Understanding local adaptation and phenotypic plasticity in fitness-related traits across the European beech range: implications under climate change

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Understanding local adaptation and phenotypic plasticity in fitness-related traits across the European beech range: implications under climate change

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Title: Understanding local adaptation and phenotypic plasticity in fitness-related traits across the European beech range: implications under climate change.

Abstract

Climate change is modifying the distribution ranges of species worldwide. To better understand and more realistically predict future species ranges, it is critical to account for local adaptation and phenotypic plasticity in populations' responses to climate. This is challenging, however, because local adaptation and phenotypic plasticity are trait dependent and because traits co-vary along climatic gradients across the range, with differential consequences for fitness. One way to address this challenge is to build models with empirical data from large-scale common-garden experiments such as those that have been established in past decades for some forest tree species. This thesis used individual measurements of several fitness-related phenotypic traits (vertical and radial tree growth, spring and autumn leaf phenology and recruit mortality) of European beech (*Fagus sylvatica* L.) recorded in the frame of BeechCOSTe52, the largest network of tree phenotypic traits measured in common gardens throughout Europe (>150,000 trees) for modeling the species' likely response to recent climate change. Specifically, I pursued the following objectives: (i) to quantify range-wide variation and co-variation of local adaptation and phenotypic plasticity for four major phenotypic traits related to fitness (vertical growth, radial growth, survival, and leaf flushing phenology), and to project its species range under current and future climate based on this information (chapter 1); (ii) to quantify variation among populations in spring and autumn leaf phenology and the resulting growing season length, and to predict their patterns at the range-wide scale under current and future climate (chapter 2); and (iii) to quantify phenotypic plasticity at different development stages for vertical growth, radial growth, survival, and spring and autumn leaf flushing phenology, and to determine the extent to which inter-annual climate variation during the 20th century is related to variation in phenotypic plasticity across the species range (chapter 3). After setting up the required databases, I performed different types of linear mixed-effect models that related trait variation and co-variation to local adaptation (i.e., trait variation related to the climate of the planted populations' origin) and phenotypic plasticity (i.e., trait variation related to the climate of plantation site). Finally, I calculated a phenotypic plasticity index for populations based on their reaction norms (i.e., the shape or specific form of the phenotypic response to the environment of an individual or genotype). My results revealed that: (i) the contribution of plasticity to intra-specific trait variation is always higher than that of local adaptation, suggesting that beech is less sensitive to (moderate) climate change than previously reported; (ii) different traits and underlying climatic drivers constrain beech populations in different parts of the species range; (iii) considering trait co-variation improves predictions based on single traits; (iv) growing season length will increase under climate change in northern beech provenances but shrink in populations from the core and the southern range; (v) northern beech populations show high phenotypic plasticity for the investigated traits; and (vi) phenotypic plasticity tends to increase with age in growth-related traits. My results underline that population responses to climate across large geographical gradients are trait-dependent, suggesting that a complete set of fitness-related traits is required to fully understand species sensitivity to climate change.

Key words: phenotypic variability, acclimation, species distribution models, provenance test, beech, trait covariation.

Titre : Comprendre l'adaptation locale et la plasticité phénotypique des caractères liés à la valeur adaptative dans l'aire de répartition du hêtre européen : implications en contexte de changement climatique

Résumé

Le changement climatique modifie l'aire de répartition des espèces dans le monde. Pour mieux comprendre et prévoir de façon plus réaliste les aires de répartition futures des espèces, il est essentiel de tenir compte de l'adaptation locale et de la plasticité phénotypique dans les réponses des populations au changement climatique. C'est un défi, cependant, parce que l'adaptation locale et la plasticité phénotypique dépendent des caractères et parce que les caractères varient le long des gradients climatiques dans toute la gamme, avec des conséquences différentes pour la condition physique. C'est un défi, cependant, parce que l'adaptation locale et la plasticité phénotypique dépendent des caractères et parce que les caractères varient le long des gradients climatiques dans toute la gamme, avec des conséquences différentes pour la valeur adaptative. Une façon de relever ce défi consiste à construire des modèles à partir de données empiriques issues d'expériences à grande échelle sur les jardins communs, comme celles qui ont été réalisées au cours des dernières décennies pour certaines essences forestières. Cette thèse a utilisé des mesures individuelles de plusieurs caractères phénotypiques liés à la valeur adaptative (croissance verticale et radiale des arbres, phénologie foliaire printanière et automnale et mortalité) du hêtre européen (Fagus sylvatica L.) enregistrés dans le cadre du projet BeechCOSTe52, le plus grand réseau de caractères phénotypiques d'arbres mesurés dans des jardins communs à travers l'Europe (>150 000 arbres) pour modéliser la réponse probable de l'espèce au changement climatique récent. Plus précisément, j'ai poursuivi les objectifs suivants : (i) quantifier la variation et la covariation à l'échelle de l'aire de répartition de l'adaptation locale et de la plasticité phénotypique pour quatre caractères phénotypiques majeurs liés à la valeur adaptative (croissance verticale, croissance radiale, survie et phénologie des feuilles au printemps), et de projeter son aire de répartition dans le climat actuel et futur en fonction de cette information (chapitre 1) ; (ii) quantifier les variations entre les populations en ce qui concerne la phénologie foliaire printanière et automnale et la durée de la période de végétation qui en résulte, et prévoir leurs tendances à l'échelle de l'aire de répartition sous le climat actuel et futur (chapitre 2) ; et (iii) quantifier la plasticité phénotypique à différents stades de développement pour la croissance verticale, la croissance radiale, la survie et la phénologie des feuilles au printemps et à l'automne, et déterminer dans quelle mesure la variation climatique interannuelle au cours du 20e siècle est liée à la variation de la plasticité phénotypique dans l'aire de répartition des espèces (chapitre 3). Après avoir mis en place les bases de données requises, j'ai réalisé différents types de modèles linéaires à effets mixtes qui relient la variation et la covariation des caractères à l'adaptation locale (c'est-à-dire la variation des caractères liée au climat d'origine des populations plantées) et la plasticité phénotypique (c'est-à-dire la variation des caractères liée au climat du site de plantation). Finalement, j'ai calculé un indice de plasticité phénotypique pour les populations en fonction de leurs normes de réaction (la forme spécifique de la réponse phénotypique à l'environnement d'un individu ou du génotype). Mes résultats l'ont révélé : (i) la contribution de la plasticité à la variation des caractères intraspécifiques est toujours plus élevée que celle de l'adaptation locale, ce qui suggère que le hêtre est moins sensible aux changements climatiques (modérés) que ce qui avait été rapporté précédemment ; ii) des caractères différents et des facteurs climatiques limitent les populations de hêtres dans différentes parties de l'aire de répartition de l'espèce ; (iii) la prise en compte de la covariation des caractères améliore les prédictions basées sur des caractères uniques ; iv) la durée de la saison de croissance augmentera sous l'effet du changement climatique dans les provenances de hêtres du nord, mais diminuera dans les populations du cœur et de l'aire de répartition du sud ; (v) les populations de hêtres du nord présentent une plasticité phénotypique élevée pour les caractères étudiés ; et (vi) la plasticité phénotypique tend à augmenter avec l'âge dans les caractères liés à la croissance. Mes résultats soulignent que les réactions des populations au climat sur de grands gradients géographiques dépendent des caractères, ce qui suggère qu'un ensemble complet de caractères liés à la valeur adaptative est nécessaire pour bien comprendre la sensibilité des espèces au changement climatique.

Mots clés : variabilité phénotypique, l'acclimatation, modèles de distribution des espèces, test de provenance, hêtre and covariation des caractéristiques.

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GLOSSARY

Common terms used in my PhD. Although other definitions are possible, this glossary reflects the terms as I used them through the thesis document.

Fitness: The capacity of individuals to survive (survival success) and to contribute to the next generation (reproductive success).

Fundamental niche: The total range of environmental conditions that is potentially suitable for an organism to exist in the absence of limiting factors (i.e., competition, predation, disease, resource availability and environmental stresses).

Genotype: The collection of genes responsible for the various traits of a given organism (Nicotra et al., 2010).

Growing season length: The number of days between the estimated dates of budburst and leaf senescence (Estiarte and Peñuelas, 2015).

Leaf budburst: The stage in leaf development when green leaves first become visible (Cole and Sheldon, 2017). Leaf budburst is referred to as leaf flushing in the second chapter of this thesis.

Leaf phenology: The timing of the leaf cycle stages and their relationship to seasonal climatic changes (Kikuzawa, 1995).

Leaf senescence: The age-dependent programmed degradation and degeneration process that leads to the death of leaves (Woo et al., 2013). In the second chapter of this thesis, leaf senescence is estimated at the tree level as the stage when 50% of the tree's leaves have changed color from green to yellow (Lang et al., 2019).

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Leading edge: Dynamic margin of a species' distribution where populations expand and occupy previously non-inhabited areas (Lenoir and Svenning, 2013).

Local adaptation: Process to measures the fitness of a population in its local environment relative to other environments (Kawecki and Ebert, 2004).

Linear mixed-effect models: linear regression model used when data have some kind of hierarchical structure or grouping such as repeated measurement designs, time series, nested designs or randomized blocks. Mixed models allow to have fixed coefficients (those whose levels are of interest to the experimenter) and random coefficients (those whose levels are only one realization of all possible levels coming from a population) and several error terms (Zuur et al., 2009).

