; Fig. 3a & b and S1a & b) than for autumn leaf senescence stages (including 50% yellow  
274 leaves; Fig. 3c & d and S1c & d). Although these differences were always statistically significant,  
275 they were larger in the Slovakian trial than in the German one (Fig. 3 and S1, Table S1 and S2).  
276 Differences in the predicted DOY of spring leaf flush and autumn leaf senescence stages were  
277 found for the two years of measurement in both trials (Fig. 3 and S1). We used the fitted data to  
278 extract the DOY for the flushing stage 2.5 (bud burst, BB) and the senescence stage 3 (= 50% of  
279 leaves yellow, LS) for each provenance (Tables S1 and S2).



Spring leaf flushing phenology stages	
2	Buds swollen and elongated.
2.5	Bud burst.
3	First green becomes visible between bud scales, bud adopts a silver-grey sheen.
4	First folded hairy leaves become visible but remain partially held by the bud.
5	Entire leaves cascade from the bud, but are still largely folded and flaccid.

Autumn leaf senescence phenology stages	
2	<5% of leaves yellow.
3	<50% of leaves yellow.
4	<100% of leaves yellow.
5	Winter state.

280

281 **Figure 3.** Predicted spring bud burst and autumn leaf senescence phenology, days of the year

282 (DOY) against the observational stages recorded in the field for the two trials. SP: spring bud burst

283 phenology; AP: autumn leaf senescence phenology. Provenance colours range from dark blue



284 (cold origin) to dark red (warm origin) for the provenances in the two trials (Fig. 2, Map & Table).  
285 The spring leaf flushing and autumn leaf senescence stages are described in the lower part of the  
286 figure. The phenology stages were recorded in the year 2006 in Germany and 2008 in Slovakia.

287

### 288 **3.2 Variable selection and best model selection**

289 Our inspection of climate variables revealed that: (i) provenance and trial variables were not  
290 correlated with each other; (ii) temperature (Tm JJA and Tm SON)- and precipitation (BIO14,  
291 Ppet Min and Prec JJA)-related variables for the provenances were correlated, whilst daily  
292 insolation (DIM JJA and DIM SON) variables for the provenances were only correlated with the  
293 latitude (Lat) of the provenances; (iii) all the trial variables were correlated among themselves;  
294 and (iv) the co-variable BB was not correlated with the rest of variables (Fig. S2).

295 In view of these results, we retained daily insolation (DIM JJA and DIM SON) and  
296 temperature-(Tm JJA and Tm SON)-related variables for the provenances, all climate variables  
297 from the trials, and BB as predictors for our models of LS. The best model according to AIC  
298 criteria (Tables S3 and S4) used the mean temperature in September, October and November (Tm  
299 SON) of the trial and of the provenance, and BB as a co-variable (Table 1 and Table S3).

300 **Table 1.** Statistics from linear mixed-effects models of leaf senescence. Obs: number of trait  
301 measurements; Variance: variance explained by the random effects; SD: standard deviation of each  
302 level of random effects; Estimate: coefficient of the regression, shown on a logarithmic scale; SE:  
303 standard error of each fixed variable; *t*: Wald statistical test that measures the point estimate  
304 divided by the estimate of its SE, assuming a Gaussian distribution of observations conditional on  
305 fixed and random effects. Fixed effects: coefficients of the fixed effects of the model; BB: bud

306 burst; Tm SON\_T: mean temperature of September, October and November of the trial; Tm  
 307 SON\_P: mean temperature of September, October and November of the provenance. Coefficients  
 308 of the interactions: BB x Tm SON\_T and BB x Tm SON\_P.  $r$ : Pearson correlation;  $R^2M$ :  
 309 percentage of the variance explained by the fixed effects (Marginal variance);  $R^2C$ : percentage of  
 310 the variance explained by the random and fixed effects (Conditional variance).

311

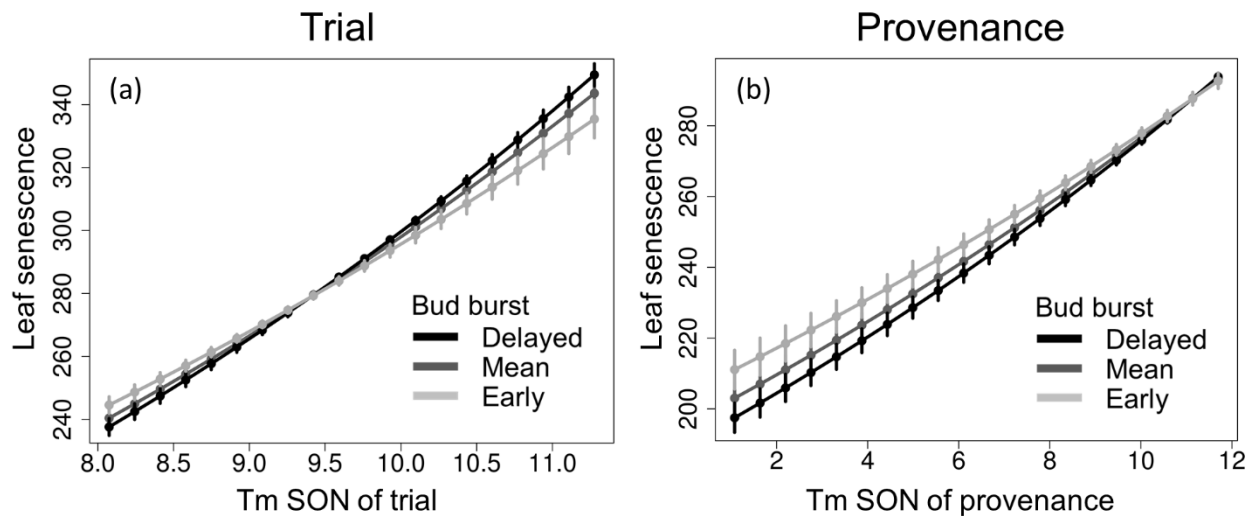
Leaf senescence			
Model	Linear Mixed Effect		
Random Effects			
	Obs	Variance	SD
Population	12	3.33E-05	5.77E-03
Trial	2	2.39E-02	1.55E-01
Trial:Block	6	9.73E-06	3.10E-03
Tree	925	1.88E-04	1.37E-02
Residuals		2.34E-04	1.53E-02
Fixed Effects			
	Estimate	SE	$t$
Intercept	5.62E+00	1.10E-01	51.16
BB	-8.18E-04	9.91E-05	-8.25
Tm SON_T	2.88E-02	1.43E-02	2.02
Tm SON_P	2.61E-02	8.10E-03	3.23
BB x Tm SON_T	5.97E-04	9.61E-05	6.21
BB x Tm SON_P	-1.96E-04	6.60E-05	-2.97
	$r$	$R^2M$	$R^2C$
	0.92	0.52	0.99

