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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 925 individual field-observations of BB and LS  
28 from six *Fagus sylvatica* provenances, covering the range of environmental conditions found  
29 across the species distribution, to: (i) estimate the dates of BB and LS of these provenances; (ii)  
30 assess the main drivers of LS; and (iii) predict the likely variation in the growing season length  
31 (GSL; defined by BB and LS timing) across populations under current and future climate  
32 scenarios. To this end, we first calibrated linear mixed-effects models for LS as a function of  
33 temperature, insolation and BB date. Secondly, we calculated the GSL for each provenance as  
34 the number of days between BB and LS. We found that: i) there were larger differences among  
35 provenances in the date of LS than in the date of BB; ii) the temperature through September,  
36 October and November was the main determinant of LS in beech, although covariation of  
37 temperature with daily insolation and precipitation-related variables suggests that all three  
38 variables may affect LS timing; and iii) GSL was predicted to increase in northern beech  
39 provenances and to shrink in populations from the core and the southern range under climate  
40 change. Consequently, the large differences in GSL across beech range in the present climate are  
41 likely to decrease under future climates where rising temperatures will alter the relationship  
42 between BB and LS, with northern populations increasing productivity by extending their  
43 growing season to take advantage of warmer conditions.

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

46

## 47 **1 Introduction**

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

65 Extensive research has identified cold winter temperatures (i.e., chilling requirements)  
66 and accumulated spring temperatures (i.e., forcing requirements) as the main drivers of BB;

67 sometimes coupled with photoperiod (Basler and Körner 2014; Fu et al. 2015) (Fig. 1). The  
68 major drivers of LS have been more difficult to identify (Gallinat et al. 2015; Brelsford et al.  
69 2019). A recent meta-analysis showed that summer and autumn temperatures, precipitation and  
70 photoperiod can all affect LS (Gill et al. 2015). Generally, temperature tends to be predominant  
71 at lower latitudes (Pudas et al. 2008; Lang et al. 2019), whereas photoperiod is more important at  
72 higher latitudes (Soolanayakanahally et al. 2013; Lang et al. 2019) (Fig. 1). Yet temperature  
73 effects on LS are not straightforward: increasing summer and autumn temperatures and even  
74 moderate drought can delay LS (Xie et al. 2015), whereas severe drought tends to promote  
75 earlier LS (Chen et al. 2015; Estiarte and Peñuelas 2015), (Fig. 1). Finally, high insolation may  
76 also delay LS (Liu et al. 2016a) (Fig. 1). The complex nature of the environmental triggers of LS  
77 has to-date hampered attempts to understand the causes of its variation across large geographical  
78 scales (Chmura et al. 2018). This uncertainty makes it very difficult to estimate GSL across  
79 species ranges. Recent studies based on *in-situ* records and satellite data have shown positive  
80 correlations between the timing of BB and LS that tend to stabilize GSL across populations  
81 (Keenan and Richardson 2015; Liu et al. 2016b). But this is not a universal finding and the  
82 extent to which GSL can change depends on the combination of many factors, as explained in  
83 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/In  | (Liu <i>et al.</i> , 2016a)                                                       |
|                                                                                                                                   | ↓ Phot     |                 |                 | ↓ Phot/In  | (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)                                                         |

84

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

95

96 *Fagus sylvatica* L. (European beech, henceforth “beech”) is one of the most dominant  
97 and widespread broadleaf forest trees in Europe (Preston and Hill 1997) of high ecological and

98 economic importance (Packham et al. 2012). In beech, BB responds to a combination of chilling  
99 and forcing temperature requirements (Heide 1993; Falusi and Calamassi 2012; Kramer et al.  
100 2017), and to photoperiod (Heide 1993; Caffarra and Donnelly 2011; Basler and Körner 2012),  
101 with the strength of these drivers changing along environmental gradients. For instance, BB is  
102 more affected by photoperiod in colder populations, and by chilling requirements in warmer  
103 populations (Gárate-Escamilla et al. 2019). Studies of LS in beech suggest that: (i) temperature  
104 may be a more important cue than photoperiod when nutrients and water are not limiting (Fu et  
105 al. 2018); (ii) non-senescent green leaves are prematurely lost as a result of severe drought  
106 conditions (Bréda et al. 2006); (iv) early BB correlates with early LS (Fu et al. 2014; Chen et al.  
107 2018; Zohner et al. 2018); (v) leaves first start to change color in autumn from the upper part of  
108 the canopy, suggesting that hydraulic conductance or the amount of solar radiation received over  
109 the growing season may play a role in triggering LS (Gressler et al. 2015; Lukasová et al. 2019),  
110 although this could also be related to an hormonal effect (Zhang et al. 2011).

111 Here, we investigate BB and LS in six different beech populations (925 trees) planted in  
112 two common gardens in central Europe (Robson et al. 2018), and use this information to infer  
113 how range-wide patterns of beech GSL might evolve under future climate warming. Specifically,  
114 we attempt to: (i) estimate the dates of BB and LS, and how they differ among populations; (ii)  
115 assess the main drivers of LS; and (iii) predict GSL and how it would vary across populations  
116 under current and future climate.