Maladaptation: refers to a decrease of the mean population fitness produced by a mismatch between the optimal and realized mean genotype frequencies, which may result from the inability to adjust to rapidly changing climates (Jaramillo-Correa et al., 2015).

Phenotype: The set of observable characteristics (traits) on an individual resulting from the interaction of its genotype with the environment (Nicotra et al., 2010).

Phenotypic plasticity: The ability of a genotype to render different phenotypes across different environments (Nicotra et al., 2010).

Phenotypic variation: The variability in phenotypes that exists in a population and among populations (Coleman et al., 1994).

Provenance: Population from a specific geographic location.

Provenance test = Common garden = Genetic trial : Experiment in which trees from different populations with known geographical origin (provenances) are planted in the same environment (trial site) to study the genetic and environmental bases of complex traits (Villemereuil et al., 2016).

Radial growth: Amount of growth a tree has as measured by the increase in the radius of its stem. The thesis uses the diameter measured at breast height (DBH).

Range core: Physical location of populations established near the center of the range (Lenoir and Svenning, 2013).

Reaction norm: The function that describes the phenotypic response of a given genotype or a population along an environmental gradient (Arnold et al., 2019).

Realized niche: Represent the environmental conditions where a species inhabit. It accounts for competition, predation, disease, resource availability and environmental stresses.

Species distribution models (SDMs): Correlational models used to explain or predict the distribution of a species or lineage across geographic space and time using environmental data (Guillera-Arroita et al., 2015).

Species range: The area where a particular species can be found during its lifetime (Lenoir and Svenning, 2013).

Trailing edge: Dynamic margin of a species distribution where the range contracts as a consequence of the extinction of local populations (Lenoir and Svenning, 2013).

Trial site: Plantation of trees from different origins (provenances).

Glossary

ΔTraitSDM: Species distribution models that consider phenotypic plasticity and local adaptation of fitness-related traits to predict the sensitivity of populations across species ranges to climate change (Benito Garzón et al., 2019).

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INTRODUCTION

1.1 Modern climate change and its impact on species ranges

During the 20th century, global average surface temperatures increased up to 2.5° C and annual precipitation decreased up to 100 mm (Fig. I1; IPCC, 2014). The increase in temperature has been greater in the continental areas of the northern hemisphere especially in high latitudes (IPCC, 2014) and most of the increase has occurred in the last decade (Rahmstorf and Coumou, 2012). Climate change causes variability in precipitation promoting droughts and unusually heavy rainfall and flooding (Fig. I1b; Hansen et al., 2012; IPCC, 2014). According to different Representative Concentrations Pathways (RCP), global average temperatures are expected to increase between 1 and 3.7° C by 2100 (IPCC, 2014).

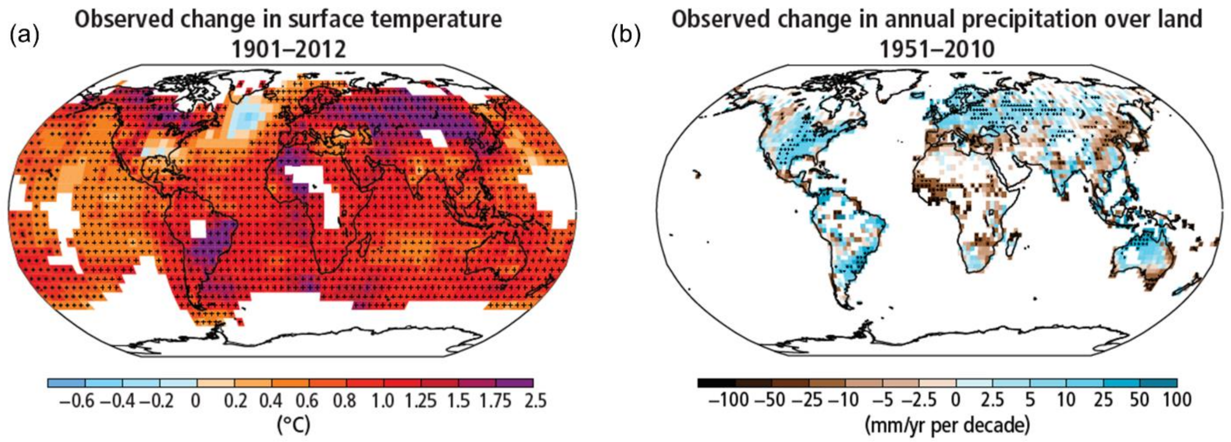

Figure I1 Observed changes of surface temperature (a) from 1901 to 2012; and precipitation (b) from 1951 to 2010 (IPCC, 2014).

Climate change is having a major impact on the geographical distribution of species worldwide (Bellard et al., 2012). Many plant and animal species are moving to higher elevations and latitudes in response to shifts of the environmental conditions to which they are adapted (Chen et al., 2011; Parmesan and Yohe, 2003). These changes in abundance and distributions result in the reshuffling of communities, mismatches between interacting organisms and changing ecosystem dynamics (Peñuelas et al., 2013). Correlative species distribution models (SDMs), the most widespread approach to model the distribution of a species as a function of environmental conditions, have now been applied to many thousands of species around the world including hundreds of tree species (Urban et al., 2016). Numerous SDMs have projected range shifts of forest tree species towards higher latitudes and elevations under contemporary climate change (Cheaib et al., 2012; Iverson and Prasad, 1998; McKenney et al., 2007; Pecchi et al., 2019). Some SDMs have predicted an average decrease of 28% in the area of distribution of forest trees in Europe, especially for widely distributed species (Hanewinkel et al., 2013), although other authors have shown that such predictions strongly depend on the underlying data (Duputié et al., 2014). Most importantly, SDMs are exclusively based in the occurrence of the species and hence provide very little information about the biological mechanisms behind range shifts (Valladares et al., 2014). Yet whether a species shifts (or contracts/expands) its range depends on the sensitivity to climate of the populations that form this range. Populations can respond to climate change in three ways: (i) by migrating to match the environmental conditions to which they are adapted, (ii) by persisting *in-situ* and acclimating to new environmental conditions or (iii) by going extinct (Aitken et al., 2008). Most traditional SDMs only consider the consequences of population migration (in form of range expansions) and population extinction (in form of range retractions), whereas they do not account for the possibility of *in-situ* population persistence based on changes of the local phenotypes and eventually genotypes in response to a changing climate (Fig. I2; Benito Garzón et al., 2011; Duputié et al., 2015; Richardson et al., 2017; Valladares et al., 2014). However, there is growing evidence that forest trees have a notable ability to acclimate to rapidly changing environmental conditions (Alberto et al., 2013).