312

313

### 314 3.3 Leaf senescence model

315 LS differed among the provenances and between the two trials. These differences were explained  
316 by the Tm SON of the trial and provenance, as well as by BB (Table 1). Interactions between BB  
317 and Tm SON of the trial and provenance were also significant (Table 1). Late LS timing was  
318 related to higher Tm SON of the trial and provenances (Fig. 4). Late LS was related to late BB at  
319 high Tm SON of the trial, whilst at low trial Tm SON the opposite effect occurred (Fig. 4a). Late  
320 LS was related to early BB irrespective of Tm SON of the population (Fig. 4b). The marginal  $R^2$   
321 was 52%, while the conditional  $R^2$  was 99% (Table 1). The capacity for generalisation from the  
322 model was  $r = 0.92$  (Table 1).



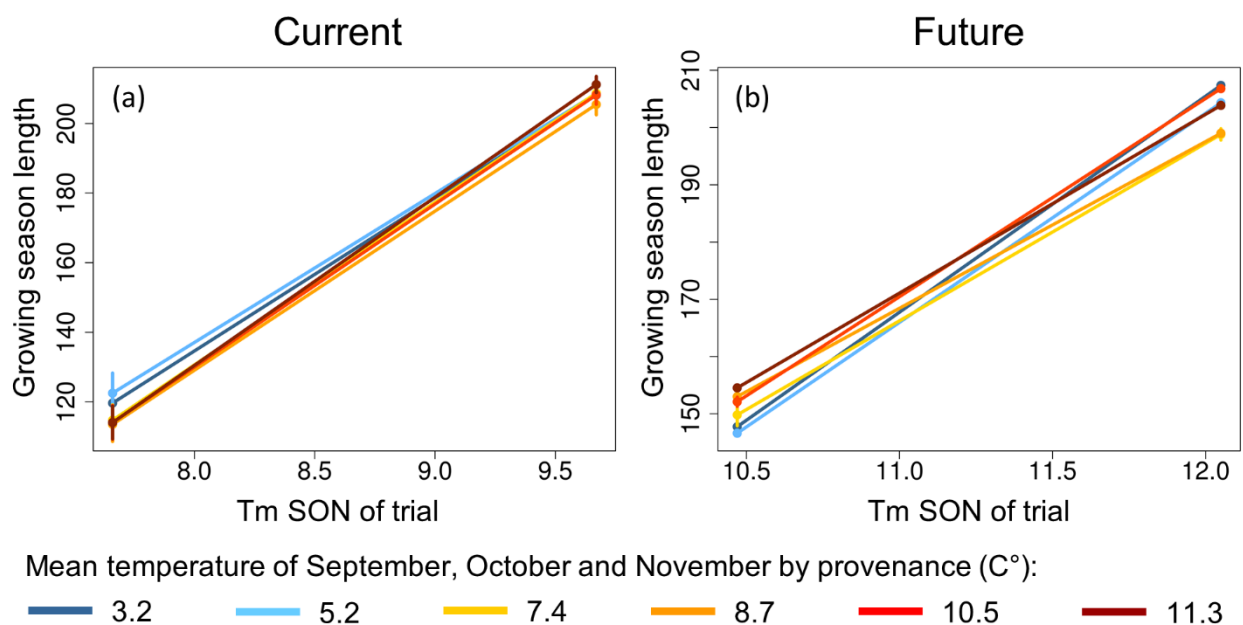
323  
324 **Figure 4.** Mathematical interaction between leaf senescence and the mean temperature in  
325 September, October and November (Tm SON) for the trial (a) and for the provenance (b). The  
326 mathematical interaction is estimated from the LS linear mixed-effects model (equation 1), where  
327 BB is considered as a co-variable. Leaf senescence is given in Julian days, and Tm SON in °C.  
328 The black line represents delayed bud burst, the dark-grey mean bud-burst and the light-grey early  
329 bud-burst. The error bars represent the 95% confidence intervals.

330

331 **3.4 Determinants of growing season length under current and future climates**

332 GSL greatly increased with higher temperatures in September, October and November in the trials,  
333 although the strength of this effect depended on the origin of the provenances (Fig. 5). The increase  
334 in GSL was greatest for cold provenances (3.2-5.2 C°), which had their longest GSL under cold  
335 conditions (7.5-8.5 C°) at the trials in the current climate (Fig. 5a). In our two trials, GSL differed  
336 more among provenances under future than under current autumn temperatures (Fig. 5b). The  
337 longest GSL under future conditions was predicted at high trial temperatures (11.5-12 C°) for the  
338 warm (10.5-11.3 C°) and cold (3.2-5.2 C°) provenances, whilst at low trial temperatures (10.5-11  
339 C°), the longest GSL was predicted for warmer (10.5-11.3 C°) populations (Fig. 5b).

340 When we extrapolate our models for the examined 2070 climate scenario, GSL is predicted to  
341 increase up to 9 days in the north-east of the range (Fig. 6). Decreases of GSL up to 8 days are  
342 predicted for much of the range including the central, southern, western and eastern areas; little or  
343 no change in GSL is predicted for the south-eastern-most range (Fig. 6).