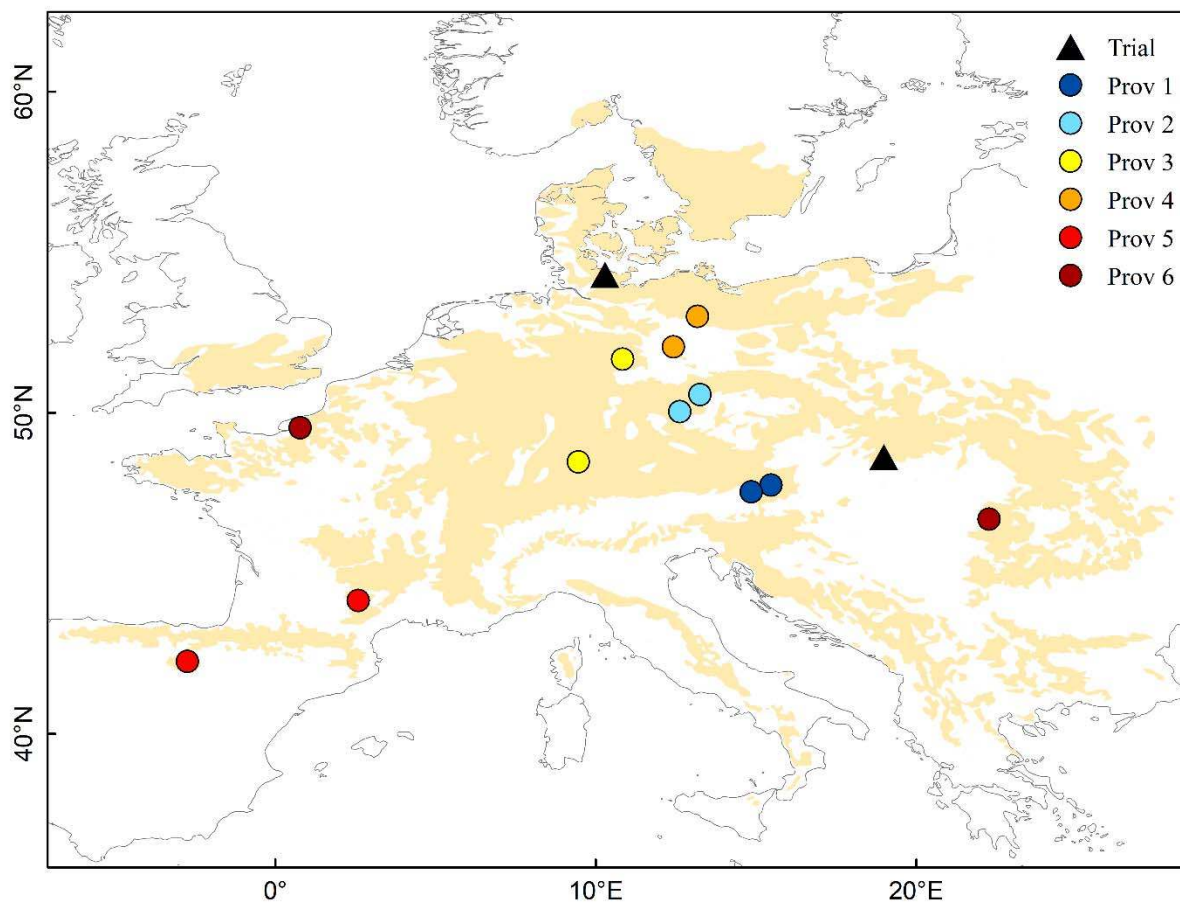
117

## 118 **2 Materials and Methods**

### 119 **2.1 Field trials and provenances**

120 Spring and autumn phenological observations came from two common-garden field-trials  
121 (hereafter “trials”), located in Schädtebek (54.30°N, 10.28°E), Germany and Tále, Mláčik,  
122 Slovakia (48.62°N, 18.98°E) (henceforth termed “Germany” and “Slovakia” trials, respectively).  
123 These trials were planted with seeds collected from 38 populations (hereafter referred to as  
124 “provenances”) that roughly cover the entire range of beech (Fig. 2). Seeds were germinated in  
125 greenhouses and planted in the trials when two years old, in 1995 (Germany) and 1998  
126 (Slovakia) (details given in Robson et al. 2018). To maintain a balanced design, we used only six  
127 provenances from each of the two trials (Supplementary Table S1, Fig. 2), chosen in pairs based  
128 on their similar climatic origin (Pearson correlation  $r \geq 0.98$ ). The provenances were ranked from  
129 colder (1) to warmer (6) origins (Fig. 2). Trees growing in Germany were measured at an age of  
130 12 and 13 years old, those in Slovakia at 11 and 12 years old (Table S1).





131

132 **Figure 2.** Geographical distribution of beech provenances (colored circles) and trials (triangles)  
133 underlying this study. Beige shading indicates the distribution range of beech. The different  
134 colors of the provenance circles indicate the pairs of similar provenances selected from each trail  
135 (blue colors indicate cold and red colors warm provenances as defined in Table S1).

136

## 137 **2.2 Estimation of bud burst, leaf senescence and growing season length**

138 We transformed the observational stages (phenophases), and score data (qualitative  
139 measurements) for BB and LS to Julian days by fitting the phenophases (Fig. 3; Table S2 and  
140 S3) for each tree in every trial using the Weibull function (Robson et al. 2011; Gárate-Escamilla

141 et al. 2019). These data were used to obtain the day of the year (DOY) when BB was attained in  
142 spring (stage 2.5; Fig. 2; Robson et al. 2013) and at the stage at which 50% of the trees' leaves  
143 had changed color from green to yellow (stage 3; Fig. 2; (Lang et al. 2019)). We calculated the  
144 GSL for each tree as the number of days between the estimated dates of BB and LS (Estiarte and  
145 Peñuelas 2015).

