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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**

4 Homero Gárate-Escamilla¹, Craig C. Brelsford², Arndt Hampe¹, T. Matthew Robson² & Marta
5 Benito Garzón^{1*}.

6 ¹BIOGECO INRA UMR 1202 University of Bordeaux, Pessac, 33400, France

7 ²Organismal and Evolutionary Biology (OEB), Viikki Plant Science Centre (ViPS), Faculty of
8 Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, Finland 00014.

9 *Corresponding author: marta.benito-garzon@inrae.fr

10 BIOGECO UMR 1202, INRAE - Université de Bordeaux, Bat B2

11 Allée Geoffroy-St-Hilaire, CS50023

12 33615 Pessac Cedex

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

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

GSL					
Reference	EV	BB _R	LS _R	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_R: bud burst
87 response; LS_R: 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 BB_R and
91 LS_R: left arrow: early bud burst/leaf senescence; right arrow: delayed bud burst/leaf senescence;
92 Green colour and green leaf: Reference, EV related to bud burst and BB_R; Orange colour and
93 orange leaf: Reference, EV related to leaf senescence and LS_R. All the combinations of bud burst
94 and leaf senescence responses defining the growing season length are possible.

95 *Fagus sylvatica* L. (European beech, henceforth “beech”) is one of the most dominant
96 and widespread broadleaf forest trees in Europe (Preston and Hill 1997), and it is of high
97 ecological and economic importance (Packham *et al.* 2012). In beech, BB responds to a
98 combination of chilling and forcing temperature requirements (Heide 1993; Falusi and Calamassi

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

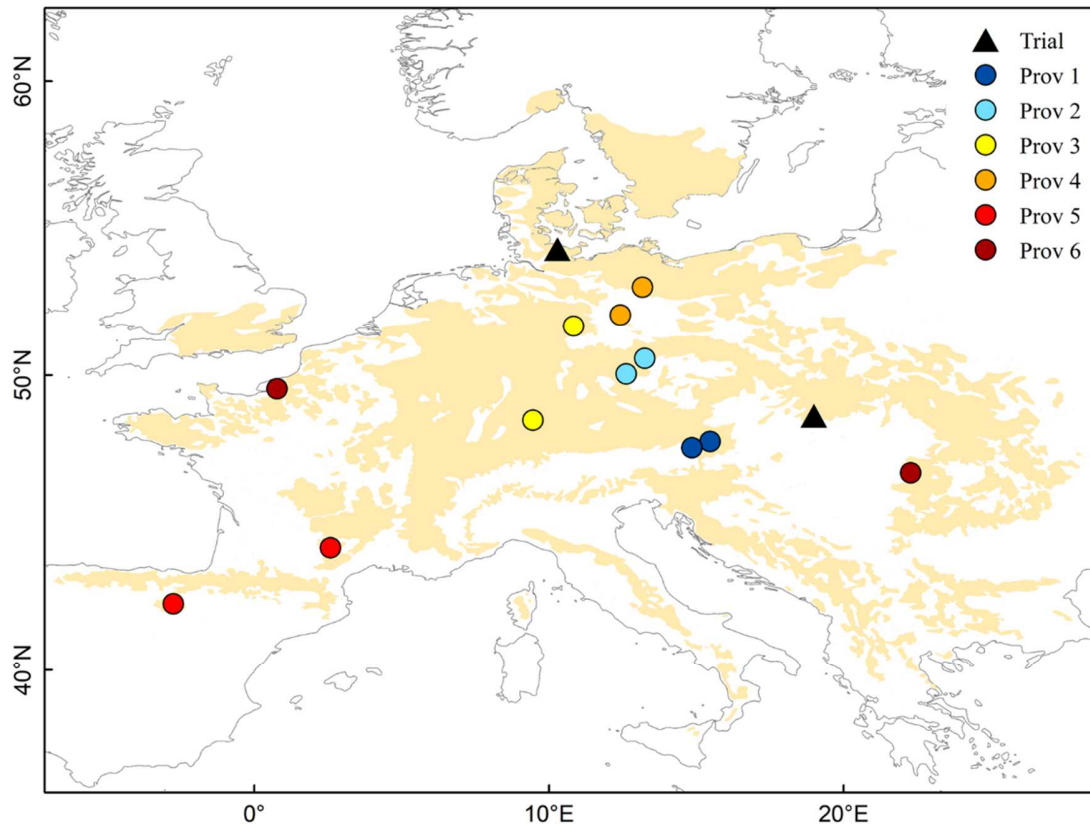
111 Here, we investigate BB and LS in six different beech provenances (905 trees) planted in
112 two common gardens in central Europe (Robson et al. 2018), and use this information to infer
113 how range-wide patterns of beech GSL might evolve under future climate warming. Specifically,
114 we attempt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