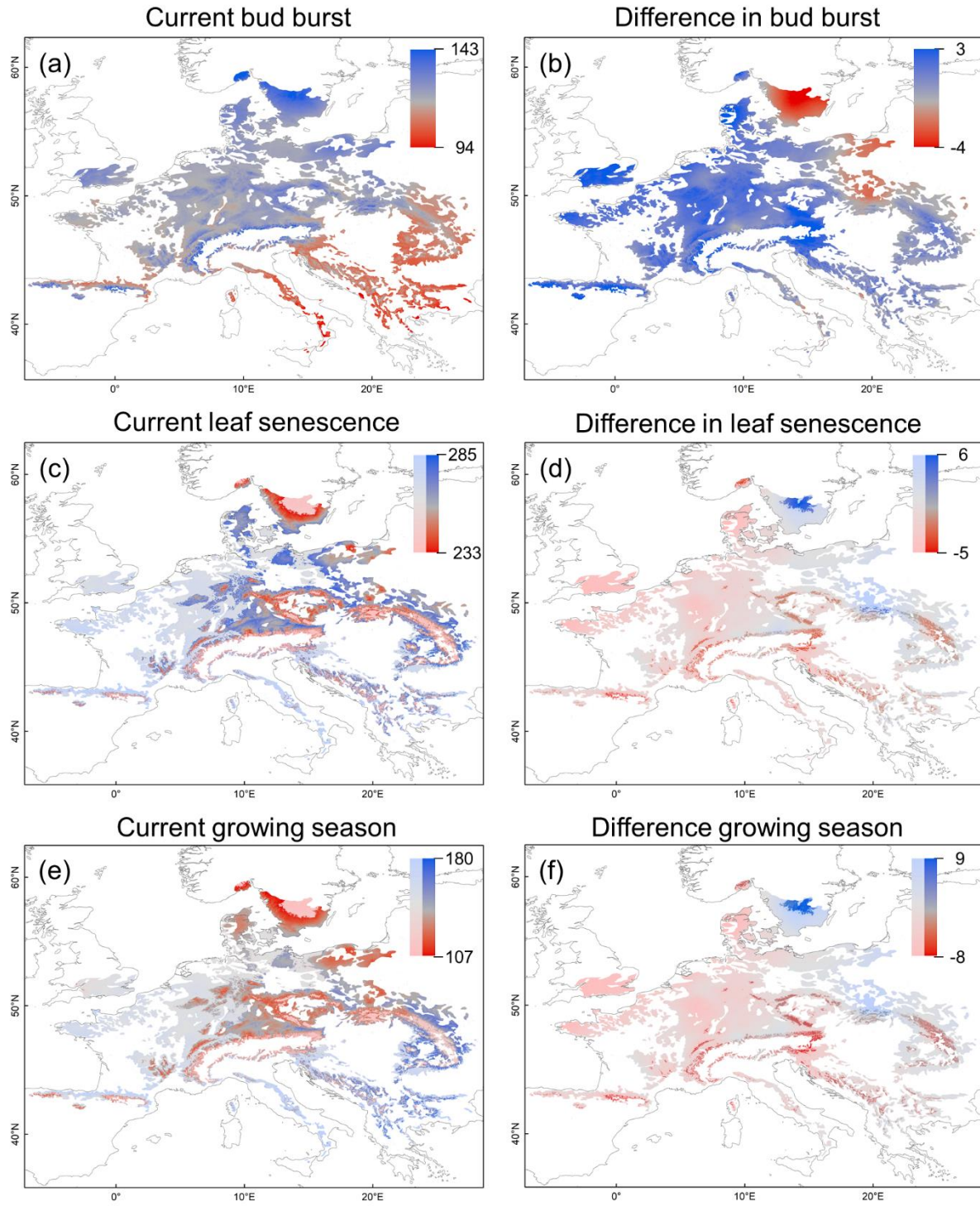


344

345 **Figure 5.** Interaction between growing season length and the mean temperature of September,  
346 October and November ( $T_m$  SON) of the trial, for (a) current climatic conditions (year of  
347 measurement minus year of plantation) and (b) the future climate scenario (RCP 8.5 for 2070).  
348 The colour gradient depicts the clinal variation from cold (blue) to warm (red) provenances ( $T_m$   
349 SON). Growing season length is represented in days. The error bars represent the 95% confidence  
350 intervals.

351

352



353

354 **Figure 6.** Spatial projections for (a) bud burst under current climatic conditions, (b) bud-burst  
 355 differences between current and future conditions, (c) leaf senescence under current climatic  
 356 conditions, (d) leaf-senescence differences between current and future conditions, (e) growing-

357 season length under current climatic conditions and (e) growing-season-length differences  
358 between current and future conditions. The growing-season length represents the difference  
359 between leaf flushing and leaf senescence. The colour gradient depicts the clinal variation from  
360 low (red) to high (blue) values of bud burst, leaf senescence and growing-season length. Growing-  
361 season length is represented in days, and leaf senescence and bud burst in Julian days. Solid colours  
362 represent the predicted geographic area without extrapolation from the climatic area covered by  
363 the trials ( $T_{mSON} = 7.5$  to  $10^{\circ}\text{C}$ ), the soft colours represent the extrapolated area (that is, outside  
364 the range of the calibration) predicted by the models. Current climate refers to the average climate  
365 calculated from 2000-2014, and difference in bud burst/leaf senescence/growing season represents  
366 the differences between the model predictions for future (2070, RCP 8.5) and contemporary  
367 climate conditions for bud burst/leaf senescence/growing season.

368

## 369 **4 Discussion**

### 370 4.1 Provenance differences in bud burst and autumn leaf senescence

371 The origin of beech provenances is a major determinant of the timing of their leaf spring and  
372 autumn phenology (Table 1), which confirms their genetic differentiation in the control of  
373 phenology (Chmura and Rozkowski 2002; Petkova et al. 2017, Alberto et al. 2013). This  
374 differentiation has often been reported to be stronger for spring phenology than for autumn  
375 phenology (Vitasse et al. 2009; Weih 2009; Firmat et al. 2017; Petkova et al. 2017), which is in  
376 agreement with what we found in our provenances. For instance, in the Slovakian trial the  
377 difference in the date of budburst between colder and warmer provenances was more than 20 days  
378 (Fig. 3 and S1). The duration of autumn leaf senescence is longer than that of leaf flushing in beech



379 (Fig. 3 and S1, Table S1 and S2) (Gömöry and Paule 2011; Petkova et al. 2017), whereas other  
380 temperate broadleaf species such as *Salix* spp. and *Quercus petraea* have a relatively long period  
381 of leaf-out and relatively abrupt autumn leaf senescence (Weih 2009; Firmat et al. 2017). Although  
382 the dates of spring and autumn leaf phenological stages varied between the two years of our study,  
383 the same response patterns persisted in both years (Fig. 3 and S1), suggesting a consistent effect  
384 of environmental conditions on the trials (Weih 2009; Friedman et al. 2011; Petkova et al. 2017).  
385 Our results also revealed larger differences among provenances for both BB and LS in the  
386 Slovakian trial than in the German one (Fig. 3 and S1), confirming that, in addition to genetic  
387 effects, the environment plays an important role in the phenological response of beech (Vitasse et  
388 al. 2013; Gárate-Escamilla et al. 2019).