146

### 147 **2.3 Environmental data**

148 To separate the effects of the provenance (genetic effects) to those of the trial (environmental  
149 effects), we used the average climate from 1901 to 1990 for each provenance and the average  
150 climate of the period between the planting year and the year of measurement for the trial (Leites  
151 et al. 2012) in our models. We used the following precipitation- and temperature-related  
152 variables from EuMedClim (Fréjaville and Benito Garzón 2018): precipitation of driest month,  
153 (BIO14, mm), precipitation (P, mm) of June, July and August (JJA), minimal (Min) monthly  
154 water balance (PPET, mm), and mean temperature ( $T_m$ , °C) of June, July and August (JJA) and  
155 September, October and November (SON). In addition, we used daily insolation, a function of  
156 day length and solar irradiance (Yeang 2007). We downloaded daily insolation data from the  
157 NASA Atmospheric Science Data Center (<https://power.larc.nasa.gov/data-access-viewer/>), and  
158 we calculated solar radiation (direct and diffuse) between 400-2700 nm incoming on a horizontal  
159 surface for a given location. We calculated the mean daily insolation (DIM,  $\text{kWh m}^{-2} \text{d}^{-1}$ )  
160 between the months of June, July and August (JJA) and September, October and November  
161 (SON). As with the climatic variables, we characterized the DIM of the trial as the average  
162 between the planting year and the year of measurement. Because the insolation data series from  
163 the NASA Atmospheric Science Data Center begins in July 1983, we characterized the DIM of

164 the provenance as the average between 1984 and 1990 for JJA, and between 1983 and 1990 for  
165 SON.

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

171

## 172 **2.4 Statistical analysis**

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

181

### 182 **2.4.1 Environmental variable selection**

183 To avoid co-linearity and reduce the number of variables to test in our models, we only retained  
184 weakly correlated variables ( $-0.5 < r < 0.5$ ) for modeling purposes. The full correlation matrix  
185 between all variables is provided in Fig. S2.

186

#### 187 2.4.2 Linear mixed-effects model of leaf senescence

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

$$\log(LS_{ijk}) = \alpha_0 + \alpha_1(EP_{ij}) + \alpha_2(ET_{ik}) + \alpha_3(BB_{ik}) + \alpha_4(EP_{ij} \times ET_{ik}) + \alpha_5(EP_{ij} \times BB_{ik}) \\ + \alpha_6(ET_{ik} \times BB_{ik}) + \beta + \varepsilon$$

194 (Equation 1)

195 Where LS = leaf senescence of the  $i^{th}$  individual of the  $j^{th}$  provenance in the  $k^{th}$  trial; EP =  
196 environmental variable that characterized the provenance site of the  $i^{th}$  individual of the  $j^{th}$   
197 provenance; ET = environmental variable that characterized the trial site of the  $i^{th}$  individual in  
198 the  $k^{th}$  trial; BB = bud burst of the  $i^{th}$  individual in the  $k^{th}$  trial;  $\beta$  = random effects and  $\varepsilon$  =  
199 residuals. In addition, the model included the following interaction terms: EP  $\times$  ET, EP  $\times$  BB,  
200 and ET  $\times$  BB. EP  $\times$  ET, interactions represent differences in LS values that can be attributed to  
201 the interactions between genetic (provenance) and environmental (site) effects. EP  $\times$  BB and ET

202 × BB interactions represent the effects of the provenance on LS related to BB and the effects of  
203 the site related to BB.

204 LS models were fitted with the ‘lmer’ function of the package ‘lme4’ (Bates et al. 2018),  
205 within R statistical framework version 3.2.0 (R Development Core Team 2015). To choose the  
206 best supported model, we followed a stepwise-model procedure: (i) we selected the most  
207 important variable related to the trial by comparing a series of models that included one  
208 environmental variable for the trial and BB, and then selected the best model using the Akaike  
209 information criterion (AIC) with criteria delta < 2 (Mazerolle 2006), and the variance explained  
210 by the fixed effects, marginal  $R^2$  (Supplementary Table S4); (ii) we chose the optimal random  
211 component of the model by comparing the battery of models that included different  
212 combinations of random effects, the previously selected environmental variable from the trial  
213 and BB using restricted maximum likelihood (REML), and selected using the AIC criterion; (iii)  
214 we retained the best environmental variable related to the provenance comparing the models that  
215 included one environmental variable from the provenance, the selected variable from the trial,  
216 the BB, the interaction between the three variables and the random terms using maximum  
217 likelihood (ML) using the AIC criterion (Supplementary Table S4); (iv) we combined the best  
218 optimal random and fixed components (previously selected) and adjusted them using REML to  
219 obtain the best performing model.

220 The goodness of fit of the final models was assessed using two approaches. First, we  
221 quantified the percentage variance explained by the model attributed to the fixed effects  
222 (marginal  $R^2$ ) and attributed to the fixed and random effects (conditional  $R^2$ ). Second, we  
223 measured the generalization capacity of the model using cross-validation with independent data.

224 To this end, we calibrated the model with 66% of the data and performed an independent  
225 validation (using Pearson correlations) with the remaining 34% of the data.

226

#### 227 2.4.3 Interactions of leaf senescence with bud burst, and environmental variables

228 For the best LS supported model, we analyzed the significant interactions (EP × ET, EP × BB,  
229 ET × BB in Equation 1) between LS and the environment (ET; represented by one environmental  
230 variable of the trial) and according to provenances showing early, mean and late BB. We also  
231 inspected gradients of GSL for the six populations by plotting GSL against the environmental  
232 variable of the trial selected in the model (ET) and population under current conditions. We  
233 predicted the date of LS for the future climate scenario RCP 8.5 using our LS model and the date  
234 of BB for the same provenances, achieved using our BB model (Gárate-Escamilla et al. 2019),  
235 and plotted the predicted future GSL against ET, for each of the populations.