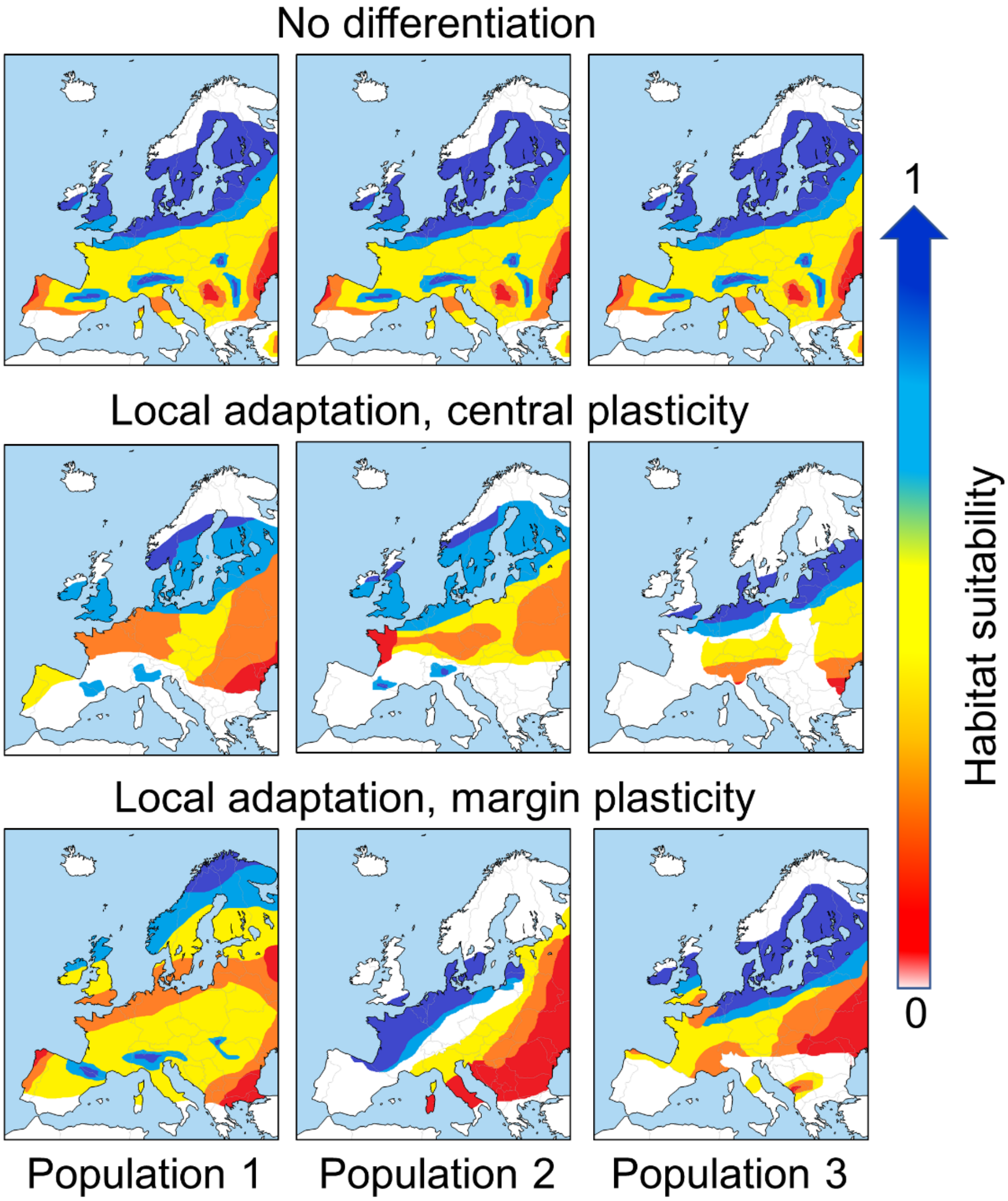

Fig. I2 Simulations of differences in climatic suitability (future-current) for three populations of a virtual species occurring in Europe in three scenarios differing in population responses to temperature. Each row corresponds to simulations for each intraspecific scenario: In first row the populations have no differentiation, in second row populations are locally adapted and have strong plasticity in the center of the range, in third row populations are locally adapted and have strong plasticity in the margins of the range. Each column represents a population. Reddish colors indicate areas of decreasing climatic suitability, bluish colors indicate increasing suitability. White represents little or no difference in future vs current climatic suitability. The figure shows that predictions are the same when no differences between populations (first row) are considered, while there are differences in predictions when differences in local adaptation and plasticity between populations (lines 2 and 3) are considered. Figure modified from Valladares et al. (2014).

1.2 Local adaptation and phenotypic plasticity

Two main evolutionary processes allow tree populations to persist locally and acclimate to a changing climate: local adaptation and phenotypic plasticity (Des Roches et al., 2018; Mclean et al., 2014; Valladares et al., 2014). Local adaptation is a process that requires several generations to change the frequency of alleles in response to changes in the environment (Savolainen et al., 2007), whilst phenotypic plasticity is a process that relies on the ability of a genotype to render different phenotypes across different environments (Fig. I3; Nicotra et al., 2010).

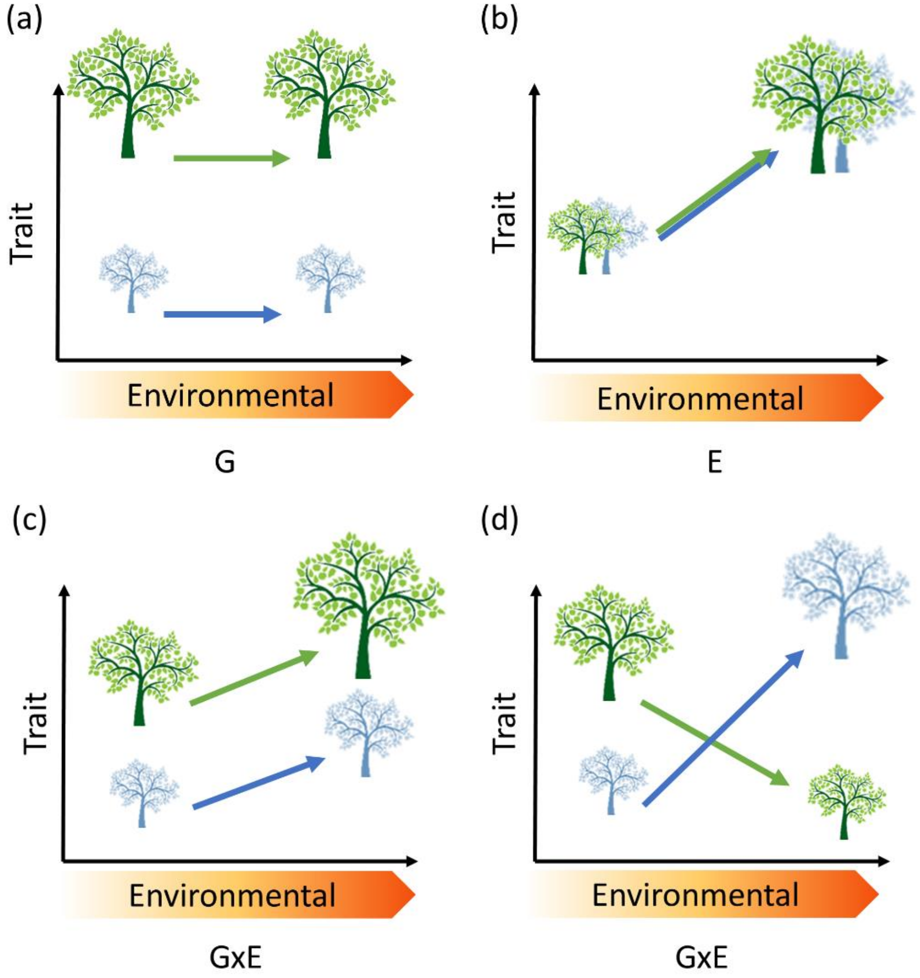

Fig. I3 Conceptual presentation of reaction norms (phenotypic expressions across environments for different genotypes or populations). Letters (G, E, GxE) indicate genetic, environmental, or gene-environment interaction variance. (a) No phenotypic plasticity (denoted by flat reaction norms) but with significant genetic effects (space between genotypes). (b) Plasticity variation for traits with no interaction variance (parallel slopes). (c) Differently sloped (positive) interaction norms indicating genetic variation for plasticity (genotype-environmental interaction). (d) Differently sloped interaction norms (both positive and negative) indicating genetic variation for plasticity. Opposite slopes indicating that the phenotypic expression across the environmental gradient goes in different directions depending on genotype. Figure modified from Strand and Weisner (2004).

Local adaptation and phenotypic plasticity are ubiquitous in natural populations and highly relevant for population responses to environmental changes (Chevin et al., 2010; Savolainen et al., 2007), although their respective importance tends to vary extensively through time and space (Des Roches et al., 2018; Reich et al., 2016). Trees are long-lived organisms with large gene flow among populations (Petit and Hampe, 2006), it implies that local adaptation is carried out at long time scales (Savolainen et al., 2007). Phenotypic plasticity is frequently the main mechanism for tree populations across species ranges to respond rapidly to climate change (Benito Garzón et al., 2019). Phenotypic plasticity changes across the developmental stages of trees life and can be driven by climatic variability (Vizcaíno-Palomar et al., In revision), suggesting that some populations may evolve towards more plastic genotypes under high variability. Hence, it is critical to identify and quantify the role of local adaptation and phenotypic plasticity in the response of local populations to a changing environment to better understand and more realistically predict future species distribution ranges (Chevin et al., 2010).

1.3 Phenotypic traits and fitness

Phenotypic traits variation is driven by local adaptation or phenotypic plasticity (Ellis and Weis, 2006). Some local environmental factors can exert a selective pressure on the phenotypic traits, causing local adaptation and affecting fitness under the new environmental conditions (Ellis and Weis, 2006; Fréjaville et al., 2019). Although with different nuances, tree fitness can be associated with several traits that putatively have a direct relationship with survival and reproduction, conforming a fitness landscape (Laughlin, 2018) that may ultimately delimit the species range. The traits that have most commonly been considered in this context are those related with tree growth, phenology and mortality (Alberto et al., 2013; Benito Garzón et al., 2018; Chuine, 2010; Stahl et al., 2014). Fitness-related traits typically vary across large geographical gradients. Values reflecting high performance are typically found in the central parts of the range where the environmental conditions are most favorable compared to more peripheral areas (Pironon et al., 2017; Sexton et al., 2009). Thus, vertical growth is generally highest near the range core and decreases towards the margins (Fréjaville et al., 2019b; Pedlar and McKenney, 2017). Similarly, recruit mortality tends to increase towards the range periphery, especially when this is delimited by drought-induced stress (Benito Garzón et al., 2018). On the contrary, phenological traits such as leaf budburst tend to show latitudinal or altitudinal trends (Duputié et al., 2015) that have been interpreted as a consequence of genetic adaptation to frost and photoperiod (Way and Montgomery, 2015). On the other hand, different traits often co-vary, either positively or negatively, across climatic gradients (Laughlin and Messier, 2015). One conspicuous case of trait co-variation is observed around the phenomenon of demographic compensation between survival and growth (Fig. I4; Benito-Garzón et al., 2013; Doak and Morris, 2010; Peterson et al., 2018; Villellas et al., 2015). New climatic conditions can result into maladaptation of some populations, which may change intra-specific patterns of trait variation and co-variation across geographical gradients, and eventually species ranges. For example, increasing temperatures at higher latitudes can translate either into higher mortality or into higher growth rates depending on whether advanced leaf budburst incites or not frost damage on tree tissues (Delpierre et al., 2017; Vitasse et al., 2014). Taking all together, we can hypothesize that species ranges are likely to be delimited by the interaction of several traits and their responses across environmental gradients (Benito-Garzón et al., 2013; Enquist et al., 2015; Stahl et al., 2014).