117

118 **2 Materials and Methods**

119 **2.1 Field trials and provenances**

120 Spring and autumn leaf phenological observations came from two common-gardens (i.e.
121 provenance tests, genetic trials; hereafter “trials”) located in Schädtebek (54.30°N, 10.28°E),
122 Germany, and Tále, Mláčik, Slovakia (48.62°N, 18.98°E) (henceforth termed “Germany” and
123 “Slovakia” trials, respectively). These two tests belong to a large network of beech common-
124 gardens planted to understand the population (i.e. provenance effect including genetics) effects
125 of climate change on fitness-related traits across the distribution range (details given in Robson
126 et al. 2018). These trials were planted with seeds collected from 38 provenances (32 provenances
127 in Slovakia and six provenances in Germany) that roughly span the entire environmental range of
128 beech (Fig. 2, Map). Seeds were germinated in the greenhouse and planted in the trials when two
129 years old, in 1995 (Germany) and 1998 (Slovakia). To maintain a balanced design (same number
130 of provenances per trial), we used only six provenances from each of the two trials (Fig. 2, Map
131 & Table). The six provenances from the Slovakian trial were chosen based on their similar
132 climatic origin to those planted in the German trial (Pearson correlation $r \geq 0.98$). The
133 provenances were ranked from colder (1) to warmer (6) origins (Fig. 2, Map & Table). Trees
134 growing in Germany were measured at an age of 12 and 13 years, those in Slovakia at 11 and 12
135 years (Fig. 2, Table).



Provenance Information

T	P	Lon	Lat	Elev	N	NT	Age	BIO 14	Ppct 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	

137

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

154

155 **2.2 Estimation of bud burst, leaf senescence and growing season length**

156 We transformed the observational stages (phenophases), and score data (qualitative
157 measurements) for BB and LS to Julian days by fitting the phenophases (Fig. 3 and S1; Table S1
158 and S2) for each tree in every trial using the Weibull function (Robson et al. 2011; Gárate-

159 Escamilla et al. 2019). The Weibull function is non-linear and asymptotic in the upper and lower
160 limits, hence it requires at least two censuses to obtain a fit of the data: the day of the year
161 (DOY) when BB is attained in spring (stage 2.5; Fig.3 and S1; Robson et al. 2013) and at the
162 stage at which 50% of the trees' leaves have changed colour from green to yellow (stage 3; Fig.
163 3 and S1; (Lang et al. 2019)). We calculated GSL for each tree as the number of days between
164 the estimated dates of BB and LS (Estiarte and Peñuelas 2015).

165

166 **2.3 Environmental data**

167 To separate the effects of the provenance (genetic effects) from those of the trial (environmental
168 effects), we used the average climate from 1901 to 1990 for each provenance and the average
169 climate during the years of measurement for the trials (Leites et al. 2012) in our models. We used
170 the following precipitation- and temperature-related variables from EuMedClim (Fréjaville and
171 Benito Garzón 2018): precipitation in the driest month (BIO14, mm), precipitation (P, mm) in
172 June, July and August (JJA), minimal (Min) monthly water balance (PPET, mm), and mean
173 temperature (Tm, °C) in June, July and August (JJA) and September, October and November
174 (SON). In addition, we used latitude as a proxy of photoperiod as well as daily insolation, a
175 function of day length and solar irradiance (Yeang 2007). We downloaded daily insolation data
176 from the NASA Atmospheric Science Data Center ([https://power.larc.nasa.gov/data-access-
177 viewer/](https://power.larc.nasa.gov/data-access-viewer/)), and we calculated solar radiation (direct and diffuse) over the wavelength range 400-
178 2700 nm incoming on a horizontal surface for a given location. We used insolation including
179 NIR and SWIR, as well as PAR, because the mode of action is still unknown, so a direct heating
180 effect from NIR and SWIR may be important. We calculated the mean daily insolation (DIM,
181 kWh m⁻² d⁻¹) between the months of June, July and August (JJA) and September, October and

182 November (SON), respectively. As with the climatic variables, we characterized the DIM of the
183 trial as the average between the planting year and the year of measurement. Because the
184 insolation data series from the NASA Atmospheric Science Data Center begins in July 1983, we
185 characterized the DIM of the population as the average between 1984 and 1990 for JJA, and
186 between 1983 and 1990 for SON.