236

#### 237 2.4.4 Spatial predictions

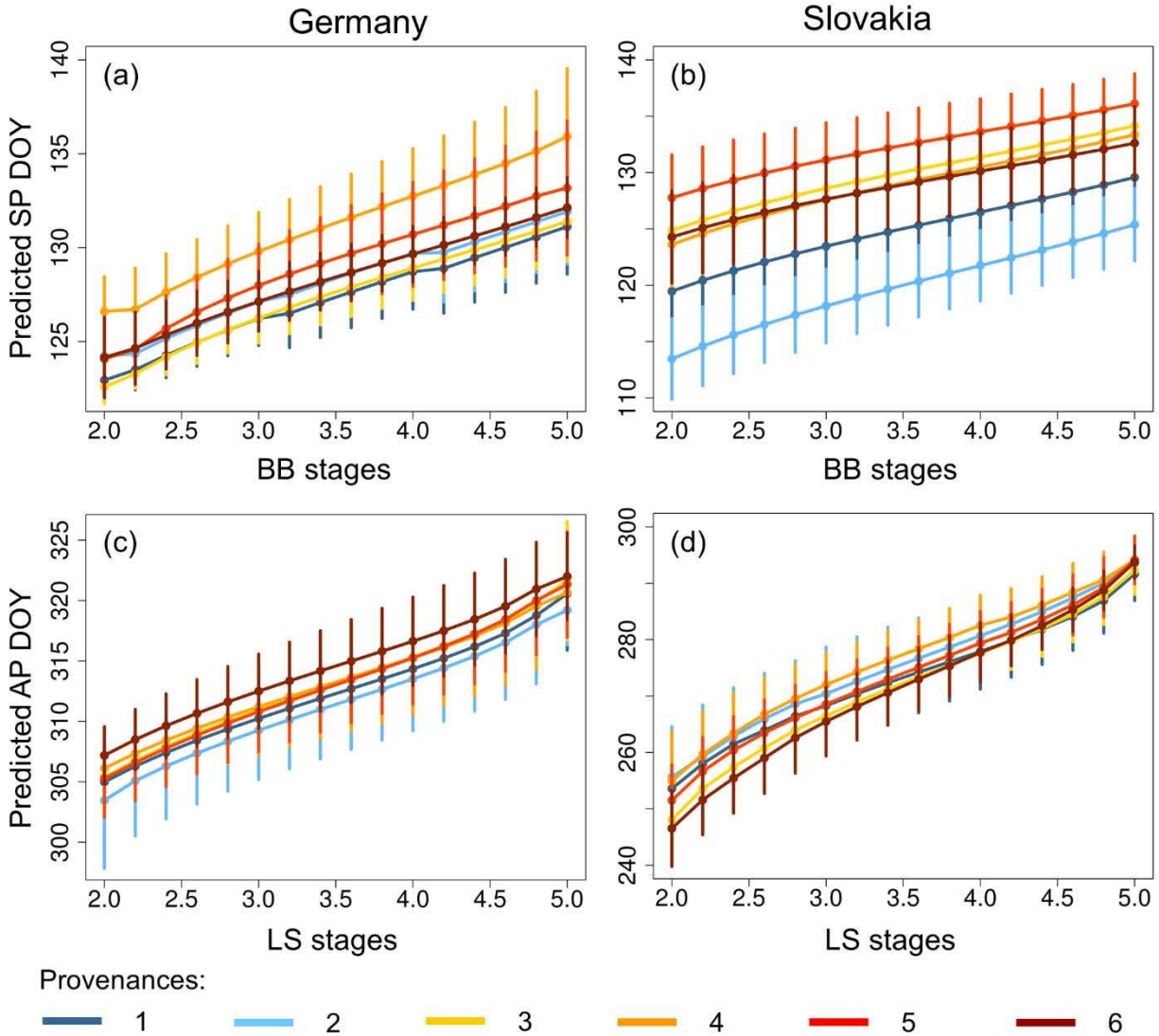
238 Spatial projections of LS were calculated using our LS model, and predictions of GSL were  
239 calculated by subtracting the predicted BB from LS for both current and future climatic  
240 conditions across the species range. All spatial predictions were delimited within the distribution  
241 range of the species (EUFORGEN 2009). Spatial analyses were performed with the ‘raster’  
242 package in R (Hijmans et al. 2017).

243

### 244 **3 Results**

### 245 **3.1 Estimation of bud burst and autumn leaf senescence dates from field observations**

246 In both trials, differences among provenances were larger for spring leaf flush stages (including  
247 bud burst; Fig. 3a & b) than for autumn leaf senescence stages (including 50% yellow leaves;  
248 Fig. 3c & d). Although these differences were always statistically significant, they were bigger in  
249 the Slovakian trial than in the German one (Fig. 3, Table S2 and S3). Differences in the predicted  
250 DOY of spring leaf flush and autumn leaf senescence stages were found for the two different  
251 years of measurement in the Slovakian trial (Figs. 3b & d; S1a & b). We used the fitted data to  
252 extract the DOY for the flushing stage 2.5 (bud burst, BB) and the senescence stage 3 (= 50% of  
253 leaves yellow, LS) for each provenance (Tables S2 and S3).