389

#### 390 4.2 Environmental variables defining leaf senescence

391 Overall, our results support the assertions that (1) high autumn temperatures, both at the site of  
392 population origin and at the planting site, delay LS in beech, and (2) early BB tends to be followed  
393 by early LS (Table 1). The delayed LS promoted by warmer temperatures that we obtained by  
394 manipulating both genetic and site factors using common-garden trials (Fig. 4), is consistent with  
395 previous studies based on *in-situ* LS records (Delpierre et al. 2009; Vitasse et al. 2011), satellite  
396 data (Yang et al. 2015; Liu et al. 2016a) and climate-controlled chambers (Gunderson et al. 2012;  
397 Fu et al. 2018). While the convergence of these studies is reassuring, the extent to which warmer  
398 temperatures promote delayed LS still remains elusive (Estiarte and Peñuelas 2015): warmer  
399 temperatures accompanied by moderate drought appear to delay LS until a certain threshold (Xie  
400 et al. 2015); but beyond this drought threshold LS is accelerated (Chen et al. 2015; Estiarte and  
401 Peñuelas 2015). The roles of temperature and drought in LS have several broader implications



402 because the delay in LS induced by warm temperatures is associated with: delayed degradation of  
403 chlorophyll (Fracheboud et al. 2009), maintenance of photosynthetic enzyme activity (Shi et al.  
404 2014), prolonged leaf life span (Liu et al. 2018a), an increased risk of early-autumn frost damage  
405 that might kill leaves before nutrient reabsorption is complete (Estiarte and Peñuelas 2015),  
406 (Hartman et al. 2013) and a possible increase in photosynthetic carbon assimilation related to a  
407 longer growing season (Liu et al. 2016b).

408 Our findings do not necessarily imply that LS timing in beech only depends on the  
409 temperature of the provenance, because this parameter co-varied with daily insolation, latitude and  
410 precipitation measured at the origin of the provenance (Fig. S2). These factors explained a low  
411 proportion of the overall variance (higher insolation and latitude promoting delayed LS and higher  
412 precipitation promoting earlier LS, although delayed LS might be temperature-related due to cold  
413 temperatures experienced at high latitudes; see Table S3), yet we cannot exclude the possibility  
414 that they may have affected LS timing to some extent. For instance, photoperiod and insolation  
415 can have a strong effect on LS at high latitudes (Liu et al. 2016a, b) where photosynthesis at the  
416 end of the growing season can be increased by high insolation (which implies high  
417 photosynthetically active radiation; Bonan 2002) and by long photoperiods before the autumn  
418 equinox. This benefit feeds back, potentially producing a delay in LS as a result of persistent  
419 chlorophyll retention under sustained high irradiance (Kim et al. 2008).

420

421 4.3 The effect of bud burst on leaf senescence

422

423 The significant carry-over effect of BB on LS timing that we found when considering the climate  
424 of the trial (Table 1; Fig. 4a) is consistent with other recent studies on beech (Fu et al. 2014;  
425 Signarbieux et al. 2017; Chen et al. 2018; Zohner and Renner 2019) and other deciduous trees  
426 across the Northern Hemisphere (Keenan and Richardson 2015; Liu et al. 2016b). The relationship  
427 between BB and LS is complex and various different mechanisms have been proposed to explain  
428 carry-over effects of BB on LS, according to the particular conditions in each study: (i) leaf  
429 structural and morphological traits constrain leaf life span (Reich et al. 1992) and programmed cell  
430 death (Lam 2004; Lim et al. 2007); (ii) once a plant's carbohydrate storage capacities are saturated,  
431 growth is inhibited ("sink limitation") and LS is promoted (Fatichi et al. 2013; Keenan and  
432 Richardson 2015; Körner 2015; Signarbieux et al. 2017); (iii) LS is itself affected by the preceding  
433 winter/spring temperature (Fu et al. 2014; Signarbieux et al. 2017; Zohner and Renner 2019); (iv)  
434 early BB could lead to soil water depletion through increased transpiration, resulting in drought  
435 stress and producing earlier LS (Buermann et al. 2013); (v) early BB might increase pest attack  
436 (Jepsen et al. 2011) and increase the probability of spring frost damage (Hufkens et al. 2012),  
437 leading to an earlier LS. Our use of multiple provenances of different climatic origin enabled us  
438 to isolate the genetic component of these carry-over effects of BB on LS from the temperature  
439 response. We only found this pattern among cold provenances (3.2-5.2 C°) (Fig. S3) and in regions  
440 with high autumn temperature (11.5-12 C°) (Fig. 4a). Yet, we can not rule out the mechanisms  
441 listed above, and more experimental testing is needed to further elucidate the relationship between  
442 BB and LF across large environmental gradients.

443 The significant interaction effect of BB and the autumn temperature of the provenances on LS is  
444 notable (Table 1), as it suggests that the relationship between BB and LS is moderated by the  
445 temperature at the site of provenance origin in a population-specific manner. Contrarily to the

446 carry-over effect that we found between delayed LS and late BB when the autumn temperature of  
447 the trial was warm (Fig. 4a), there was an interaction effect between delayed LS and early BB only  
448 when the autumn temperatures of the populations were low (Fig. 4b), suggesting that early BB is  
449 correlated with delayed senescence only when provenances have cold origins (e.g. from the  
450 northern range).

451

#### 452 4.4 Variation in growing season length based on bud burst, leaf senescence and the environment 453 under present and future climates

454 Our results, based on two trials located in the core of the distribution range, predict that almost all  
455 the provenances monitored (except number 3 with an average autumn temperature of 7.4°C)  
456 would extend their GSL by up to 10 days under future climatic conditions with increased autumn  
457 temperatures (11.5-12 C°) (Fig. 5b). However, caution is required when scaling this result up over  
458 large geographical areas with our models based on only two trials. When the models predict  
459 phenology for locations within the climatic range of the trials, only trees in northern regions are  
460 expected to increase their GSL up-to 9 days. This trend can be attributed to the positive relationship  
461 between early BB and delayed LS in cold provenances (Figure 4b), which would extend to north-  
462 eastern regions of the species distribution when we extrapolate our results outside the climatic  
463 range of the trials (Fig. 6f). The GSL of trees in the rest of the range is predicted by our model to  
464 decrease by at least 8 days without extrapolation (Fig. 6). Several recent studies based on field or  
465 satellite data have also predict an increase in GSL (Barnard et al. 2018; Liu et al. 2018b; Gaertner  
466 et al. 2019) at high latitudes, coincident with cold beech populations. Yet Chen et al. (2018), a  
467 study including cold southern beech populations like those considered here, did not detect increases  
468 in the GSL of southern populations of four temperate European tree species (*Quercus robur*, *F.*

469 *sylvatica*, *Betula pendula* and *Aesculus hippocastanum*) over the last two decades; a study  
470 including cold southern populations of beech like those we consider here. These two trends are  
471 both consistent with our spatial projection of GSL (Fig. 6). The predicted larger GSL differences  
472 in the central and southern range are mostly the result of later leaf senescence predicted for these  
473 regions (Fig. 6), which is likely due to an expected increase in autumn temperatures in these  
474 regions. We should however note that our spatial modelling results, although covering a wide  
475 climatic range, should be interpreted with caution since they are based on empirical data from only  
476 two trials, which can limit their scope.