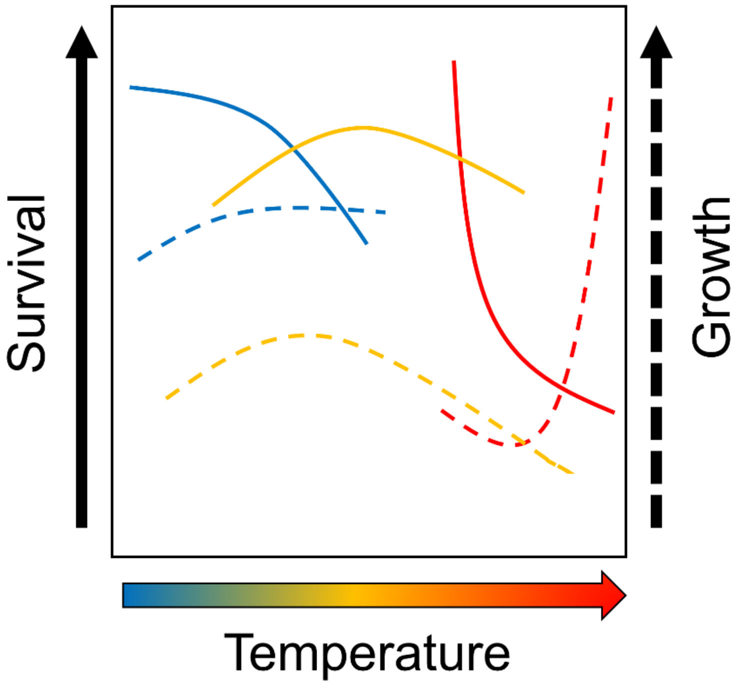

Fig. I4 Temperature responses of survival and growth rates show temporal demographic compensation in natural populations of a virtual species. Survival (solid line) and growth (dashed line) rates as functions of temperature under field conditions in cold (blue), mean (orange), and warm (red) populations. The color gradient in the arrow depicts the clinal variation from low (blue) to high (red) values of temperatures. The demographic compensation in the figure shows that in warm and cold populations, survival decreases as growth increases. Figure modified from Peterson et al. (2018).

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MATERIALS AND METHODS

1.1 Provenance tests

Provenance tests (common-garden experiment with replication of sites) provide us with the necessary experiments to quantify the effects of phenotypic plasticity, local adaptation and genotype-by-environment interactions (Alberto et al., 2011; Villemereuil et al., 2016). They consist in the controlled plantation of individuals from different origins (provenances) in experimental sites (trial sites) distributed across environmental gradients (Figure M1; Alberto et al., 2013; Villemereuil et al., 2016). Seedlings grown in the greenhouse are planted outside in a spaced arrangement, avoiding effects of germination and initial establishment as well as early intra- and interspecific competition (Alberto et al., 2013). Individuals are subsequently monitored, and a series of variables are repeatedly measured (ideally using standardized survey protocols). Local adaptation and phenotypic plasticity for the measured variables can then be quantified along geographical or environmental gradients (Alberto et al., 2013) or across contrasting environments (Villemereuil et al., 2016). Through the past decades, extensive provenance tests experiments with hundred thousands of trees have been established for several major European forest tree species (*Quercus* spp., *Fagus sylvatica*, *Pinus* spp., *Abies alba*, etc.; Benito Garzón et al., 2019). Although these experiments were originally launched for breeding and economical purposes, they are now also used to estimate tree responses to climate change in those cases where the species range is sufficiently represented (Alberto et al., 2011; Arnold et al., 2019; Fréjaville et al., 2019b; Savolainen et al., 2007; Vizcaíno-Palomar et al., 2019). For example, the climatic sources of genetic differentiation and plastic responses of growth and survival of for *Quercus petrea*, *Abies alba*, *Picea mariana* and *Pinus banskiana* have been identified based on provenance tests networks (Fréjaville et al., 2019a; Pedlar and McKenney, 2017; Sáenz-Romero et al., 2017). Most of the studies using provenance tests data rely exclusively on tree growth, an important trait for tree breeding (Fréjaville et al., 2019b). Meanwhile, the responses of many other life history traits to changes in climate and their implication in defining species ranges remain virtually unexplored (but see e.g. Sáenz-Romero et al., 2017 for tree mortality).

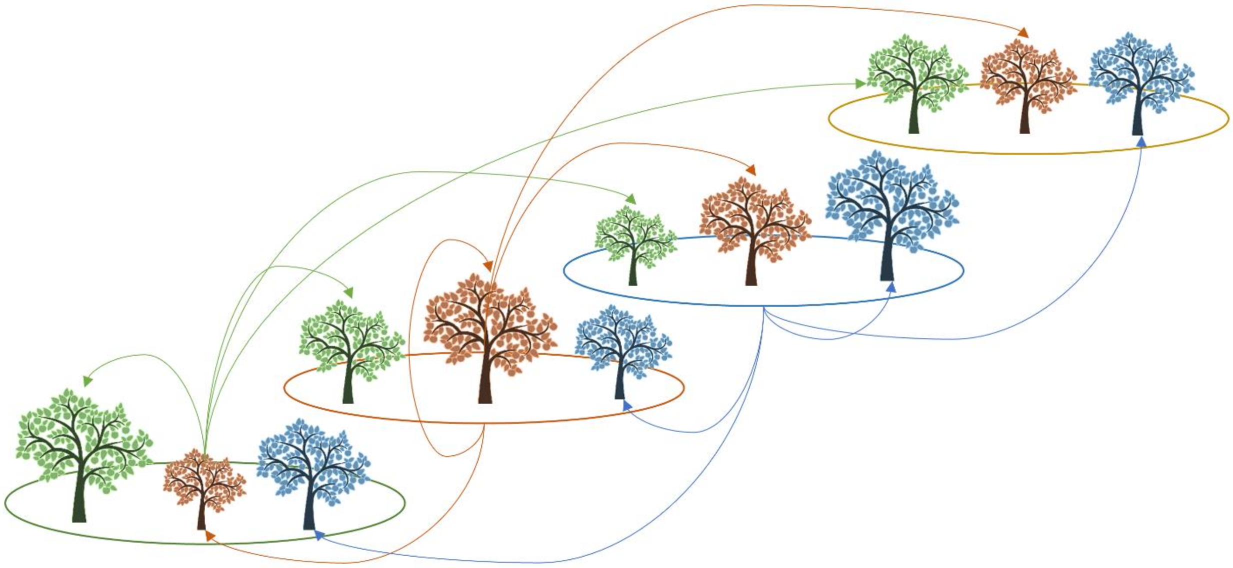


Fig. M1 Experimental design of common-garden networks across different climates (colored oval shapes), where trees originate from different provenances (indicated by three colors: blue, red and yellow). Tree performance is represented by tree size. Figure modified from Benito Garzón et al. (2019).

1.2 Modeling

To know the direction and magnitude of the phenotypic response of each genotype in response to environmental variation, reaction norms can be calculated for a given trait from provenance tests experiments (Figure I3; Arnold et al., 2019; Wilczek et al., 2014). Reaction norms can have sharply contrasting shapes for different traits across the same environmental range within the same species (Vitasse et al., 2010). In plants, reaction norms are regularly analyzed assuming a linear response to environmental variables (Chevin and Lande, 2011). Linear mixed-effect models provide a statistically appropriate method of describing both the population-level response and the variation among individuals in that response (Benito Garzón et al., 2019). Mixed models are composed of two predictive elements: "fixed" effects (the variable(s) of interest due to their direct effects on the predictor variable) and "random" effects (the variable(s) that contribute to the variance between predictor values) (Zuur et al., 2009). An advantage of linear mixed-effects models is that they combine the provenance and trial site effect into a single equation, while including random effects that control differences between experimental sites that are not climate-related (Fig. M2; Leites et al., 2012). These models have been recently named ΔTraitSDMs that in addition to preserving the statistical simplicity of the SDMs, provide a link to traits related to fitness dividing the phenotypic variation of traits into components of local adaptation (i.e., related to the climate of origin of the provenance) and phenotypic plasticity (i.e., related to the climate of the trial site) (Benito Garzón et al., 2019). In addition, these models make it possible to evaluate changes with age (Arnold et al., 2019) and covariations between different traits (Benito Garzón et al., 2019; Gárate-Escamilla et al., 2019). For some of the phenotypic traits, reaction norms are curves when samples are taken over a sufficiently wide range of environmental conditions (Cochrane et al., 2014; Gunderson et al., 2010; Jochner et al., 2016). In these cases, characterizing the form of the reaction norms as non-linear functions of the environment will allow the response of the reaction norm to be expressed in a more realistic way (Stinchcombe et al., 2012). In mixed models, non-linearity can be handled using polynomial quadratic functions (Arnold et al., 2019).