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.           |

254

255 **Figure 3.** Predicted spring bud burst and autumn leaf senescence phenology days of the year  
 256 (DOY) against the observational stages recorded in the field for the two trials. SP: spring bud  
 257 burst phenology; AP: autumn leaf senescence phenology. Provenance colors range from dark



258 blue (cold origin) to dark red (warm origin) for the provenances in the two trials (Figure 1 &  
259 Table S1). The spring leaf flushing and autumn leaf senescence stages are described in the lower  
260 part of the figure. The phenology stages were recorded in the year 2006 in Germany and 2008 in  
261 Slovakia.

262

### 263 **3.2 Variable selection and best model selection**

264 Our inspection of climate variables revealed that: (i) provenance and trial variables were not  
265 correlated with each other; (ii) temperature (TmJJA and TmSON)- and precipitation (BIO14,  
266 PpetMin and PrecJJA)-related variables for the provenances were correlated, whilst daily  
267 insolation (DIMJJA and DIMSON) variables for the provenances were only correlated with the  
268 latitude (Lat) of the provenances; (iii) all the trial variables were correlated among themselves;  
269 and (iv) the BB co-variable was not correlated with the rest of variables (Fig. S2).

270 In view of these results, we retained daily insolation (DIMJJA and DIMSON) and  
271 temperature-(TmJJA and TmSON)-related variables for the provenances, all climate variables  
272 from the trials, and BB as predictors for our models of LS. The best model according to AIC  
273 criteria (Tables S4 and S5) used the mean temperature in September, October and November  
274 (Tm SON) of the trial and of the provenance, and BB as a co-variable (Table 1 and Table S4).

275

|            | <b>Leaf senescence</b> |          |          |
|------------|------------------------|----------|----------|
| Model      | Linear Mixed Effect    |          |          |
|            | Random Effects         |          |          |
|            | Obs                    | Variance | SD       |
| Provenance | 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       | <i>t</i> |
| 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    |
|               | <i>r</i>      | $R^2M$   | $R^2C$   |
|               | 0.92          | 0.52     | 0.99     |

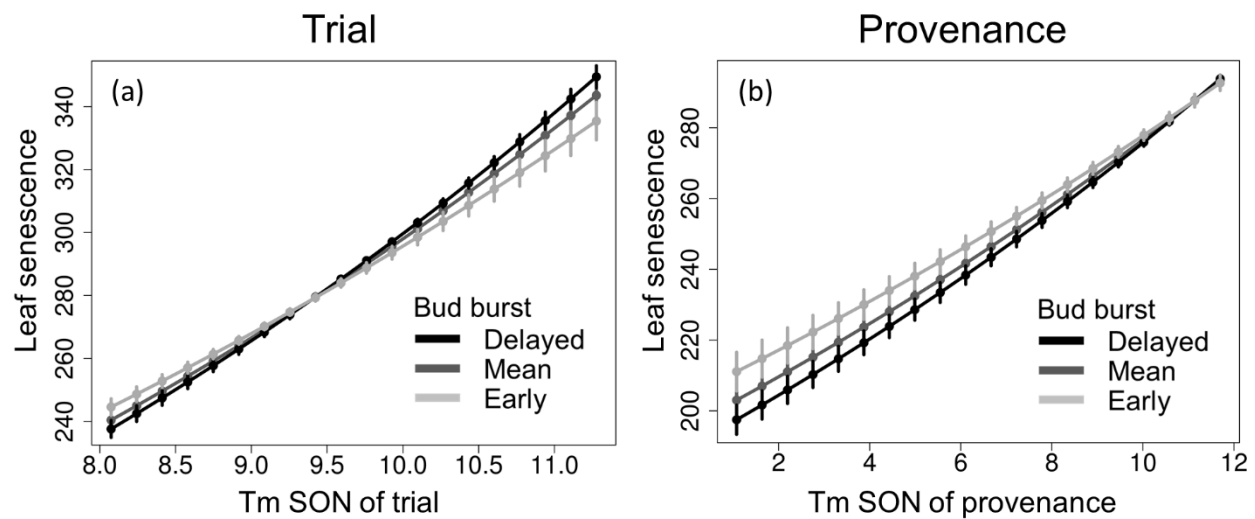
276

277 **Table 1.** Statistics from linear mixed-effects models of leaf senescence. Obs: number of trait  
 278 measurements; Variance: variance explained by the random effects; SD: standard deviation of  
 279 each level of random effects; Estimate: coefficient of the regression, shown on a logarithmic  
 280 scale; SE: standard error of each fixed variable; *t*: Wald statistical test that measures the point  
 281 estimate divided by the estimate of its SE, assuming a Gaussian distribution of observations  
 282 conditional on fixed and random effects. Fixed effects: Coefficients of the fixed effects of the  
 283 model; BB: bud burst; Tm SON\_T: mean temperature of September, October and November of  
 284 the trial; Tm SON\_P: mean temperature of September, October and November of the  
 285 provenance. Coefficients of the interactions: BB x Tm SON\_T and BB x Tm SON\_P. *r*: Pearson  
 286 correlation;  $R^2M$ : percentage of the variance explained by the fixed effects (Marginal variance);  
 287  $R^2C$ : percentage of the variance explained by the random and fixed effects (Conditional  
 288 variance).