477

## 478 **5 Conclusions**

479 European beech is characterised by extensive plasticity in many of its life history traits (Gárate-  
480 Escamilla et al. 2019) compared to other tree species (Benito Garzón et al. 2019). Yet, strong  
481 genetic control over beech phenology, particularly in spring (Kramer et al. 2017), can constrain  
482 the acclimative response of populations to climatic changes and hence potentially compromise  
483 their future performance. Our analyses provide important insights into the complex relationships  
484 driving spring and autumn phenology across the species range. Although our extrapolations are  
485 only based on two trials, and hence they do not represent the entire climate conditions that  
486 populations encounter across the species range, we found large range-wide differences in GSL (as  
487 inferred from BB and LS) under present climate conditions. However, these differences are likely  
488 to diminish in the future, because the GSL of southern and core populations (i.e. those with a  
489 relatively long current GSL) is predicted to decrease, whilst that of northern and north-eastern  
490 populations (i.e. those with a relatively short current GSL) is predicted to increase. These trends  
491 are largely driven by an increase in temperatures that would modify phenology. Taken together,

492 our results suggest that northern populations should increase productivity in the coming years,  
493 extending their growing season to take advantage of warmer conditions in the northern part of the  
494 range.

## 495 **Funding**

496 This study was funded by the Investments for the Future programme (IdEx) Bordeaux (ANR-10-  
497 IDEX-03-02). HGE was funded by the Consejo Nacional de Ciencia y Tecnologia (CONACYT-  
498 Mexico; grant number: 636246) and by the Institute of Innovation and Technology Transfer of  
499 Nuevo Leon, Mexico. CCB and TMR were funded by the Academy of Finland (decision 304519).  
500 We have no conflicts of interest to declare.

501

## 502 **References**

- 503 Alberto FJ, Aitken SN, Alía R, et al (2013) Potential for evolutionary responses to climate  
504 change - evidence from tree populations. *Global Change Biology* 19:1645–1661. doi:  
505 10.1111/gcb.12181
- 506 Barnard DM, Knowles JF, Barnard HR, et al (2018) Reevaluating growing season length  
507 controls on net ecosystem production in evergreen conifer forests. *Scientific Reports* 8:1–  
508 10. doi: 10.1038/s41598-018-36065-0
- 509 Basler D, Körner C (2014) Photoperiod and temperature responses of bud swelling and bud burst  
510 in four temperate forest tree species. *Tree Physiology* 34:377–388. doi:  
511 10.1093/treephys/tpu021
- 512 Basler D, Körner C (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree  
513 species. *Agricultural and Forest Meteorology* 165:73–81. doi:  
514 10.1016/j.agrformet.2012.06.001
- 515 Bates D, Maechler M, Bolker B, et al (2018) lme4: Linear mixed-effects models using Eigen and  
516 S4. R package version 1.1-18-1. Available at: <http://CRAN.R-project.org/package=lme4>.  
517 In: Available at: <http://CRAN.R-project.org/package=lme4>
- 518 Benito Garzón M, Robson TM, Hampe A (2019)  $\Delta$ TraitSDM: Species distribution models that  
519 account for local adaptation and phenotypic plasticity. *New Phytologist* 222:1757–1765
- 520 Bonan GB (2002) *Ecological Climatology: Concepts and Applications*
- 521 Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe  
522 drought : a review of ecophysiological responses , adaptation processes and long-term

- 523 consequences. *Annals of Forest Science* 63:625–644. doi: 10.1051/forest
- 524 Brelsford CC, Nybakken L, Kotilainen TK, Robson TM (2019) The influence of spectral  
525 composition on spring and autumn phenology in trees. *Tree Physiology* 1–26. doi:  
526 10.1093/treephys/tpz026
- 527 Buermann W, Bikash PR, Jung M, et al (2013) Earlier springs decrease peak summer  
528 productivity in North American boreal forests. *Environmental Research Letters* 8:. doi:  
529 10.1088/1748-9326/8/2/024027
- 530 Caffarra A, Donnelly A (2011) The ecological significance of phenology in four different tree  
531 species: Effects of light and temperature on bud burst. *International Journal of*  
532 *Biometeorology* 55:711–721. doi: 10.1007/s00484-010-0386-1
- 533 Chen D, Wang S, Xiong B, et al (2015) Carbon/nitrogen imbalance associated with drought-  
534 induced leaf senescence in sorghum bicolor. *PLoS ONE* 10:1–17. doi:  
535 10.1371/journal.pone.0137026
- 536 Chen L, Huang JG, Ma Q, et al (2018) Long-term changes in the impacts of global warming on  
537 leaf phenology of four temperate tree species. *Global Change Biology* 997–1004. doi:  
538 10.1111/gcb.14496
- 539 Chmura DJ, Rozkowski R (2002) Variability of beech provenances in spring and autumn  
540 phenology. *Silvae Genetica* 51:123–127
- 541 Chmura HE, Kharouba HM, Ashander J, et al (2018) The mechanisms of phenology: the patterns  
542 and processes of phenological shifts. *Ecological Monographs* 0–2. doi: 10.1002/ecm.1337
- 543 Cooper HF, Grady KC, Cowan JA, et al (2018) Genotypic variation in phenological plasticity:  
544 Reciprocal common gardens reveal adaptive responses to warmer springs but not to fall  
545 frost. *Global Change Biology* 187–200. doi: 10.1111/gcb.14494
- 546 Dantec C ecile F oise, Ducasse H, Capdevielle X, et al (2015) Escape of spring frost and disease  
547 through phenological variations in oak populations along elevation gradients. *Journal of*  
548 *Ecology* 103:1044–1056. doi: 10.1111/1365-2745.12403
- 549 Delpierre N, Dufrière E, Soudani K, et al (2009) Modelling interannual and spatial variability of  
550 leaf senescence for three deciduous tree species in France. *Agricultural and Forest*  
551 *Meteorology* 149:938–948. doi: 10.1016/j.agrformet.2008.11.014
- 552 Estiarte M, Peñuelas J (2015) Alteration of the phenology of leaf senescence and fall in winter  
553 deciduous species by climate change: Effects on nutrient proficiency. *Global Change*  
554 *Biology* 21:1005–1017. doi: 10.1111/gcb.12804
- 555 EUFORGEN (2009) Distribution map of Beech (*Fagus sylvatica*). Available at:  
556 [www.euforgen.org](http://www.euforgen.org). In: [www.euforgen.org](http://www.euforgen.org)
- 557 Falusi M, Calamassi R (2012) Bud dormancy in beech (*Fagus sylvatica* L.). Effect of chilling  
558 and photoperiod on dormancy release of beech seedlings. *Tree Physiology* 6:429–438. doi:  
559 10.1093/treephys/6.4.429
- 560 Fatichi S, Luezing S, Korner C, Ecosystem T (2013) Moving beyond photosynthesis : from

