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

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

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

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

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

BIOGECO UMR 1202, INRAE - Université de Bordeaux, Bat B2
Allée Geoffroy-St-Hilaire, CS50023
33615 Pessac Cedex

Abstract

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

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

1 Introduction

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

Extensive research has identified cold winter temperatures (i.e., chilling requirements) 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.






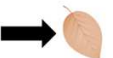






		GSL			
Reference	EV	BB _R	LS _R	EV	Reference
(Gárate-Escamilla <i>et al.</i> , 2019; Ibáñez <i>et al.</i> , 2010; Signarbieux <i>et al.</i> , 2017; Yang <i>et al.</i> , 2017)	↑ Twin/spr			↑ Tsum/aut	(Ibáñez <i>et al.</i> , 2010; Yang <i>et al.</i> , 2017; Fu <i>et al.</i> , 2018)
	↓ Twin/spr			↓ Tsum/aut	
(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)

Figure 1. Environmental drivers of growing season length through their effects on bud burst and leaf senescence. GSL: growing season length; EV: environmental variables; BB_R: bud burst response; LS_R: leaf senescence response; Twin/spr: winter and spring temperatures; Tsum/aut: summer and autumn temperatures; Phot: photoperiod; In: insolation; Chill: chilling requirements; Psum: summer precipitation; Drou: drought; Columns EV: up arrow: increase in the environmental variable; down arrow: decrease in the environmental variable; Columns BB_R and LS_R: left arrow: early bud burst/leaf senescence; right arrow: delayed bud burst/leaf senescence; Green colour and green leaf: Reference, EV related to bud burst and BB_R; Orange colour and orange leaf: Reference, EV related to leaf senescence and LS_R. All the combinations of bud burst and leaf senescence responses defining the growing season length are possible.

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

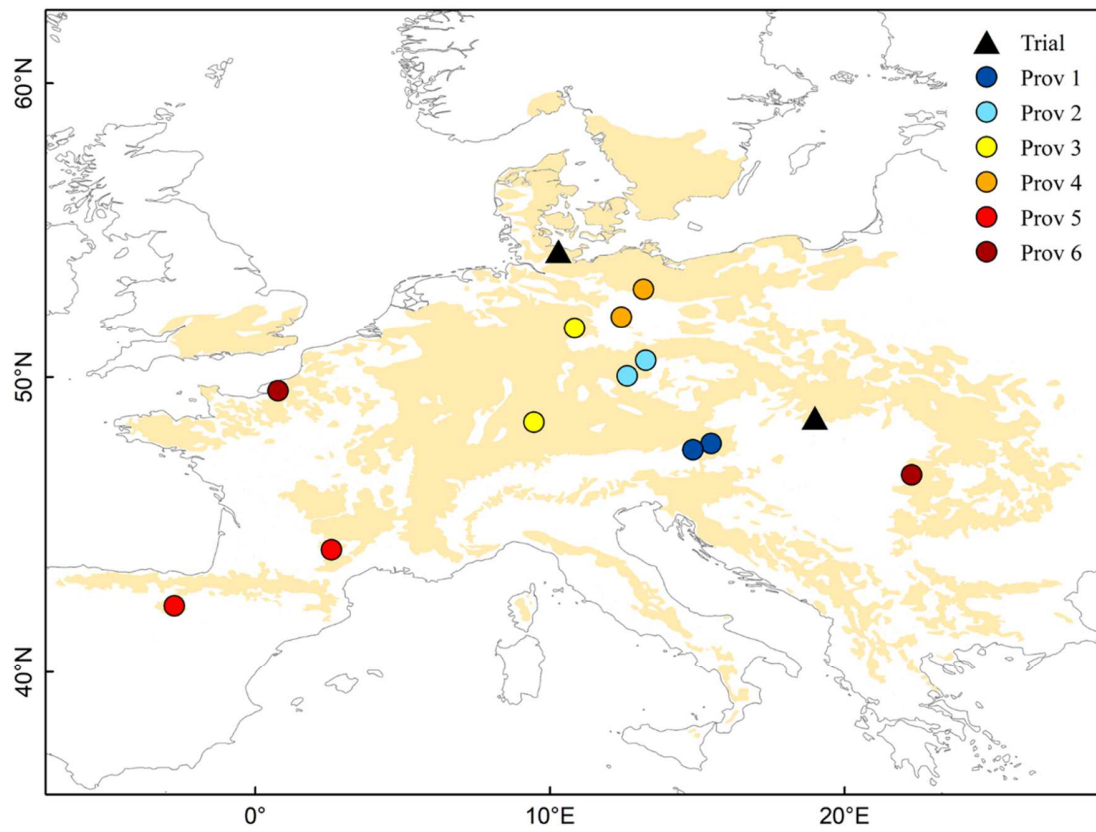
2012; Kramer et al. 2017) as well as to photoperiod (Heide 1993; Caffarra and Donnelly 2011; Basler and Körner 2012), with the strength of these drivers changing along environmental gradients. For instance, BB is more affected by photoperiod in colder climates, and by chilling requirements in warmer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