289

### 290 3.3 Leaf senescence model

291 LS differed among the provenances and between the two trials. These differences were explained  
292 by the Tm SON of the trial and provenance, as well as BB (Table 1). Interactions between BB  
293 and Tm SON of the trial and provenance were also significant (Table 1). Late BB timing was  
294 related to higher Tm SON of the trial and provenances (Fig. 4). Late LS was related to late BB at  
295 high Tm SON of the trial, whilst at low trial TM SON the opposite effect occurred (Fig. 4a). Late  
296 LS was related to early BB irrespective of Tm SON of the provenance (Fig. 4b). The marginal  $R^2$   
297 was 52%, while the conditional  $R^2$  was 99% (Table 1). The capacity for generalization from the  
298 model was  $r = 0.92$  (Table 1).



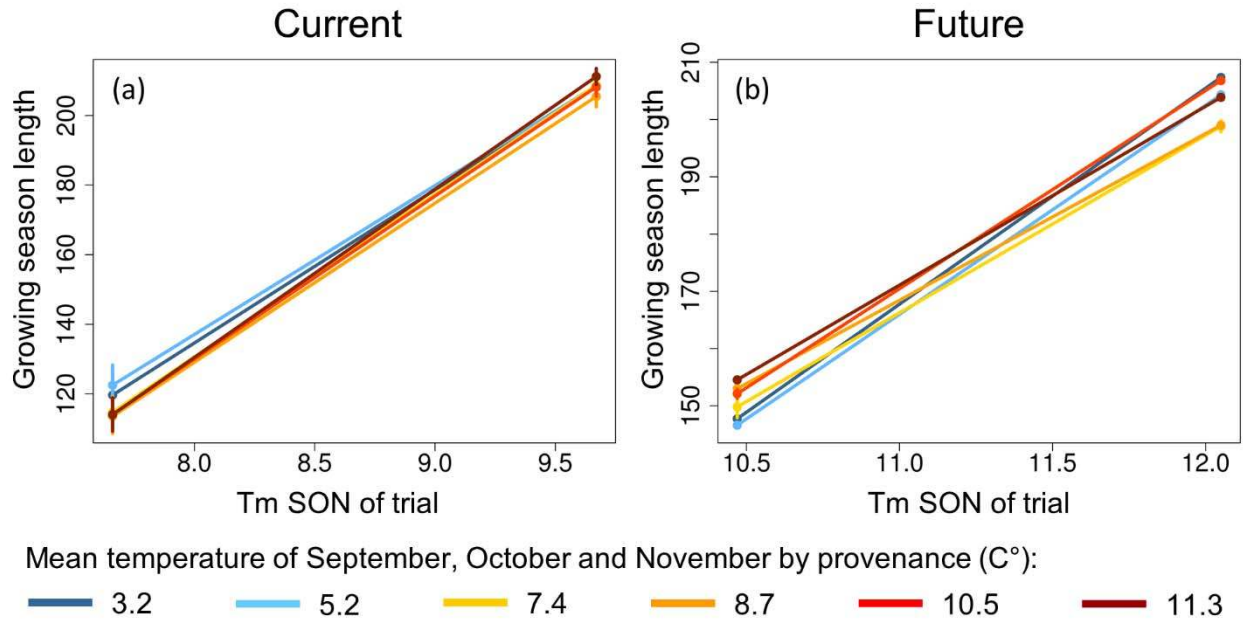
299 **Figure 4.** Interaction between leaf senescence and the mean temperature in September, October  
300 and November (Tm SON) in the (a) trial and for the (b) provenance. Leaf senescence is given in  
301 Julian days, and Tm SON in °C. The black line represents delayed bud burst, the dark gray mean  
302 bud burst dates and the light gray early bud burst. The error bars represent the 95% confidence  
303 intervals.

305

### 306 **3.4 Determinants of growing season length under current and future climates**

307 GSL greatly increased with higher temperatures in September, October and November in the  
308 trials, although the strength of this effect depended on the origin of the provenances (Fig. 5).  
309 Specifically, this increase in GSL was greatest for cold provenances (3.2-5.2 C°), which have  
310 their longest GSL under cold conditions (7.5-8.5 C°) at the trials in the current climate (Fig. 5a).  
311 In this two specific trials, GSL differed more among provenances under future than under current  
312 autumn temperatures (Fig. 5b). The longest GSL under future conditions was predicted at high  
313 trial temperatures (11.5-12 C°) for the warm (10.5-11.3 C°) and cold (3.2-5.2 C°) provenances,  
314 whilst at low trial temperatures (10.5-11 C°), the longest GSL was predicted for warmer (10.5-  
315 11.3 C°) provenances (Fig. 5b).