561 carbon source to sink-driven vegetation modeling. *New Phytologist*

562 Firmat C, Delzon S, Louvet JM, et al (2017) Evolutionary dynamics of the leaf phenological  
563 cycle in an oak metapopulation along an elevation gradient. *Journal of Evolutionary*  
564 *Biology* 30:2116–2131. doi: 10.1111/jeb.13185

565 Fracheboud Y, Luquez V, Bjorken L, et al (2009) The Control of Autumn Senescence in  
566 European Aspen. *Plant Physiology* 149:1982–1991. doi: 10.1104/pp.108.133249

567 Fréjaville T, Benito Garzón M (2018) The EuMedClim Database : Yearly Climate Data ( 1901 –  
568 2014 ) of 1 km Resolution Grids for Europe and the Mediterranean Basin. *Frontiers in*  
569 *Ecology and Evolution* 6:1–5. doi: 10.3389/fevo.2018.00031

570 Friedman JM, Roelle JE, Cade BS (2011) Genetic and environmental influences on leaf  
571 phenology and cold hardiness of native and introduced riparian trees. *International Journal of*  
572 *Biometeorology* 55:775–787. doi: 10.1007/s00484-011-0494-6

573 Fu YH, Piao S, Delpierre N, et al (2018) Larger temperature response of autumn leaf senescence  
574 than spring leaf-out phenology. *Global Change Biology* 24:2159–2168. doi:  
575 10.1111/gcb.14021

576 Fu YH, Piao S, Vitasse Y, et al (2015) Increased heat requirement for leaf flushing in temperate  
577 woody species over 1980-2012: Effects of chilling, precipitation and insolation. *Global*  
578 *Change Biology* 21:2687–2697. doi: 10.1111/gcb.12863

579 Fu YSH, Campioli M, Vitasse Y, et al (2014) Variation in leaf flushing date influences autumnal  
580 senescence and next year’s flushing date in two temperate tree species. *Proceedings of the*  
581 *National Academy of Sciences* 111:7355–7360. doi: 10.1073/pnas.1321727111

582 Gaertner BA, Zegre N, Warner T, et al (2019) Climate, forest growing season, and  
583 evapotranspiration changes in the central Appalachian Mountains, USA. *Science of the*  
584 *Total Environment* 650:1371–1381. doi: 10.1016/j.scitotenv.2018.09.129

585 Gallinat AS, Primack RB, Wagner DL (2015a) Autumn, the neglected season in climate change  
586 research. *Trends in Ecology and Evolution* 30:169–176. doi: 10.1016/j.tree.2015.01.004

587 Gallinat AS, Primack RB, Wagner DL (2015b) Autumn , the neglected season in climate change  
588 research. *Trends in Ecology & Evolution* 30:169–176. doi: 10.1016/j.tree.2015.01.004

589 Gárate-Escamilla H, Hampe A, Vizcaíno-Palomar N, et al (2019) Range-wide variation in local  
590 adaptation and phenotypic plasticity of fitness-related traits in *Fagus sylvatica* and their  
591 implications under climate change. *Global Ecology and Biogeography*. doi: 10.1101/513515

592 Ghelardini L, Berlin S, Weih M, et al (2014) Genetic architecture of spring and autumn  
593 phenology in *Salix*. *BMC Plant Biology* 14:1–18. doi: 10.1186/1471-2229-14-31

594 Gill AL, Gallinat AS, Sanders-DeMott R, et al (2015) Changes in autumn senescence in northern  
595 hemisphere deciduous trees: A meta-analysis of autumn phenology studies. *Annals of*  
596 *Botany* 116:875–888. doi: 10.1093/aob/mcv055

597 Gömöry D, Paule L (2011) Trade-off between height growth and spring flushing in common  
598 beech (*Fagus sylvatica* L.). *Annals of Forest Science* 68:975–984. doi: 10.1007/s13595-011-