187 We used the 2070 Representative Concentration Pathway (RCP) 8.5 GISS-E2-R
188 (http://www.worldclim.org/cmip5_30s) scenario for GSL predictions under future climate. We
189 deliberately chose only this pessimistic scenario because, for long-lived organisms such as forest
190 trees, it makes little difference whether the projected situation will be reached in 2070 or some
191 decades later.

192

193 **2.4 Statistical analysis**

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

202

203 **2.4.1 Environmental variable selection**

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

207

208 2.4.2 Linear mixed-effects model of leaf senescence

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

$$\begin{aligned} 215 \quad \log(LS_{ijk}) = & \alpha_0 + \alpha_1(EP_{ij}) + \alpha_2(ET_{ik}) + \alpha_3(BB_{ik}) + \alpha_4(EP_{ij} \times ET_{ik}) + \alpha_5(EP_{ij} \times BB_{ik}) \\ 216 \quad & + \alpha_6(ET_{ik} \times BB_{ik}) + \beta + \varepsilon \end{aligned}$$

217 (Equation 1)

218 Where LS = leaf senescence of the i^{th} individual of the j^{th} provenance in the k^{th} trial; EP =
219 environmental variable that characterizes the provenance site of the i^{th} individual of the j^{th}
220 provenance; ET = environmental variable that characterizes the trial site of the i^{th} individual in
221 the k^{th} trial; BB = bud burst of the i^{th} individual in the k^{th} trial; β = random effects and ε =
222 residuals. In addition, the model included the following interaction terms: EP \times ET, EP \times BB,
223 and ET \times BB. EP \times ET interactions represent differences in LS values that can be attributed to
224 the interactions between genetic (provenance) and environmental (site) effects. EP \times BB and ET

225 × BB interactions represent the effects of the provenance on LS related to BB and the effects of
226 the site related to BB.

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

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

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

250

251 2.4.3 Interactions of leaf senescence with bud burst and environmental variables

252 For the best supported LS model, we analysed the significant interactions (EP × ET, EP × BB,
253 and ET × BB in Equation 1) between LS and the environment (ET; represented by the
254 environmental variable from the trial selected by the best supported LS model) and according to
255 provenances showing early, mean and late BB. We also inspected gradients of GSL for the six
256 provenances by plotting GSL against the environmental variable of the trial selected in the model
257 (ET) and provenance under current conditions. We predicted the date of LS for the future climate
258 scenario RCP 8.5 using our LS model and the date of BB for the same provenances achieved
259 using our BB model (Gárate-Escamilla et al. 2019), and plotted the predicted future GSL against
260 ET for each of the provenances.

261

262 2.4.4 Spatial predictions

263 Spatial projections of LS were calculated using our LS model for current and future climatic
264 conditions and predictions of BB were taken from Gárate Escamilla et al. (2019). Predictions of
265 GSL were calculated by subtracting the predicted BB from LS for both current and future
266 climatic conditions across the species range. For the current and future predictions, the climate
267 for provenances was represented by the average of the period from 1900 to 1990. The climate for
268 the trials was represented by the average of the period from 2000 to 2014 for current predictions,
269 and by the mean value for the year 2070 (RCP 8.5) for future predictions.