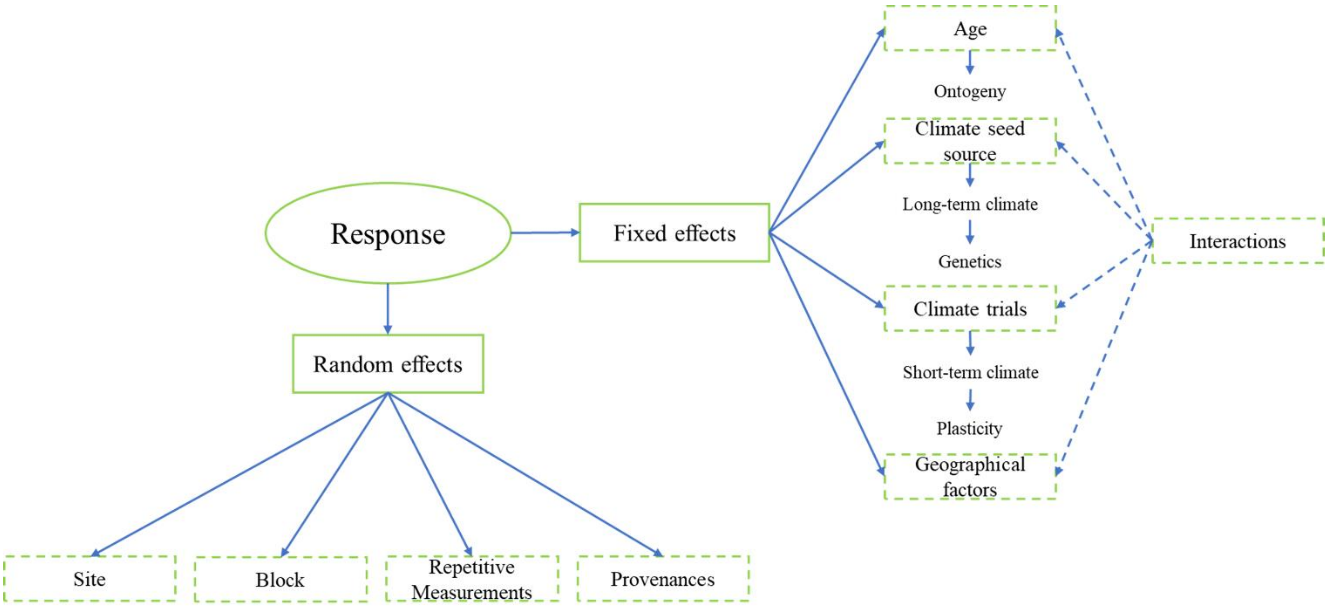
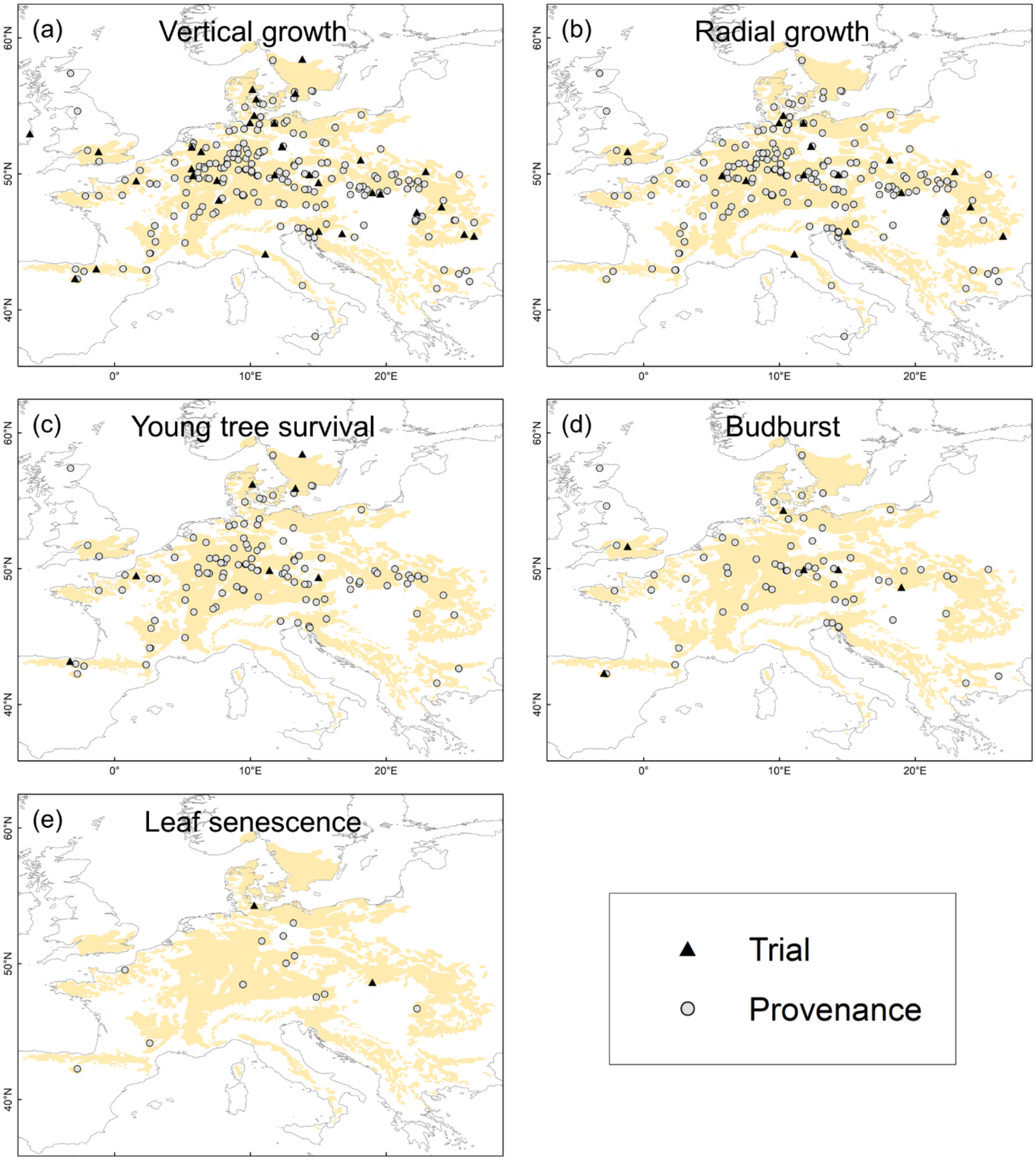


Fig. M2 Graphical summary of the fitted linear mixed-effects model. Oval shape indicates response variable, rectangular solid lines shapes indicate fixed and random effects, and rectangular dashes lines shapes indicate explanatory variables of fixed and random effects. Figure modified from Leites et al. (2012).

1.3 *Fagus sylvatica*

Fagus sylvatica L. (European beech, henceforth “beech”) is a deciduous broadleaved temperate tree (Preston and Hill, 1997) that is widely distributed across Europe and of high ecological and economic importance (Packham et al., 2012). This dominant forest tree species covers a wide range of environmental conditions from northern Spain to Bulgaria and from southern Sweden to the Italian mountains (Leuschner et al., 2006). The adaptive responses of beech to climate change have been intensively studied on a local basis for several fitness related traits including growth (vertical and radial growth, survival, and leaf budburst and senescence) (Gömöry and Paule, 2011; Kramer et al., 2017, 2010; Robson et al., 2013). Overall, leaf phenology tends to be more strongly driven by local adaptation than the other parameters, suggesting that under new climates, leaf phenology could constrain species ranges rather than the more plastic traits (Duputié et al., 2015). At present, beech is expanding at its northern distribution limit and showing apparent stability in the southern part of the range (Farahat and Linderholm, 2018; Stojnic et al., 2018). The extent to which this pattern will continue in the future depends, among others, on the species' fitness-related traits and their capacity to rapidly respond (via plasticity) to new climates. However, to date, most studies considering more than one trait and eventual trait interactions have been performed at local scale. Thus, it has been shown that late budburst is positively correlated with high rates of mortality (Gömöry and Paule, 2011) and negatively with tree growth (Delpierre et al., 2017; Robson et al., 2013), whilst vertical and radial growth are positively correlated (Albert and Schmidt, 2010; Heym et al., 2017). The recently assembled BeechCOSTe52 (Robson et al., 2018) now allows to test such relationships across multiple experimental sites, providing phenotypic variation information of tree growth (vertical and radial), survival and leaf phenology (spring and autumn) across a network of 38 provenance tests whose trees originating 205 provenances represent the entire distribution range of the species (Fig. M3).

Fig. M3 Map: Distribution range of *Fagus sylvatica* L. (shaded in beige) and location of the provenances and trial sites by trait. Circles indicate the locations of the provenances and triangles those of the trial sites for (a) vertical growth (Vg), (b) radial growth (RG), (c) young tree survival (YTS), (d) budburst (BB) and (e) leaf senescence (LS). Table: The extent of data from the BeechCOSTe52 database (Robson et al., 2018) used for modelling. Measurements = total number of measurements; Trees = total number of individual trees; Trials = total number of trial sites; Provenances = total number of provenances, Age = the age at which the trees were measured.



	VG	RG	YTS	BB	LS
Measurements	203 105	34 237	41 309	7 863	1227
Trees	108 415	31 339	37 433	7 863	905
Trials	36	19	7	7	2
Provenances	205	186	114	62	12
Age	2 to 15	8 to 15	2 to 6	12	9 to 11

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OBJECTIVES AND THESIS STRUCTURE

1.1 Objectives

Here, I apply a new modeling approach that quantifies range-wide variation of local adaptation and phenotypic plasticity of five fitness related traits (vertical and radial growth, survival, and budburst and leaf senescence phenology) and their interactions, to delimit the distribution range of beech under current and future climates. For this purpose, I use the measurements of beech recorded in BeechCOSTe52 database, the largest network of provenance tests for a forest tree species in Europe. The specifics objectives of this thesis are:

1. To quantify range-wide variation and co-variation of local adaptation and phenotypic plasticity for vertical growth, radial growth, survival, and leaf budburst phenology, and to project beech species range based on this information.
2. To quantify variation among populations in spring and autumn leaf phenology and the resulting growing season length, and to predict their patterns at the range-wide scale.
3. To quantify phenotypic plasticity at different development stages for vertical growth, radial growth, survival, and spring and autumn leaf budburst phenology, and to determine the extent to which inter-annual climate variation during the 20th century is related to variation in phenotypic plasticity across the species range.