- 600 Gressler E, Jochner S, Capdevielle-Vargas RM, et al (2015) Vertical variation in autumn leaf  
601 phenology of *Fagus sylvatica* L. in southern Germany. *Agricultural and Forest Meteorology*  
602 201:176–186. doi: 10.1016/j.agrformet.2014.10.013
- 603 Gunderson CA, Edwards NT, Walker A V., et al (2012) Forest phenology and a warmer climate  
604 - growing season extension in relation to climatic provenance. *Global Change Biology*  
605 18:2008–2025. doi: 10.1111/j.1365-2486.2011.02632.x
- 606 Hartman DL, Klein Tank AMG, Rusicucci M, et al (2013) Observations: atmosphere and  
607 Observations: atmosphere and surface. In: *Climate Change 2013: The Physical Science*  
608 *Basis. Contribution of Working Group I to the Fifth Assessment Report of the*  
609 *Intergovernmental Panel on Climate Change.* In: Cambridge University Press, Cambridge,  
610 UK and New York, NY, USA. pp 159–254
- 611 Heide OM (1993) Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and  
612 long days. *Physiologia Plantarum* 89:187–191. doi: 10.1111/j.1399-3054.1993.tb01804.x
- 613 Hijmans RJ, Van Etten J, Cheng J, et al (2017) Package ‘ raster ’: Geographic Data Analysis and  
614 Modeling. Available at: <https://cran.r-project.org/web/packages/raster/raster.pdf>.
- 615 Hufkens K, Friedl MA, Keenan TF, et al (2012) Ecological impacts of a widespread frost event  
616 following early spring leaf-out. *Global Change Biology* 18:2365–2377. doi: 10.1111/j.1365-  
617 2486.2012.02712.x
- 618 Jepsen JU, Kapari L, Hagen SB, et al (2011) Rapid northwards expansion of a forest insect pest  
619 attributed to spring phenology matching with sub-Arctic birch. *Global Change Biology*  
620 17:2071–2083. doi: 10.1111/j.1365-2486.2010.02370.x
- 621 Keenan TF, Richardson AD (2015) The timing of autumn senescence is affected by the timing of  
622 spring phenology: Implications for predictive models. *Global Change Biology* 21:2634–  
623 2641. doi: 10.1111/gcb.12890
- 624 Kim J-H, Moon YR, Wi SG, et al (2008) Differential Radiation Sensitivities of Arabidopsis  
625 Plants at Various Developmental Stages. *Photosynthesis Energy from the Sun* 1491–1495.  
626 doi: 10.1007/978-1-4020-6709-9\_320
- 627 Körner C (2015) Paradigm shift in plant growth control. *Current Opinion in Plant Biology*  
628 25:107–114. doi: 10.1016/j.pbi.2015.05.003
- 629 Kramer K, Ducouso A, Gomory D, et al (2017) Chilling and forcing requirements for foliage  
630 bud burst of European beech (*Fagus sylvatica* L.) differ between provenances and are  
631 phenotypically plastic. *Agricultural and Forest Meteorology* 234–235:172–181. doi:  
632 10.1016/j.agrformet.2016.12.002
- 633 Lam E (2004) Controlled cell death, plant survival and development. *Nature Reviews Molecular*  
634 *Cell Biology* 5:305–315. doi: 10.1038/nrm1358
- 635 Lang W, Chen X, Qian S, et al (2019) A new process-based model for predicting autumn  
636 phenology: How is leaf senescence controlled by photoperiod and temperature coupling?  
637 *Agricultural and Forest Meteorology* 268:124–135. doi: 10.1016/j.agrformet.2019.01.006



638 Leites LP, Robinson AP, Rehfeldt GE, et al (2012) Height-growth response to changes in climate  
639 differ among populations of interior Douglas-fir: a novel analysis of provenance-test data.  
640 Ecological Applications 22:154–165. doi: 10.1890/11-0150.1

641 Liang L (2019) A spatially explicit modeling analysis of adaptive variation in temperate tree  
642 phenology. Agricultural and Forest Meteorology 266–267:73–86. doi:  
643 10.1016/j.agrformet.2018.12.004

644 Liang L (2015) Geographic variations in spring and autumn phenology of white ash in a  
645 common garden. Physical Geography 36:489–509. doi: 10.1080/02723646.2015.1123538

646 Lim P, Kim H, Gil Nam H (2007) Leaf Senescence. Annual Review of Plant Physiology 58:115–  
647 136. doi: 10.1016/B978-0-12-394807-6.00081-2

648 Liu G, Chen X, Zhang Q, et al (2018a) Antagonistic effects of growing season and autumn  
649 temperatures on the timing of leaf coloration in winter deciduous trees. Global Change  
650 Biology 24:3537–3545. doi: 10.1111/gcb.14095

651 Liu Q, Fu YH, Zeng Z, et al (2016a) Temperature, precipitation, and insolation effects on  
652 autumn vegetation phenology in temperate China. Global Change Biology 22:644–655. doi:  
653 10.1111/gcb.13081

654 Liu Q, Fu YH, Zhu Z, et al (2016b) Delayed autumn phenology in the Northern Hemisphere is  
655 related to change in both climate and spring phenology. Global Change Biology 22:3702–  
656 3711. doi: 10.1111/gcb.13311

657 Liu Q, Piao S, Janssens IA, et al (2018b) Extension of the growing season increases vegetation  
658 exposure to frost. Nature Communications 9:. doi: 10.1038/s41467-017-02690-y

659 Lukasová V, Bucha T, Škvareninová J, Škvarenina J (2019) Validation and Application of  
660 European Beech Phenological Metrics Derived from MODIS Data along an Altitudinal  
661 Gradient. Forests 10:60. doi: 10.3390/f10010060

662 Luquez V, Hall D, Albrechtsen BR, et al (2008) Natural phenological variation in aspen (*Populus*  
663 *tremula*): The SwAsp collection. Tree Genetics and Genomes 4:279–292. doi:  
664 10.1007/s11295-007-0108-y

665 Mazerolle MJ (2006) Improving data analysis in herpetology: Using Akaike’s information  
666 criterion (AIC) to assess the strength of biological hypotheses. Amphibia Reptilia 27:169–  
667 180. doi: 10.1016/j.jclepro.2013.10.062

668 Michelson IH, Eriksson ME, Nilsson O, et al (2018) Autumn senescence in aspen is not triggered  
669 by day length. Physiologia Plantarum 162:123–134. doi: 10.1111/ppl.12593

670 Packham JR, Thomas PA, Atkinson MD, Degen T (2012) Biological Flora of the British Isles:  
671 *Fagus sylvatica*. Journal of Ecology 100:1557–1608. doi: 10.1111/j.1365-  
672 2745.2012.02017.x

673 Petkova K, Molle E, Huber G, et al (2017) Spring and autumn phenology of Bulgarian and  
674 German provenances of Common beech (*Fagus sylvatica* L.) under similar climatic  
675 conditions. Silvae Genetica 66:24–32. doi: 10.1515/sg-2017-0004