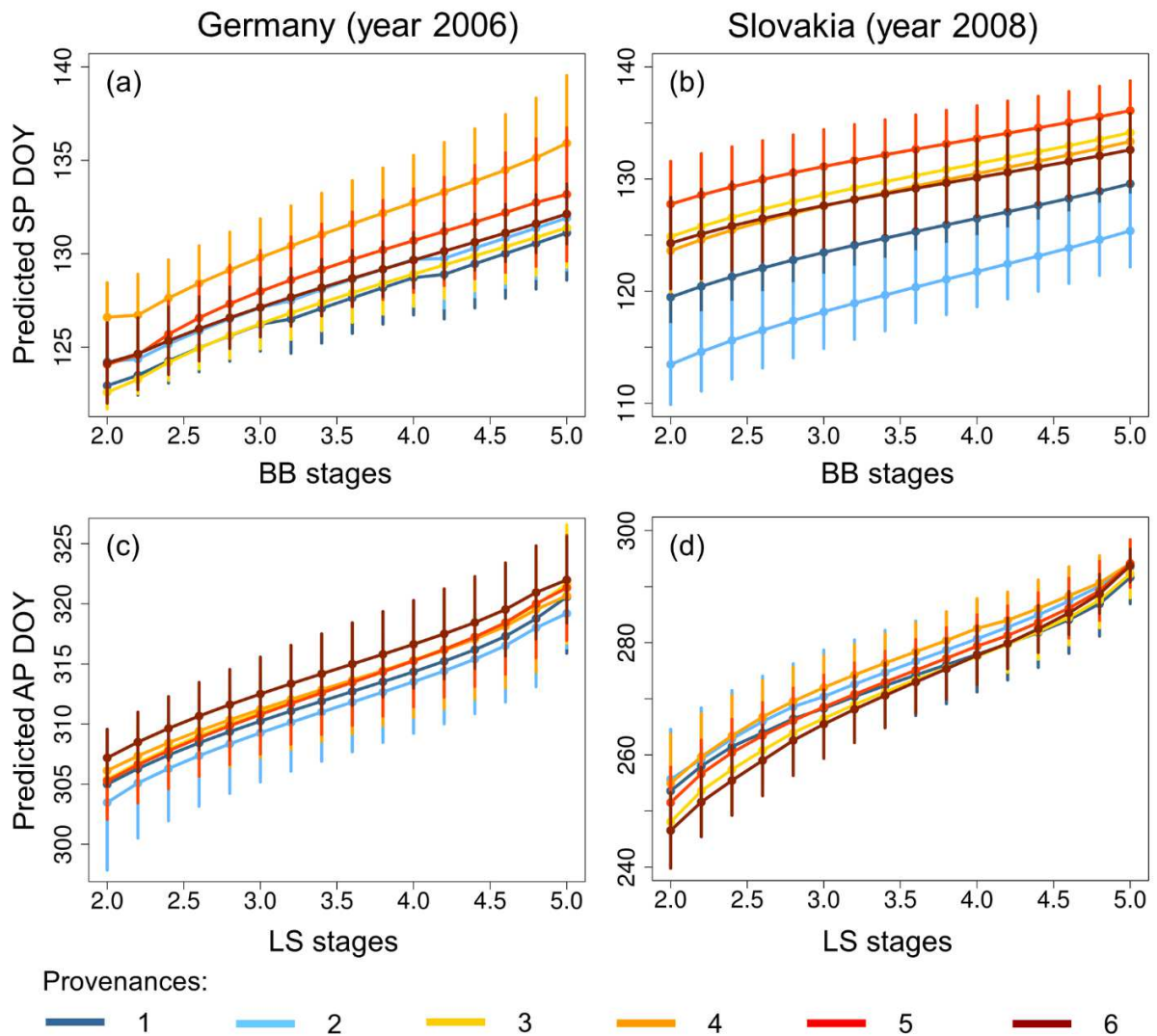
270 The current and future spatial predictions of BB and LS include a non-extrapolated area (i.e.,
271 predictions including exclusively the climatic range of the two trials, 7.5 to 10°C) and an
272 extrapolated area (i.e., predictions outside the climatic range of the trials) delimited within the
273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

275

276 **3 Results**

277 **3.1 Estimation of bud burst and autumn leaf senescence dates from field observations**

278 In both trials, differences among provenances were larger for spring leaf flush stages (including
279 bud burst; Fig. 3a & b and S1a & b) than for autumn leaf senescence stages (including 50%
280 yellow leaves; Fig. 3c & d and S1c & d). Although these differences were always statistically
281 significant, they were larger in the Slovakian trial than in the German one (Fig. 3 and S1, Table
282 S1 and S2). Differences in the predicted DOY of spring leaf flush and autumn leaf senescence
283 stages were found for the two years of measurement in both trials (Fig. 3 and S1). We used the
284 fitted data to extract the DOY for the flushing stage 2.5 (bud burst, BB) and the senescence stage
285 3 (= 50% of 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. |

286

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

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

294

295 **3.2 Variable selection and best model selection**

296 Our inspection of climate variables revealed that: (i) provenance and trial variables were not
297 correlated with each other; (ii) temperature (T_m JJA and T_m SON)- and precipitation (BIO14,
298 P_{pet} Min and Prec JJA)-related variables for the provenances were correlated, whilst daily
299 insolation (DIM JJA and DIM SON) variables for the provenances were only correlated with the
300 latitude (Lat) of the provenances; (iii) all the trial variables were correlated among themselves;
301 and (iv) the co-variable BB was not correlated with the rest of variables (Fig. S2).