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

2 Materials and Methods

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	Ppet Min	P JJA	Tm JJA	Tm SON	DIM JJA	DIM SON	r
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-

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

2.3 Environmental data

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

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

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

2.4 Statistical analysis

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

2.4.1 Environmental variable selection

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

2.4.2 Linear mixed-effects model of leaf senescence

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

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

(Equation 1)

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

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

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

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

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

2.4.3 Interactions of leaf senescence with bud burst and environmental variables

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

2.4.4 Spatial predictions

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

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

3 Results

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

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

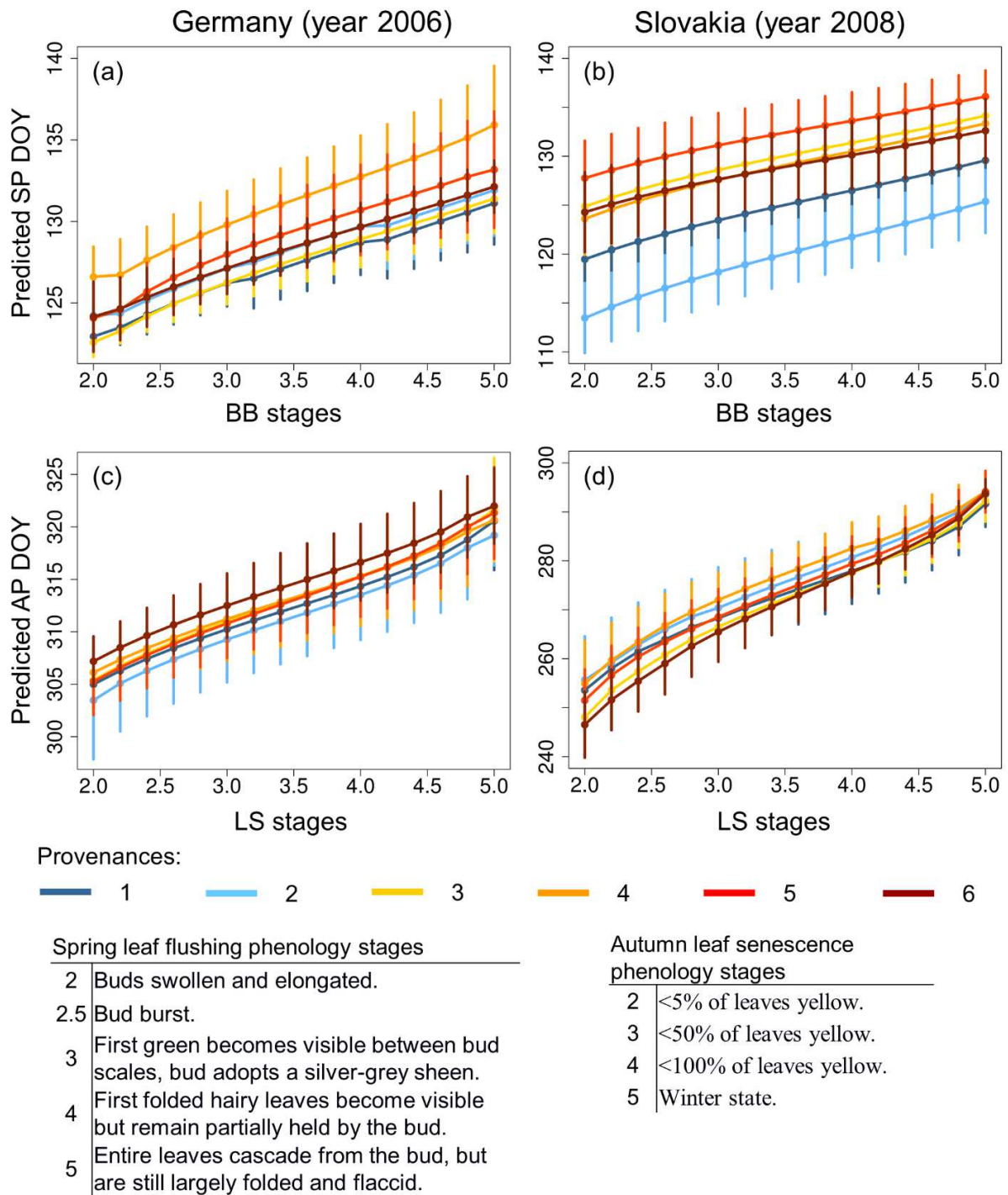


Figure 3. Predicted spring bud burst and autumn leaf senescence phenology, days of the year (DOY) against the observational stages recorded in the field for the two trials. SP: spring bud burst phenology; AP: autumn leaf senescence phenology. Provenance colours range from dark

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

3.2 Variable selection and best model selection

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

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

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

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

Model	Leaf senescence		
	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

3.3 Leaf senescence model

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

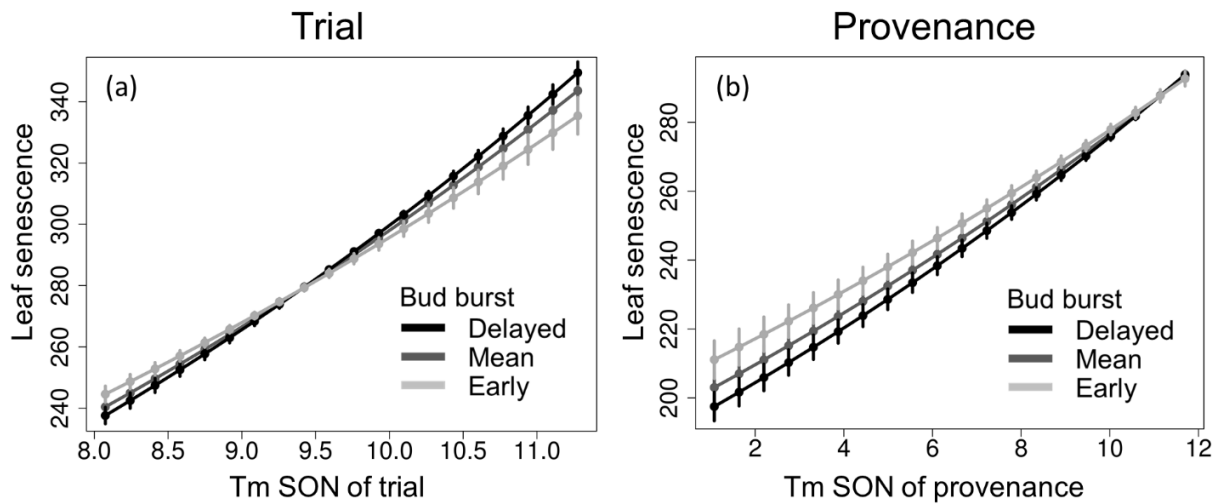


Figure 4. The interactive relationship between leaf senescence and the mean temperature in September, October and November (Tm SON) for (a) the trial and (b) for the provenance. The relationship was estimated from the LS linear mixed-effects model (equation 1), where BB was included as a co-variable.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