1.2 Thesis structure

The thesis is divided into General Introduction, General Materials & Methods, three research chapters (chapters 1, 2 and 3) that have been structured as scientific manuscripts (see summary of specific objectives and approach of each research chapter in Table I1). At the moment of submitting the thesis document, the manuscript corresponding to chapter 1 has been published in Global Ecology and Biogeography, the manuscript corresponding to chapter 2 is in second review in Agricultural and Forest Meteorology and the manuscript corresponding to chapter 3 is expected to be submitted at the end of the year. Finally, the General Discussion integrates the contributions of the three research papers in the context of evolutionary processes modifying species ranges across large temporal and geographical scales in a context of modern rapid climate change.

Table O1. Overview of the research chapters and related publications presented in this thesis.

	Title	Objectives	Processes	Main Drivers	Methods		Publications
					Study area Data source	Major statistical approaches	
Chapter 1	Range-wide variation in local adaptation and phenotypic plasticity of fitness-related traits in *Fagus sylvatica* and their implications under climate change	Quantify range-wide variation and co-variation of local adaptation and phenotypic plasticity for traits related to growth, mortality and leaf phenology, and to project the species range under current and future climate based on this information	Local adaptation and phenotypic plasticity	Vertical and radial growth, young tree survival, budburst, tree age, and climate variables	Global range BeechCOSTe52 database	Linear mixed-effect models Nonlinear models Linear models	Gárate-Escamilla H. et al. (2019) Global Ecology and Biogeography 28: 1336-1350.
Chapter 2	Greater capacity to exploit warming temperatures in northern populations of European beech is partly driven by delayed leaf senescence	Quantify variation among populations in spring and autumn leaf phenology and the resulting growing season length, and to predict their patterns at the range-wide scale under current and future climate	Local adaptation and phenotypic plasticity	Budburst, leaf senescence, growing season and climate variables	Germany and Slovakia BeechCOSTe52 database	Linear mixed-effect models Nonlinear models	Gárate-Escamilla H.et al. Agricultural and Forest Meteorology, in revision
Chapter 3	The legacy of 20th inter-annual climate variation in European beech populations' phenotypic plasticity	Quantify phenotypic plasticity at different development stages for traits related to growth, mortality and leaf phenology and to determine the extent to which inter-annual climate variation during the 20th century is related to variation in phenotypic plasticity across the species range	Phenotypic plasticity	Vertical and radial growth, young tree survival, budburst leaf senescence, tree age, and climate variables	Global range BeechCOSTe52 database	Linear mixed-effect models Phenotypic plasticity index Linear models	Gárate-Escamilla H.et al., in preparation

CHAPTER 1

Range-wide variation in local adaptation and phenotypic plasticity of fitness-related traits in *Fagus sylvatica* and their implications under climate change

Homero Gárate-Escamilla, Arndt Hampe, Natalia Vizcaíno-Palomar, T. Matthew Robson & Marta Benito Garzón. 2019. *Global Ecology and Biogeography*.

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RESEARCH PAPER

Global Ecology and Biogeography A Journal of Macroecology WILEY

Range-wide variation in local adaptation and phenotypic plasticity of fitness-related traits in *Fagus sylvatica* and their implications under climate change

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Editor: Benjamin Blonder

Abstract

Aim: To better understand and more realistically predict future species distribution ranges, it is critical to account for local adaptation and phenotypic plasticity in populations' responses to climate. This is challenging because local adaptation and phenotypic plasticity are trait-dependent and traits covary along climatic gradients, with differential consequences for fitness. Our aim is to quantify local adaptation and phenotypic plasticity of vertical and radial growth, leaf flushing and survival across the range of *Fagus sylvatica* and to estimate the contribution of each trait to explaining the species' occurrence.

Location: Europe.

Time period: 1995–2014; 2070.

Major taxa studied: *Fagus sylvatica* L.

Methods: We used vertical and radial growth, flushing phenology and mortality of *F. sylvatica* L. recorded in the BeechCOSTe52 database (>150,000 trees). Firstly, we performed linear mixed-effect models that related trait variation and covariation to local adaptation (related to the planted populations' climatic origin) and phenotypic plasticity (accounting for the climate of the plantation), and we made spatial predictions under current and representative concentration pathway (RCP 8.5) climates. Secondly, we combined spatial trait predictions in a linear model to explain the occurrence of the species.

Results: The contribution of plasticity to intraspecific trait variation is always higher than that of local adaptation, suggesting that the species is less sensitive to climate change than expected; different traits constrain beech's distribution in different parts of its range: the northernmost edge is mainly delimited by flushing phenology (mostly driven by photoperiod and temperature), the southern edge by mortality (mainly driven by intolerance to drought), and the eastern edge is characterized by decreasing radial growth (mainly shaped by precipitation-related variables in our model); considering trait covariation improved single-trait predictions.

Main conclusions: Population responses to climate across large geographical gradients are dependent on trait × environment interactions, indicating that each trait responds differently depending on the local environment.

KEYWORDS
acclimation, beech, common gardens, phenotypic variation, species distribution models, trait covariation

1 | INTRODUCTION

Climate change is having a major impact on the structure, composition and distribution of forests worldwide (Trumbore, Brando, & Hartmann, 2015). Accordingly, numerous models have projected significant range shifts of forest tree species towards higher latitudes and elevations (Urban et al., 2016). However, to date, the two most important processes in the response of tree populations to a rapidly changing climate, local adaptation and phenotypic plasticity (Aitken, Yeaman, Holliday, Wang, & Curtis-Mclane, 2008; Savolainen, Pyhäjärvi, & Knürr, 2007), are not systematically considered by species distribution models (Duputié, Rutschmann, Ronce, & Chuine, 2015; Richardson, Chaney, Shaw, & Still, 2017; Valladares et al., 2014). Phenotypic plasticity enables a given genotype to express different phenotypes in response to changing environments, while local adaptation produces new genotypes with a greater ability to cope with the new environment. The two mechanisms are ubiquitous in natural populations, although their respective importance is considered to vary extensively through time and across species ranges (Des Roches et al., 2018; Reich et al., 2016). To persist under rapid climatic change, organisms with short generation times can take advantage of evolutionary responses and phenotypic plasticity (Scheepens, Deng, & Bossdorf, 2018), whereas organisms with long generation cycles will rely predominantly on phenotypic plasticity (Fox, Donelson, Schunter, Ravasi, & Gaitán-Espitia, 2019). To better understand and more realistically predict future species distribution ranges, it is therefore critical to identify and quantify the respective importance of local adaptation and phenotypic plasticity in the response of local populations to a changing climate.

From an ecological perspective, fitness can be associated with several phenotypic traits that directly affect survival and reproduction, creating a fitness landscape (Laughlin, 2018) that allows them to be used to bound species ranges (Benito-Garzón, Ruiz-Benito, & Zavala, 2013; Stahl, Reu, & Wirth, 2014). From a biogeographical perspective, higher fitness can be associated with higher probabilities of occurrence of a species in a given environment (Jiménez, Soberón, Christen, & Soto, 2019). Fitness-related traits vary across large geographical gradients, mainly depending on how natural selection drove differences among populations in the past. For instance, tree height is generally greatest at the core of a species' range and decreases towards its margins (Pedlar & McKenney, 2017; Purves, 2009). Climate-driven mortality commonly increases towards the driest part of a species' range, which is related to drought-induced stress conditions (Benito Garzón et al., 2018). The onset of flushing phenology tends to be delayed towards high latitudes (Duputié et al., 2015) as a consequence of genetic adaptation to late frost and fluctuating photoperiod (Way & Montgomery, 2015). Moreover, traits tend to covary across climatic gradients (Laughlin & Messier, 2015). A conspicuous example is the demographic compensation found between survival and growth near range margins (Benito-Garzón et al., 2013; Doak & Morris, 2010; Peterson, Doak, & Morris, 2018), and further delimitation of species ranges based on demographic approaches (Merow, Bois, Allen, Xie, & Silander, 2017). New climatic conditions can result in maladaptation of some populations, which may change intraspecific patterns of trait variation and covariation across geographical gradients, and eventually, species ranges. For example, increasing temperatures at high-latitude or high-elevation range margins are likely to produce higher growth rates, but they can also induce higher mortality owing to late frosts (Delpierre, Guillemot, Dufrêne, Cecchini, & Nicolas, 2017; Vitasse, Lenz, Hoch, & Korner, 2014). Hence, species ranges are likely to be delimited by the interaction of multiple traits and their responses across environmental gradients (Benito-Garzón et al., 2013; Enquist et al., 2015; Stahl et al., 2014).