- 676 Piao S, Tan J, Chen A, et al (2015) Leaf onset in the northern hemisphere triggered by daytime  
677 temperature. *Nature Communications* 6:. doi: 10.1038/ncomms7911
- 678 Porth I, Klápště J, McKown AD, et al (2015) Evolutionary quantitative genomics of *Populus*  
679 *trichocarpa*. *PLoS ONE* 10:1–25. doi: 10.1371/journal.pone.0142864
- 680 Preston CD, Hill MO (1997) The geographical relationships of British and Irish vascular plants.  
681 *Botanical Journal of the Linnean Society* 124:1–120. doi: 10.1006/boj.1996.0084
- 682 Pudas E, Leppälä M, Tolvanen A, et al (2008) Trends in phenology of *Betula pubescens* across  
683 the boreal zone in Finland. *International Journal of Biometeorology* 52:251–259. doi:  
684 10.1007/s00484-007-0126-3
- 685 R Development Core Team R (2015) R: A Language and Environment for Statistical Computing.  
686 R Foundation for Statistical Computing, Vienna, Austria. Available at:  
687 <http://www.Rproject.org>.
- 688 Reich PB, Walters MB, Ellsworth DS (1992) Leaf life-span in relation to leaf, plant, and stand  
689 characteristics among diverse ecosystems. *Ecological monographs* 62:365–392. doi:  
690 10.2307/2937116
- 691 Robson M, Alia R, Bozic G, et al (2011) The timing of leaf flush in European beech (*Fagus*  
692 *sylvatica* L.) saplings. *Genetic Resources of European Beech (Fagus sylvatica L) for*  
693 *Sustainable Forestry : Proceedings of the COST E52 Final Meeting SERIE FORESTAL*  
694 22:61–80
- 695 Robson M, Benito Garzón M, BeechCOSTe52 database consortium (2018) Data Descriptor :  
696 Phenotypic trait variation measured on European genetic trials of *Fagus sylvatica* L.  
697 *Scientific Data* 5:1–7. doi: 10.1038/sdata.2018.149
- 698 Robson TM, Rasztovits E, Aphalo PJ, et al (2013) Flushing phenology and fitness of European  
699 beech (*Fagus sylvatica* L.) provenances from a trial in La Rioja, Spain, segregate according  
700 to their climate of origin. *Agricultural and Forest Meteorology* 180:76–85. doi:  
701 10.1016/j.agrformet.2013.05.008
- 702 Sampaio T, Branco M, Guichoux E, et al (2016) Does the geography of cork oak origin influence  
703 budburst and leaf pest damage? *Forest Ecology and Management* 373:33–43. doi:  
704 10.1016/j.foreco.2016.04.019
- 705 Shi C, Sun G, Zhang H, et al (2014) Effects of warming on chlorophyll degradation and  
706 carbohydrate accumulation of alpine herbaceous species during plant senescence on the  
707 tibetan plateau. *PLoS ONE* 9:. doi: 10.1371/journal.pone.0107874
- 708 Signarbieux C, Toledano E, Sanginés de Carcer P, et al (2017) Asymmetric effects of cooler and  
709 warmer winters on beech phenology last beyond spring. *Global Change Biology* 23:4569–  
710 4580. doi: 10.1111/gcb.13740
- 711 Soolanayakanahally RY, Guy RD, Silim SN, Song M (2013) Timing of photoperiodic  
712 competency causes phenological mismatch in balsam poplar (*Populus balsamifera* L.).  
713 *Plant, Cell and Environment* 36:116–127. doi: 10.1111/j.1365-3040.2012.02560.x
- 714 Vitasse Y, Delzon S, Bresson CC, et al (2009) Altitudinal differentiation in growth and

715 phenology among populations of temperate-zone tree species growing in a common garden.  
716 Canadian Journal of Forest Research 39:1259–1269. doi: 10.1139/X09-054

717 Vitasse Y, François C, Delpierre N, et al (2011) Assessing the effects of climate change on the  
718 phenology of European temperate trees. Agricultural and Forest Meteorology 151:969–980.  
719 doi: 10.1016/j.agrformet.2011.03.003

720 Vitasse Y, Hoch G, Randin CF, et al (2013) Elevational adaptation and plasticity in seedling  
721 phenology of temperate deciduous tree species. Oecologia 171:663–678. doi:  
722 10.1007/s00442-012-2580-9

723 Walther GR, Post E, Convey P, et al (2002) Ecological responses to recent climate change.  
724 Nature 416:389–395. doi: 10.1038/416389a

725 Wang J, Ding J, Tan B, et al (2018) A major locus controls local adaptation and adaptive life  
726 history variation in a perennial plant. Genome Biology 19:1–17. doi: 10.1186/s13059-018-  
727 1444-y

728 Way DA, Montgomery RA (2015) Photoperiod constraints on tree phenology, performance and  
729 migration in a warming world. Plant, Cell & Environment 38:1725–1736. doi:  
730 10.1111/pce.12431

731 Weih M (2009) Genetic and environmental variation in spring and autumn phenology of biomass  
732 willows (*Salix* spp.): Effects on shoot growth and nitrogen economy. Tree Physiology  
733 29:1479–1490. doi: 10.1093/treephys/tpp081

734 Xie Y, Wang X, Silander JA (2015) Deciduous forest responses to temperature, precipitation,  
735 and drought imply complex climate change impacts. Proceedings of the National Academy  
736 of Sciences 112:13585–13590. doi: 10.1073/pnas.1509991112

737 Yang B, He M, Shishov V, et al (2017) New perspective on spring vegetation phenology and  
738 global climate change based on Tibetan Plateau tree-ring data. Proceedings of the National  
739 Academy of Sciences 114:6966–6971. doi: 10.1073/pnas.1616608114

740 Yang Y, Guan H, Shen M, et al (2015) Changes in autumn vegetation dormancy onset date and  
741 the climate controls across temperate ecosystems in China from 1982 to 2010. Global  
742 Change Biology 21:652–665. doi: 10.1111/gcb.12778

743 Yeang H (2007) Synchronous flowering of the rubber tree (*Hevea brasiliensis*) induced by high  
744 solar radiation intensity. New Phytol 175:283–9. doi: 10.1111/j.1469-8137.2007.02089.x

745 Zhang S wu, Wang C fa, Yao Y hua (2011) Inverse Leaf Aging Sequence (ILAS) and Its  
746 Significance of Wheat. Agricultural Sciences in China 10:207–219. doi: 10.1016/S1671-  
747 2927(09)60307-2

748 Zohner CM, Renner SS (2019) Ongoing seasonally uneven climate warming leads to earlier  
749 autumn growth cessation in deciduous trees. Oecologia. doi: 10.1007/s00442-019-04339-7

750 Zohner CM, Rockinger A, Renner SS (2018) Increased autumn productivity permits temperate  
751 trees to compensate for spring frost damage. New Phytologist 221:789–795. doi:  
752 10.1111/nph.15445

753

754