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

307 **Table 1.** Statistics from linear mixed-effects models of leaf senescence. Obs: number of trait
308 measurements; Variance: variance explained by the random effects; SD: standard deviation of
309 each level of random effects; Estimate: coefficient of the regression, shown on a logarithmic
310 scale; SE: standard error of each fixed variable; *t*: Wald statistical test that measures the point
311 estimate divided by the estimate of its SE, assuming a Gaussian distribution of observations

312 conditional on fixed and random effects. Fixed effects: coefficients of the fixed effects of the
 313 model; BB: bud burst; Tm SON_T: mean temperature of September, October and November of
 314 the trial; Tm SON_P: mean temperature of September, October and November of the
 315 provenance. Coefficients of the interactions: BB x Tm SON_T and BB x Tm SON_P. *r*: Pearson
 316 correlation; R^2M : percentage of the variance explained by the fixed effects (Marginal variance);
 317 R^2C : percentage of the variance explained by the random and fixed effects (Conditional
 318 variance).

319

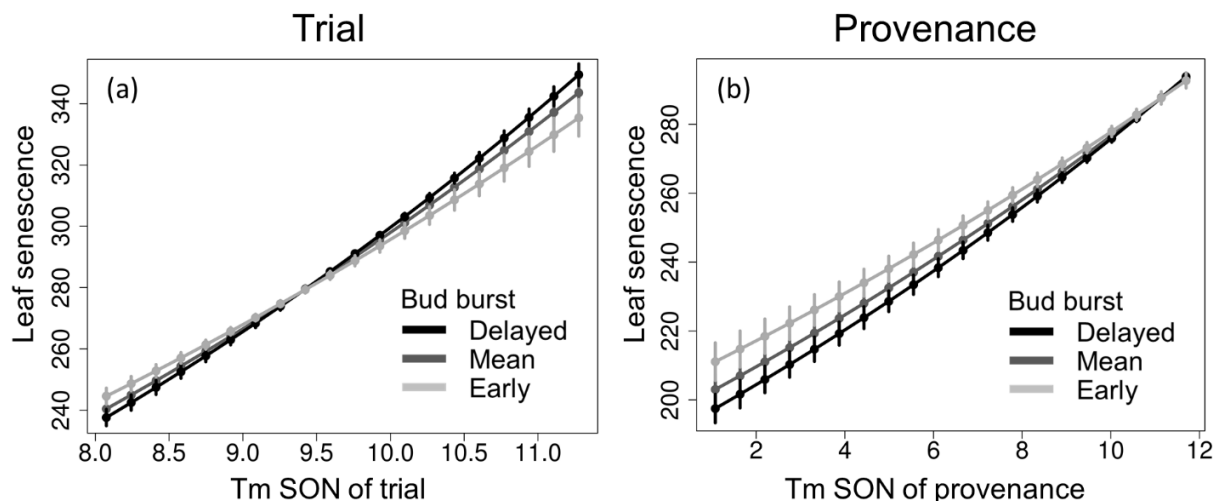
Leaf senescence			
Model	Linear Mixed Effect		
	Random Effects		
	Obs	Variance	SD
Population	12	3.33E-05	5.77E-03
Trial	2	2.39E-02	1.55E-01
Trial:Block	6	9.73E-06	3.10E-03
Tree	925	1.88E-04	1.37E-02
Residuals		2.34E-04	1.53E-02
	Fixed Effects		
	Estimate	SE	<i>t</i>
Intercept	5.62E+00	1.10E-01	51.16
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