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



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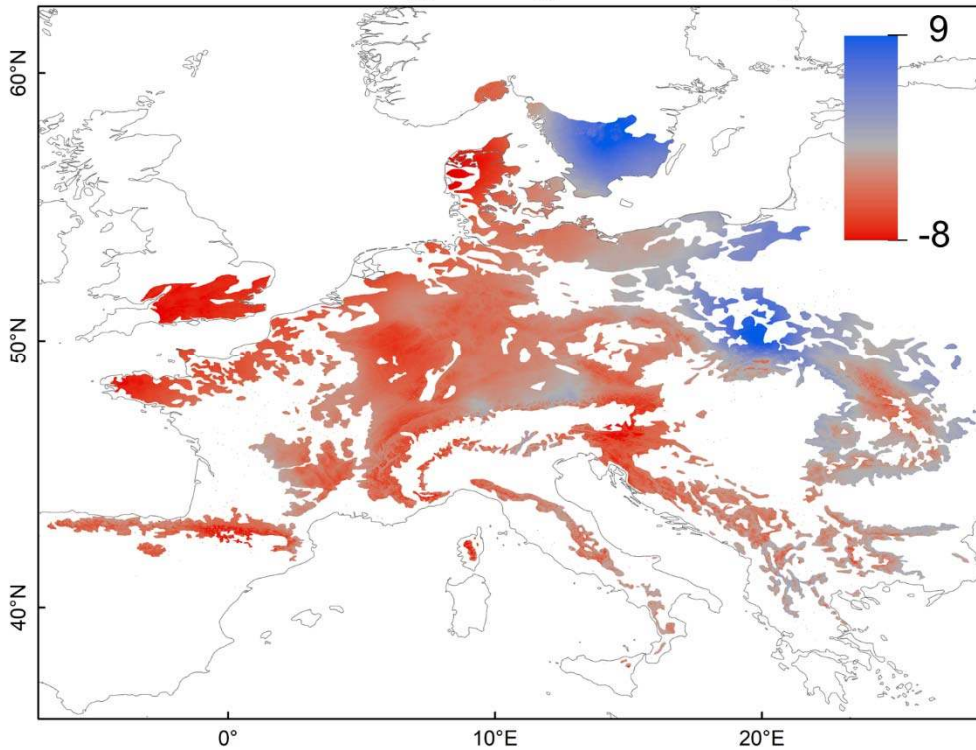
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**Figure 5.** Interaction between growing season length and the mean temperature of September, October and November (Tm SON) of the trial, for (a) current climatic conditions (year of measurement minus year of plantation) and (b) the future climate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

## Differences in growing season length



328

329 **Figure 6.** Spatial projections for growing season length: differences between current and future  
330 climate conditions. Growing season length is the difference between leaf flushing and leaf  
331 senescence spatial predictions (Figure S4). The color gradient depicts the number of days  
332 difference in growing season length between current (average climate calculated from 2000-  
333 2014) and future conditions (2070, RCP 8.5) from strong decrease (red) to strong increase (blue).

334

## 335 **4 Discussion**

### 336 4.1 Provenance differences in bud burst and autumn leaf senescence

337 The origin of beech populations is a major determinant of the timing of their leaf spring and leaf  
338 autumn phenology (Table 1), which confirms their genetic differentiation in the control of

339 phenology (Chmura and Rozkowski 2002; Petkova et al. 2017, Alberto et al. 2013). This  
340 differentiation is often stronger for spring phenology than for autumn phenology (Vitasse et al.  
341 2009; Weih 2009; Firmat et al. 2017; Petkova et al. 2017), which is in agreement with what we  
342 found in our beech provenances (Fig. 3a & b). The duration of autumn leaf senescence is longer  
343 than that of leaf flushing in beech (Fig. 3, Table S2, S3) (Gömöry and Paule 2011; Petkova et al.  
344 2017), whereas other temperate broadleaf species such as *Salix spp.* and *Quercus petraea* have a  
345 relatively long period of leaf-out and relatively abrupt autumn leaf senescence (Weih 2009;  
346 Firmat et al. 2017). Although the dates of spring and autumn leaf phenological stages varied  
347 between the two years of our study, the same response-patterns persisted in both years (Figs. 3  
348 and S1), suggesting a consistent effect of environmental conditions on the trials (Weih 2009;  
349 Friedman et al. 2011; Petkova et al. 2017). Our results also revealed larger differences among  
350 populations for both BB and LS in the Slovakian trial than in the German one (Fig. 3),  
351 confirming that, in addition to genetic effects, the environment plays an important role in the  
352 phenological response of beech (Vitasse et al. 2013; Gárate-Escamilla et al. 2019).

353

#### 354 4.2 Environmental variables defining leaf senescence

355 Overall, our results support the assertions that (1) high autumn temperatures, of the provenance  
356 and at the planting site, delay LS in beech, and (2) early BB tends to be followed by early LS  
357 (Table 1). The delayed LS promoted by warmer temperatures, that we obtained by manipulating  
358 both genetic and site factors using common-garden trials (Fig. 4), is consistent with previous  
359 studies based on *in-situ* LS records (Delpierre et al. 2009; Vitasse et al. 2011), satellite data  
360 (Yang et al. 2015; Liu et al. 2016a) and climate-controlled chambers (Gunderson et al. 2012; Fu  
361 et al. 2018). While the convergence of these studies is reassuring, the extent to which warmer

362 temperatures promote delayed LS still remains elusive (Estiarte and Peñuelas 2015): warmer  
363 temperatures accompanied by moderate drought appear to delay LS until a certain threshold (Xie  
364 et al. 2015); but beyond this drought threshold LS is accelerated (Chen et al. 2015; Estiarte and  
365 Peñuelas 2015). The roles of temperature and drought in LS have several broader implications  
366 because the delay in LS induced by warm temperatures is associated with delayed degradation of  
367 chlorophyll (Fracheboud et al. 2009), maintenance of photosynthetic enzyme activity (Shi et al.  
368 2014), prolonged leaf life span (Liu et al. 2018a), reduced potential for autumn frost damage  
369 (Hartman et al. 2013) and a possible increase of photosynthetic carbon assimilation related to a  
370 longer growing season (Liu et al. 2016b).

371         The finding of our study does not necessarily imply that LS timing in beech only depends  
372 on temperature, because this parameter covaried with daily insolation and precipitation (Fig. S2).  
373 Both explained a lower proportion of the overall variance (higher insolation promoting delayed  
374 LS and higher precipitation promoting earlier LS; see Table S4), yet we cannot exclude the  
375 possibility that they may have affected LS timing to some extent (e.g. in parts of the species  
376 range not well captured by our model). For instance, insolation can have a strong effect on LS at  
377 high latitudes (Liu et al. 2016b) where increasing photosynthetically active radiation with  
378 insolation supports increased photosynthesis (Bonan 2002), allowing a delay in LS as a result of  
379 persistent chlorophyll retention under sustained high irradiances (Kim et al. 2008).