Common gardens or provenance tests provide us with the necessary experiments to quantify phenotypic plasticity and local adaptation of fitness-related traits in response to climate (Mátyás, 1999). Models based on reaction norms of phenotypic traits using measurements recorded in common gardens show that: (a) geographical variation in populations' responses to climate is more strongly based on phenotypic plasticity than on local adaptation (Benito Garzón, Robson, & Hampe, 2019); (b) phenotypic variation can strongly differ among traits, in particular for survival of young trees, growth, and flushing phenology—traits that are directly related to fitness and typically measured in common gardens (Benito Garzón, Alía, Robson, & Zavala, 2011; Duputié et al., 2015; Richardson et al., 2017; Valladares et al., 2014); (c) as a consequence, predictions of future species ranges are likely to be strongly influenced by the combined response of different fitness-related traits to climate (Laughlin, 2018), but this structured combination of intraspecific multi-trait variation defining species ranges has not been explored with empirical data.

Fagus sylvatica L. (European beech, henceforth "beech") is a widely distributed deciduous broadleaf temperate tree. In some parts of its range, beech has a late flushing strategy to avoid late frosts, which has a generally detrimental effect on tree growth (Delpierre et al., 2017; Gömöry & Paule, 2011; Robson, Rasztovits, Aphalo, Alia, & Aranda, 2013). Beech is currently expanding at its northern distribution edge, whereas it experiences drought-induced radial growth decline and increasing mortality at its southern edge (Farahat & Linderholm, 2018; Stojnic et al., 2018). The extent to which this pattern will continue in the future depends on how the combination of several fitness-related traits will influence the species' response to new climates.

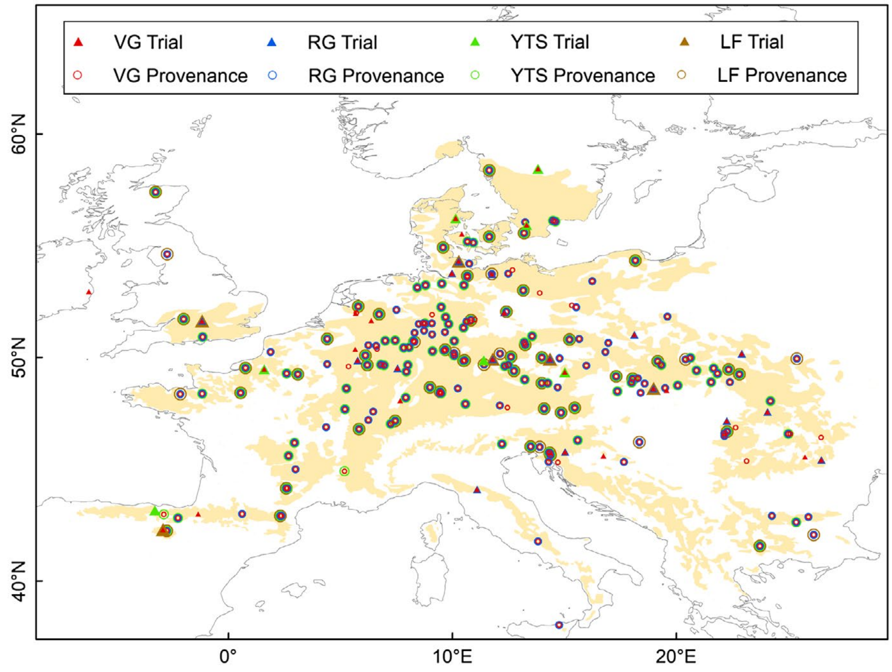
Here, we propose a new modelling approach that quantifies local adaptation and phenotypic plasticity of four major phenotypic traits related to fitness (vertical and radial growth, young tree survival, and flushing phenology) and their interactions, to delimit species ranges under current and future climates. The four traits studied are expected to be under natural selection and show high heritability (Delpierre et al., 2017; Etterson, 2002). Radial and vertical growth are directly related to biomass and thus reproduction (Younginger, Sirová, Cruzan, & Ballhorn, 2017), and the timing of flushing can affect fitness through reproduction success and growth by delimiting the growth season (Chuine, 2010). We use the phenotypic measurements recorded in the BeechCOSTe52 database (Robson et al., 2018), the largest network of common gardens for forest trees in Europe, covering virtually the entire distribution range of the species. Our specific objectives are: (a) to quantify range-wide patterns of phenotypic plasticity and local adaptation in growth, young tree survival and flushing phenology; (b) to identify interactions among the different traits and the extent of their geographical variation in local adaptation and phenotypic plasticity; (c) to discuss how these fitness-related traits delimit species ranges, and (d) to better understand species ranges under new climate scenarios and the role of trait variation in shaping future species ranges.

2 | MATERIAL AND METHODS

We calibrated two types of linear mixed-effect models using a combination of trait measurements from common gardens where seeds with different origins have been planted (provenances) and of environmental variables that we obtained for these common gardens and provenances. The first model type (one-trait models) used single traits as response variables and environmental data as explanatory variables. The second model type (two-trait models) added a second trait as a covariate, which allowed the interaction of both traits to be accounted for in the model. Finally, to quantitatively estimate the contribution of each trait to explain beech's range, we performed a binomial model using the occurrence of the species as the response variable (presence/absence) and the spatial predictions of all traits as explanatory variables.

2.1 | Trait measurements

We analysed total tree height (vertical growth), diameter at breast height (DBH; radial growth), young tree survival and flushing phenology measured on a total of 153,711 individual beech trees that originated from seeds collected from 205 populations (hereafter referred to as "provenances") across Europe and planted at 38 common gardens (hereafter "trials") (Figure 1). Briefly, the seeds were germinated in greenhouses and planted in the trials at an age of 2 years. Planting was carried out in two consecutive campaigns, the first campaign (comprising 14 trials) in 1995 and the second one (comprising 24 trials) in 1998 (Robson et al., 2018). This experimental design allowed us to attribute the effect of the climate at the



	VG	RG	YTS	LF	VG-RG	VG-LF
Measurements	203 105	34 237	41 309	7 863	34 237	12 087
Trees	108 415	31 339	37 433	7 863	31 339	10 634
Trials	36	19	7	7	19	6
Provenances	205	186	114	62	186	150
Age	2 to 15	8 to 15	2 to 6	12	8 to 15	6, 9, 11, 12, 15

FIGURE 1 Map: Distribution range of *Fagus sylvatica* L. (shaded in beige) and location of the provenances and trials by trait. Circles indicate the locations of the provenances and triangles those of the trials. Different colours have been employed to indicate the different traits (VG = vertical growth; RG = radial growth; YTS = young tree survival; LF = leaf flushing). Table: The extent of data from the BeechCOSTe52 database (Robson et al., 2018) used for modelling. Measurements = total number of measurements; Trees = total number of individual trees; Trials = total number of trials; Provenances = total number of provenances, Age = the age at which the trees were measured. Columns indicate sample sizes for the traits used in the one-trait models and in the two-trait models

trials to phenotypic plasticity and the effect of the climate at the provenance origin to genetics, including both the genetic structure and adaptive potential of the provenances. Young tree survival was recorded as individual tree survival. Leaf flushing was transformed from observational-stage score data (qualitative measurements that slightly differ among trials) to Julian days by adjusting flushing stages for each tree in every trial using the Weibull function (Robson et al., 2011, 2013).

2.2 | Environmental data

We used the EuMedClim database that gathers climatic information from 1901 to 2014 gridded at 1 km (Fréjaville & Benito Garzón, 2018). The climate of the provenances was averaged for the period from 1901 to 1990, with the rationale that the seeds planted in the common gardens stemmed from trees growing during that period (Leites, Robinson, Rehfeldt, Marshall, & Crookston, 2012). To characterize the climate of the common gardens, we calculated average values for the period between the date of planting (either 1995 or 1998) and the year of measurement of each trait for 21 climate variables (Supporting Information Appendix S1: Table S1.2). In addition, we used the latitude and longitude of the provenance and of the trial as proxies for the photoperiod and continentality, respectively (used in our flushing phenology models).

Phenotypic predictions under future climates were performed using the representative concentration pathway (RCP 8.5) in GISS-E2-R from WorldClim (http://www.worldclim.org/cmip5_30s) for 2070. 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.

2.3 | Statistical analysis

2.3.1 | Spatial autocorrelation analysis

We performed a Moran's *I* analysis to check for spatial autocorrelation of vertical and radial growth, young tree survival and leaf flushing. Correlograms were used to check autocorrelation variation with distance. We used the Moran.I function of the "ape" package (Paradis et al., 2018) and the "Correlog" function of the "pgirmess" package (Giraudoux, Antonietti, Beale, Pleydell, & Treglia, 2018).

2.3.2 | Environmental variable selection

To avoid collinearity and reduce the number of environmental variables to use in models, we performed two principal component analyses (PCAs), one for the climate variables related to the provenance site and one for the climate variables related to the trial site. For tree height, DBH and young tree survival, we considered 21 variables for the provenance and 21 variables for the trial (Supporting Information Appendix S1: Figure S1.3); whereas for leaf flushing, we only included the temperature-related variables as well as latitude and longitude (a total of 20 variables), because leaf flushing is known to be mainly driven by them (Basler & Körner, 2014).

The retained variables after the PCA screening were combined in models containing one variable to characterize the climate of the provenance and one variable to characterize the climate of the trial (Supporting Information Appendix S1: Table S1.3).