320

321

322 3.3 Leaf senescence model

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



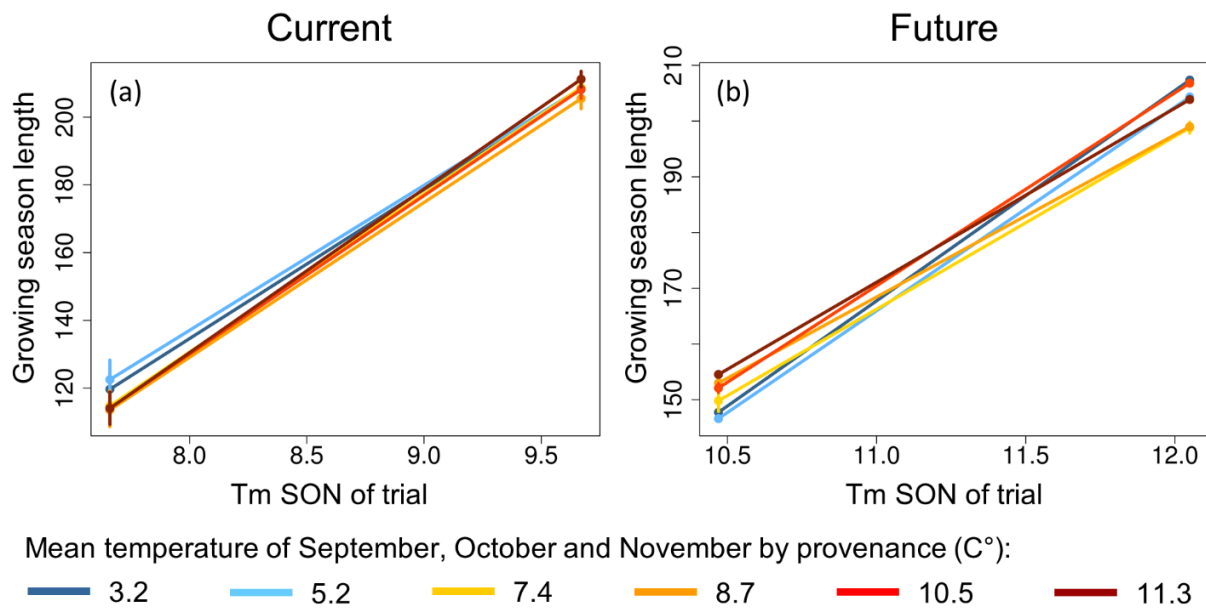
331
 332 **Figure 4.** The interactive relationship between leaf senescence and the mean temperature in
 333 September, October and November (Tm SON) for (a) the trial and (b) for the provenance. The
 334 relationship was estimated from the LS linear mixed-effects model (equation 1), where BB was
 335 included as a co-variable. Leaf senescence is given in Julian days, and Tm SON in °C. The black
 336 line represents delayed bud burst, the dark-grey mean bud-burst and the light-grey early bud-
 337 burst. The error bars represent the 95% confidence intervals.

338

339 **3.4 Determinants of growing season length under current and future climates**

340 GSL greatly increased with higher temperatures in September, October and November in the
341 trials, although the strength of this effect depended on the origin of the provenances (Fig. 5). The
342 increase in GSL was greatest for cold provenances (3.2-5.2 C°), which had their longest GSL
343 under cold conditions (7.5-8.5 C°) at the trials in the current climate (Fig. 5a). In our two trials,
344 GSL differed more among provenances under future than under current autumn temperatures
345 (Fig. 5b). The longest GSL under future conditions was predicted at high trial temperatures
346 (11.5-12 C°) for the warm (10.5-11.3 C°) and cold (3.2-5.2 C°) provenances, whilst at low trial
347 temperatures (10.5-11 C°), the longest GSL was predicted for warmer (10.5-11.3 C°) populations
348 (Fig. 5b).