380

#### 381 4.3 The effect of bud burst on leaf senescence

382 The significant carry-over effect of BB on LS timing that we found is consistent with other  
383 recent studies on beech (Fu et al. 2014; Signarbieux et al. 2017; Chen et al. 2018; Zohner and



384 Renner 2019), and other deciduous trees across the northern hemisphere (Keenan and  
385 Richardson 2015; Liu et al. 2016b). However, it can be difficult to disentangle the effects of  
386 temperature on both BB and LS, from their interdependency. In this respect, the significant  
387 interaction-effect of BB and the autumn temperature of the provenances on LS is notable (Table  
388 1; Fig. 4), as it suggests that the relationship between BB and LS is moderated by the  
389 temperature at provenance origin in a provenance-specific manner. The relationship between BB  
390 and LS is complex and various different mechanisms that have been proposed to explain carry-  
391 over effects of BB on LS, according to the particular conditions in each study: (i) leaf structural  
392 and morphological traits constrain leaf life span (Reich et al. 1992) and programmed cell death  
393 (Lam 2004; Lim et al. 2007); (ii) once a plant's carbohydrate storage capacities are saturated,  
394 growth is inhibited ("sink limitation") and LS is promoted (Fatichi et al. 2013; Keenan and  
395 Richardson 2015; Körner 2015; Signarbieux et al. 2017); (iii) LS is itself affected by the  
396 preceding winter/spring temperature (Fu et al. 2014; Signarbieux et al. 2017; Zohner and Renner  
397 2019); (iv) early BB could lead to soil water depletion through increased transpiration and  
398 resulting in drought stress, producing earlier LS (Buermann et al. 2013); (v) earlier BB might  
399 increase pest attack (Jepsen et al. 2011) and increase the probability of spring frost damage  
400 (Hufkens et al. 2012), leading to an earlier LS. Our use of multiple provenances of different  
401 climatic origin enabled us to isolate the genetic component of these carry-over effects of BB on  
402 LS from the temperature response. We only found this pattern among cold provenances (3.2-5.2  
403 C°) (Fig. S3) and in regions with high autumn temperature (11.5-12 C°) (Fig. 4a). Consequently,  
404 of the potential causes of this effect, we can discard effects of the preceding winter/spring  
405 temperature and of frost damage, neither of which affected the timing of LS in our analysis  
406 (results not shown). Yet, we can not rule out the other mechanisms listed above, and more

407 experimental testing is needed to tease apart the relationship between BB and LF across large  
408 environmental gradients.

409

410 4.4 Variation in growing season length based on bud burst, leaf senescence and the environment  
411 under present and future climates

412 Our results, based on two trials located in the core of the distribution range, predict that almost  
413 all the provenances monitored (except number 3 – with an average autumn temperature of 7.4°C)  
414 would extend their GSL by up to 10 days under future climatic conditions with increased autumn  
415 temperatures (11.5-12 C°) (Fig. 5b). However, when we extrapolate our models to the entire  
416 distribution range of the species, only trees in northern and north-eastern regions of the species  
417 range are predicted to increase their GSL by up-to 9 days, while the GSL of trees in the rest of the  
418 range would decrease by up to 8 days (Fig. 6). While several recent studies based on field or  
419 satellite data also predict an increase in GSL (Barnard et al. 2018; Liu et al. 2018b; Gaertner et  
420 al. 2019) at the high latitudes coincident with cold beech provenances, there have been no  
421 recorded increases in the GSL for southern populations of four temperate European species  
422 (*Quercus robur*, *Fagus sylvatica*, *Betula pendula* and *Aesculus hippocastanum*) over the last two  
423 decades (Chen et al. 2018). These two trends are both reflected in our spatial projection of GSL  
424 (Fig. 6). The predicted larger differences in GSL in the central and southern range are mostly due  
425 to a later leaf senescence predicted for these regions (Fig. S4), which is likely due to an expected  
426 increase in autumn temperatures in these regions. We should however note that our spatial  
427 modelling results, despite covering a wide climatic range, should be interpreted with caution  
428 since they are based on empirical data from only two trials, which can limit their scope.

429

## 430 **5 Conclusions**

431 European beech is characterised by extensive plasticity in many of its life history traits (Gárate-  
432 Escamilla et al. 2019) compared to other tree species (Benito Garzón et al. 2019). Yet strong  
433 genetic control over beech phenology, particularly in spring (Kramer et al. 2017), can constrain  
434 the acclimative response of populations to climatic changes and hence potentially compromise  
435 their future performance. Our analyses provide important insights into the complex relationships  
436 driving spring and autumn phenology across the species range. We found large differences in  
437 GSL (as inferred from BB and LS) under present climate conditions that are however likely to  
438 decrease in the future, because GSLs of southern and core populations (i.e. those with a  
439 relatively long current GSL) are predicted to decrease, whilst those of northern and north-eastern  
440 populations (i.e. those with a relatively short current GSL) are predicted to increase. These trends  
441 are largely driven by an increase in temperatures that would modify phenology. Taken  
442 altogether, our results suggest that northern populations would increase productivity in the  
443 coming years, extending their growing season to take advantage of warmer conditions in the  
444 northern part of the range.

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452

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