3.4 Determinants of growing season length under current and future climates

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

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

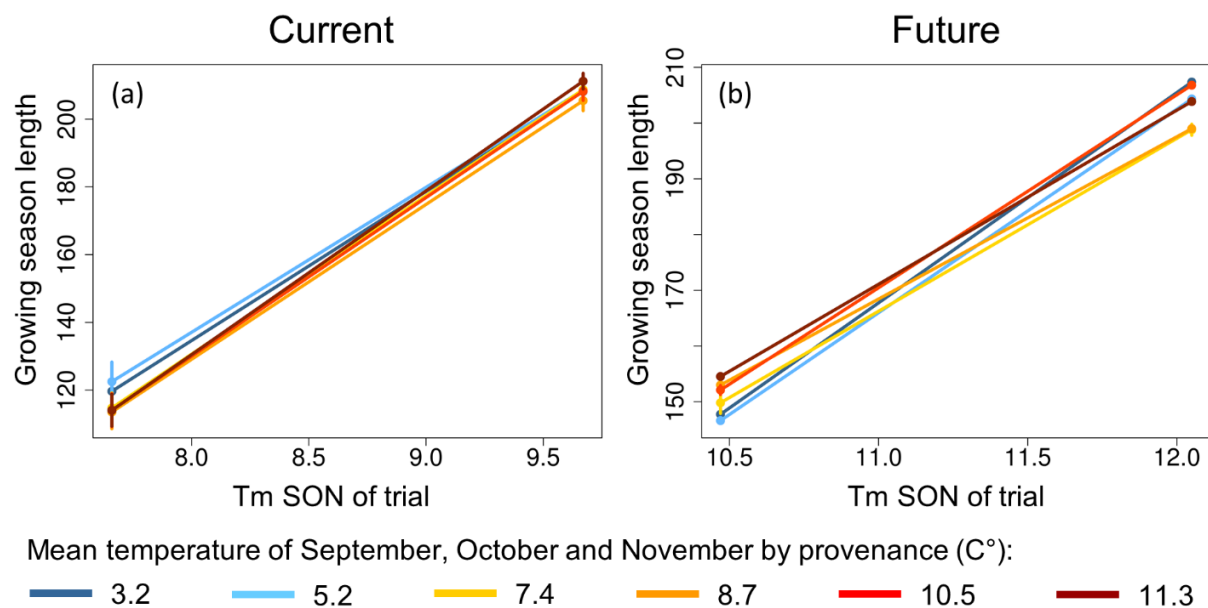


Figure 5. Interactive relationship between growing season length and the mean temperature of September, October and November (Tm SON) of the trial, for (a) current climatic conditions (year of measurement minus year of plantation) and (b) the future climate scenario (RCP 8.5 for 2070). The colour gradient 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.