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

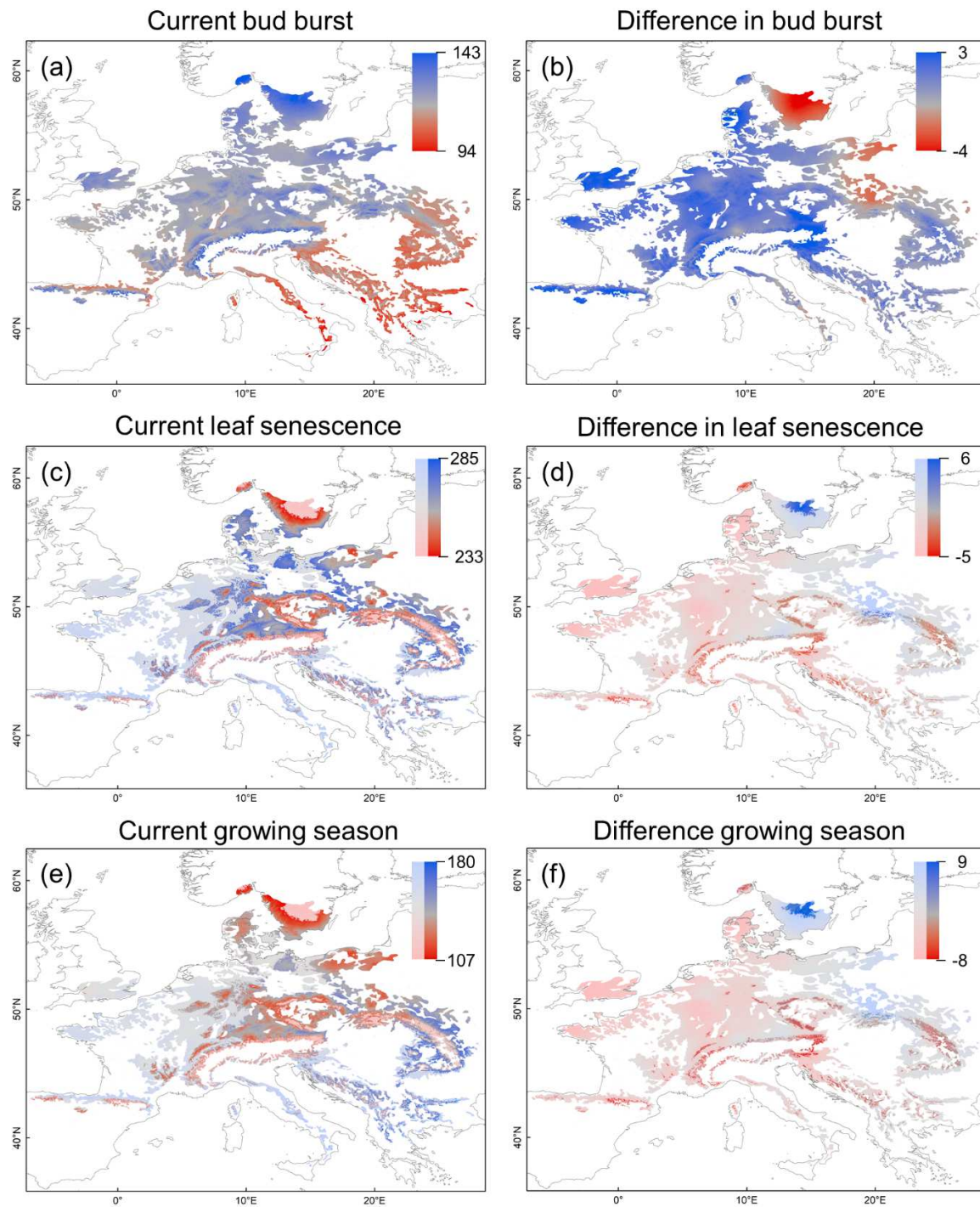


353

354 **Figure 5.** Interactive relationship between growing season length and the mean temperature of
 355 September, October and November (Tm SON) of the trial, for (a) current climatic conditions
 356 (year of measurement minus year of plantation) and (b) the future climate scenario (RCP 8.5 for
 357 2070). The colour gradient depicts the clinal variation from cold (blue) to warm (red)
 358 provenances (Tm SON). Growing season length is represented in days. The error bars represent
 359 the 95% confidence intervals.

360

361



362

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

366 season length under current climatic conditions and (e) growing-season-length differences
367 between current and future conditions. The growing-season length represents the difference
368 between leaf flushing and leaf senescence. The colour gradient depicts the clinal variation from
369 low (red) to high (blue) values of bud burst, leaf senescence and growing-season length.
370 Growing-season length is represented in days, and leaf senescence and bud burst in Julian days.
371 Solid colours represent the predicted geographic area without extrapolation from the climatic
372 area covered by the trials ($T_{mSON} = 7.5$ to 10°C), the soft colours represent the extrapolated
373 area (that is, outside the range of the calibration) predicted by the models. Current climate refers
374 to the average climate calculated from 2000-2014, and difference in bud burst/leaf
375 senescence/growing season represents the differences between the model predictions for future
376 (2070, RCP 8.5) and contemporary climate conditions for bud burst/leaf senescence/growing
377 season.

378

379 **4 Discussion**

380 4.1 Provenance differences in bud burst and autumn leaf senescence

381 The origin of beech provenances is a major determinant of the timing of their leaf spring and
382 autumn phenology (Table 1), which confirms their genetic differentiation in the control of
383 phenology (Chmura and Rozkowski 2002; Petkova et al. 2017, Alberto et al. 2013). This
384 differentiation is often stronger for spring phenology than for autumn phenology (Vitasse et al.
385 2009; Weih 2009; Firmat et al. 2017; Petkova et al. 2017), which is in agreement with what we
386 found in our provenances. For instance, in the Slovakian trial the difference in the date of
387 budburst between colder and warmer provenances was more than 20 days (Fig. 3 and S1). The

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

399

400 4.2 Environmental variables defining leaf senescence

401 Overall, our results support the assertions that (1) high autumn temperatures, both at the site of
402 population origin and at the planting site, delay LS in beech, and (2) early BB tends to be
403 followed by early LS (Table 1). The delayed LS promoted by warmer temperatures that we
404 obtained by manipulating both genetic and site factors using common-garden trials (Fig. 4), is
405 consistent with previous studies based on *in-situ* LS records (Delpierre et al. 2009; Vitasse et al.
406 2011), satellite data (Yang et al. 2015; Liu et al. 2016a) and climate-controlled chambers
407 (Gunderson et al. 2012; Fu et al. 2018). While the convergence of these studies is reassuring, the
408 extent to which warmer temperatures promote delayed LS still remains elusive (Estiarte and
409 Peñuelas 2015): warmer temperatures accompanied by moderate drought appear to delay LS
410 until a certain threshold (Xie et al. 2015); but beyond this drought threshold LS is accelerated

411 (Chen et al. 2015; Estiarte and Peñuelas 2015). The roles of temperature and drought in LS have
412 several broader implications because the delay in LS induced by warm temperatures is associated
413 with: delayed degradation of chlorophyll (Fracheboud et al. 2009), maintenance of
414 photosynthetic enzyme activity (Shi et al. 2014), prolonged leaf life span (Liu et al. 2018a), an
415 increased risk of early-autumn frost damage that might kill leaves before nutrient reabsorption is
416 complete (Estiarte and Peñuelas 2015), (Hartman et al. 2013) and a possible increase in
417 photosynthetic carbon assimilation related to a longer growing season (Liu et al. 2016b).

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

431

432 4.3 The effect of bud burst on leaf senescence

433 The significant interaction effect of BB and the autumn temperature of the provenances on LS is
434 notable (Table 1), as it suggests that the relationship between BB and LS is moderated by the
435 temperature at the site of provenance origin in a population-specific manner. Contrarily to the
436 carry-over effect that we found between delayed LS and late BB when the autumn temperature
437 of the trial was warm (Fig. 4a), there was an interaction effect between delayed LS and early BB
438 only when the autumn temperatures of the populations were low (Fig. 4b), suggesting that early
439 BB is correlated with delayed senescence only when provenances have cold origins (e.g. from
440 the northern range).

441 The significant carry-over effect of BB on LS timing that we found when considering the climate
442 of the trial (Table 1; Fig. 4a) is consistent with other recent studies on beech (Fu et al. 2014;
443 Signarbieux et al. 2017; Chen et al. 2018; Zohner and Renner 2019) and other deciduous trees
444 across the Northern Hemisphere (Keenan and Richardson 2015; Liu et al. 2016b). The
445 relationship between BB and LS is complex and various different mechanisms have been
446 proposed to explain carry-over effects of BB on LS, according to the particular conditions in
447 each study: (i) leaf structural and morphological traits constrain leaf life span (Reich et al. 1992)
448 and programmed cell death (Lam 2004; Lim et al. 2007); (ii) once a plant's carbohydrate storage
449 capacities are saturated, growth is inhibited ("sink limitation") and LS is promoted (Fatichi et al.
450 2013; Keenan and Richardson 2015; Körner 2015; Signarbieux et al. 2017); (iii) LS is itself
451 affected by the preceding winter/spring temperature (Fu et al. 2014; Signarbieux et al. 2017;
452 Zohner and Renner 2019); (iv) early BB could lead to soil water depletion through increased
453 transpiration, resulting in drought stress and producing earlier LS (Buermann et al. 2013); (v)
454 early BB might increase pest attack (Jepsen et al. 2011) and increase the probability of spring
455 frost damage (Hufkens et al. 2012), leading to an earlier LS. Our use of multiple provenances of

456 different climatic origin enabled us to isolate the genetic component of these carry-over effects
457 of BB on LS from the temperature response. We only found this pattern among cold provenances
458 (3.2-5.2 C°) (Fig. S3) and in regions with high autumn temperature (11.5-12 C°) (Fig. 4a). Yet,
459 we can not rule out the mechanisms listed above, and more experimental testing is needed to
460 further elucidate the relationship between BB and LF across large environmental gradients.

461

462 4.4 Variation in growing season length based on bud burst, leaf senescence and the environment 463 under present and future climates

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

479 *pendula* and *Aesculus hippocastanum*) over the last two decades. These two trends are both
480 consistent with our spatial projection of GSL (Fig. 6). The predicted larger differences in GSL in
481 the central and southern range are mostly the result of later leaf senescence predicted for these
482 regions (Fig. 6), which is likely due to an expected increase in autumn temperatures in these
483 regions. We should however note that our spatial modelling results, although covering a wide
484 climatic range, should be interpreted with caution since they are based on empirical data from
485 only two trials, which can limit their scope.

486

487 **5 Conclusions**

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

502 coming years, extending their growing season to take advantage of warmer conditions in the
503 northern part of the range.

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510 We have no conflicts of interest to declare.

511

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