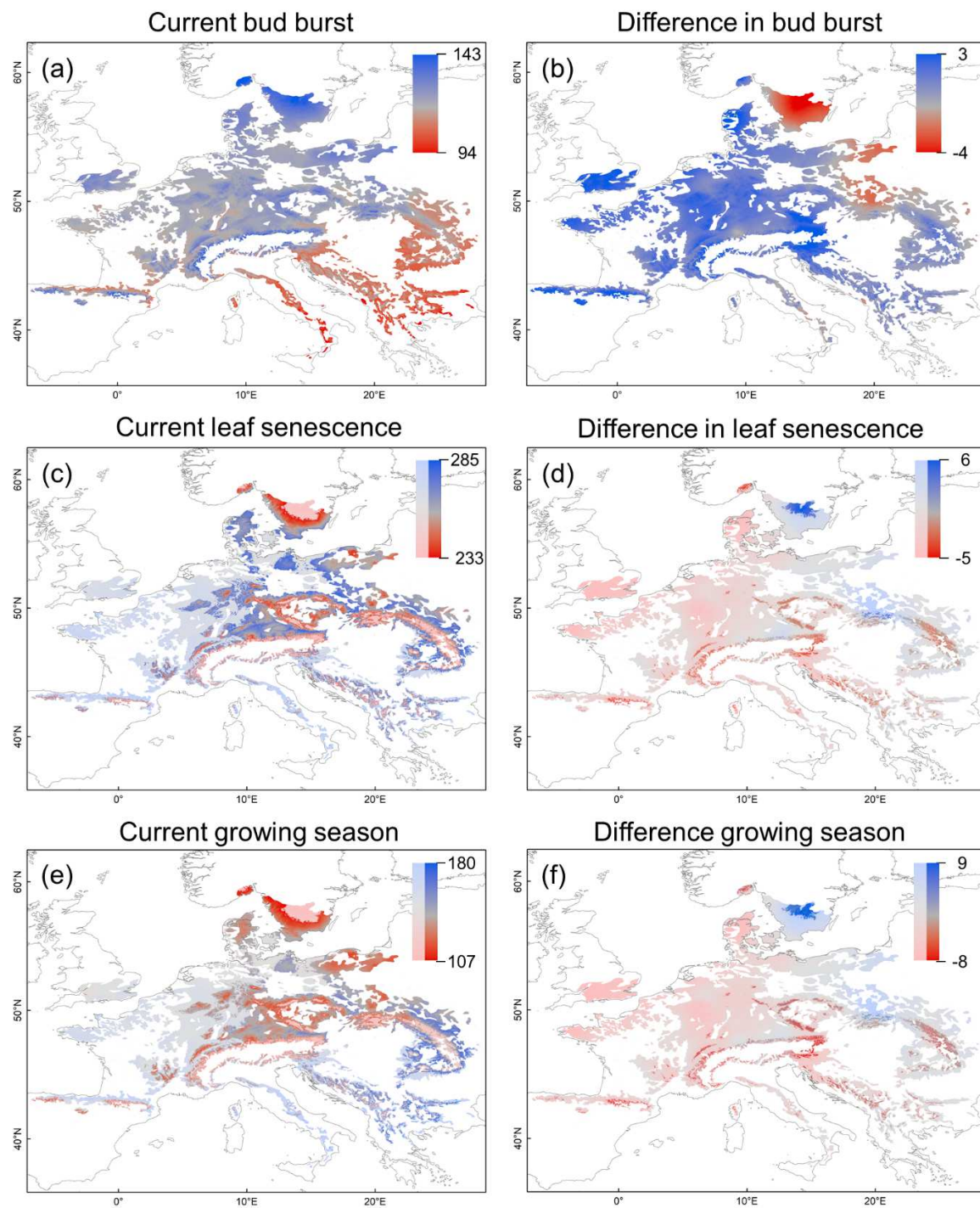


Figure 6. Spatial projections for (a) bud burst under current climatic conditions, (b) bud-burst differences between current and future conditions, (c) leaf senescence under current climatic conditions, (d) leaf-senescence differences between current and future conditions, (e) growing-

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

4 Discussion

4.1 Provenance differences in bud burst and autumn leaf senescence

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

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

4.2 Environmental variables defining leaf senescence

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

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

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

4.3 The effect of bud burst on leaf senescence

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

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

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

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

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

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

5 Conclusions

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

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

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We have no conflicts of interest to declare.

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