2.3.3 | One-trait and two-trait mixed-effect models

We used linear mixed-effect models to analyse the response of individual traits (one-trait models) and the covariation between two traits (two-trait models) to climate. We included the climate at the provenance and the trial site as previously selected (Supporting Information Appendix S1: Table S1.3), the age of trees, and for the leaf flushing model also latitude and longitude as fixed effects. The trial, blocks nested within the trial and trees nested within block and trial were included as random effects to control for differences among sites and for repeated measurements of the same trees. The random effect of the provenance was also included in the model. The common form of the one-trait model was:

$$
\begin{aligned}
\log\left(\mathrm{TR}_{ijk}\right) = {} & \alpha_0 + \alpha_1\left(\mathrm{Age}_{ik}\right) + \alpha_2\left(\mathrm{CP}_{ij}\right) + \alpha_3\left(\mathrm{CT}_{ik}\right) + \alpha_4\left(\mathrm{CP}_{ij}^2\right) \\
& + \alpha_5\left(\mathrm{CT}_{ik}^2\right) + \alpha_6\left(\mathrm{Age}_{ik} \times \mathrm{CP}_{ij}\right) \\
& + \alpha_7\left(\mathrm{Age}_{ik} \times \mathrm{CT}_{ik}\right) + \alpha_8\left(\mathrm{CP}_{ij} \times \mathrm{CT}_{ik}\right) + \beta + \varepsilon
\end{aligned}
\tag{1}
$$

Where TR = trait response of the *i*th individual of the *j*th provenance in the *k*th trial; Age = tree age of the *i*th individual in the *k*th trial; CP = climate at the provenance site of the *i*th individual of the *j*th provenance; CT = climate at the trial site 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: Age and CP, Age and CT, and CP and CT.

We analysed trait covariation across the species' range by adding two specific traits of interest in the same model. The common form of the two-trait model was:

$$
\begin{aligned}
\log\left(\mathrm{TR}_{ijk}\right) = {} & \alpha_0 + \alpha_1\left(\mathrm{Age}_{ik}\right) + \alpha_2\left(\mathrm{Cov}_{ij}\right) + \alpha_3\left(\mathrm{CP}_{ij}\right) \\
& + \alpha_4\left(\mathrm{CT}_{ik}\right) + \alpha_5\left(\mathrm{Cov}_{ik} \times \mathrm{CP}_{ij}\right) + \alpha_6\left(\mathrm{Cov}_{ik} \times \mathrm{CT}_{ik}\right) + \alpha_7\left(\mathrm{Cov}_{ik} \times \mathrm{Age}_{ik}\right) \\
& + \alpha_8\left(\mathrm{Age}_{ik} \times \mathrm{CP}_{ij}\right) + \alpha_9\left(\mathrm{Age}_{ik} \times \mathrm{CT}_{ik}\right) + \alpha_{10}\left(\mathrm{CP}_{ij} \times \mathrm{CT}_{ik}\right) + \beta + \varepsilon
\end{aligned}
\tag{2}
$$

where TR = trait response of the *i*th individual of the *j*th provenance in the *k*th trial; Age = tree age of the *i*th individual in the *k*th trial; Cov = trait covariate of the *i*th individual in the *k*th trial; CP = climate at the provenance site of the *i*th individual of the *j*th provenance; CT = climate at the trial site 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: Cov and CP, Cov and CT, Cov and Age, Age and CP, Age and CT, and CP and CT.

The one-trait and two-trait models for vertical and radial growth and leaf flushing were fitted with the "lmer" function, while the one-trait model for young tree survival was fitted with the "glmer" function to accommodate logistic regressions (binomial family) in the analysis. We implemented a stepwise-model procedure with four main steps to choose the best supported model (Akaike, 1992): (a) we fitted saturated models that included all the variables in the fixed part of the model; (b) we chose the optimal random component of the model by comparing the battery of models using restricted maximum likelihood (REML), and selected the best model using the Akaike information criterion (AIC) with criteria ΔAIC < 2 (Mazerolle, 2006); (c) we compared the battery of models using maximum likelihood (ML) and selected the optimal fixed component using the AIC criterion; (c) we combined the best optimal random and fixed component previously selected and adjusted them using REML to obtain the best performing model. All model fits were done using the package "lme4" (Bates et al., 2018).

For the best supported models, we visually analysed the interactions of vertical growth, radial growth, young tree survival and leaf flushing with the environment (one-trait models) and between traits (between the response and covariate variable, i.e., the two-trait models). To do so, tree age was fixed to 12 years for the radial and vertical growth and leaf flushing models and to 6 years for the young tree survival model. Mathematical interactions in one-trait models (CP × CT in Equation 1) represent the differences in trait values that can be attributed to the provenance (interpretable as local adaptation) and those that can be attributed to the trial (interpretable as phenotypic plasticity). Mathematical interactions in two-trait models (Cov × CT in Equation 2) represent the differences in trait values that can be attributed to a second trait that covaries across the species' range with the first trait, mediated by the climate of the trial (representing phenotypic plasticity). Unfortunately, young tree survival could not be included in the two-trait models because there were insufficient measurements shared with other traits in the same trials.

We estimated the percentage of the variance explained by the model attributed to the fixed effects alone (marginal R^2) and attributed to the fixed and random effects together (conditional R^2). We measured the generalization capacity (Pearson correlation) of the model using cross-validation (64% of the data used for calibration and the remaining 34% for validation).

2.3.4 | Spatial predictions

We made spatial predictions for each trait across the species' range for current and future climatic conditions using the "raster" package (Hijmans et al., 2017). For the prediction of current and future trait variation, the climate variable for provenance was represented by the average climate over the period from 1901 to 1990. The climate of the trial was set as the average climate from 2000 to 2014, for current trait predictions, and to 2070 for future predictions. For two-trait models, the predicted values of the covariate (DBH and leaf flushing) in the present were used to estimate the predictions of vertical growth in the future. We calculated the spatial difference between the future and the current conditions (future values minus current values) to illustrate the amount of change that traits can accommodate. All spatial predictions of traits were delimited within the distribution range of the species (EUFORGEN, 2009).

2.3.5 | Quantification of the trait contribution to delimit the range of beech

Following the rationale that fitness-related, demographic and functional traits can shape species ranges (Merow et al., 2017; Stahl et al., 2014), we regressed the occurrence (presence/absence) of the species (EUFORGEN, 2009) against the trait values obtained by the one-trait models using the "glm" function to accommodate logistic regressions (binomial family). The equation takes the form:

$$\begin{aligned}(\mathrm{RV}) = {} & \alpha_0 + \alpha_1\,(\mathrm{Vg}) + \alpha_2\,(\mathrm{Rg}) + \alpha_3\,(\mathrm{S}) + \alpha_4\,(\mathrm{Lf}) \\ & + \alpha_5\,(\mathrm{Vg}\times\mathrm{S}) + \alpha_6\,(\mathrm{Rg}\times\mathrm{S}) + \alpha_7\,(\mathrm{Lf}\times\mathrm{S}) \\ & + \alpha_8\,(\mathrm{Vg}\times\mathrm{Rg}) + \alpha_9\,(\mathrm{Vg}\times\mathrm{Lf}) + \alpha_{10}\,(\mathrm{Rg}\times\mathrm{Lf}) + \varepsilon\end{aligned} \tag{3}$$

where RV = presence/absence of beech; Vg = vertical growth; Rg = radial growth; S = young tree survival; Lf = leaf flushing; ε = residuals. In addition, the model included all possible pairwise linear interactions of the included traits. The total deviance explained by the model was calculated using the function "Dsquared" of the package "modEvA" (Barbosa, Brown, & Real, 2014). Then, we performed an analysis of variance (ANOVA) of the model to obtain trait and trait interaction deviances to estimate the percentage of the variance attributable to each trait.

All the models were performed with the R statistical framework version 3.2.0 (R Development Core Team, 2015).

3 | RESULTS

3.1 | Spatial autocorrelation analysis

Overall, the four studied traits were not significantly autocorrelated (Supporting Information Appendix S1: Table S1.1), although one autocorrelation point was found for young tree survival and leaf flushing using distance correlograms (Supporting Information Appendix S1: Figure S1.1).

3.2 | Environmental variable selection

The two PCAs performed (provenance PCA and trial PCA) revealed two groups of variables, one related to temperature and another more related to precipitation (Supporting Information Appendix S1: Figure S1.2). The two most important axes of the provenance PCA explained 53.52 and 24.03% of the total variance, and those of the trial PCA explained 38.93 and 24.19% (Supporting Information Appendix S1: Figure S1.2). To avoid collinearity in the variables that we used in the model stepwise procedure, we retained the following variables for tree growth and young tree survival: annual mean temperature (BIO1), maximal temperature of the warmest month (BIO5), minimal temperature of the coldest month (BIO6), annual precipitation (BIO12), precipitation of the wettest month (BIO13), precipitation of the driest month (BIO14), annual potential evapotranspiration (PET Mean) and maximal monthly potential evapotranspiration (PET Max). For the leaf flushing models, we retained BIO1, BIO5, BIO6, mean temperature of December, January and February (MTdjf), mean temperature of

TABLE 1 Summary of the variables included in the final best supported models (one- and two-trait) for each trait analysed

		One-trait models				Two-trait models	
		Height	DBH	Young tree survival	Leaf flushing	H-DBH	H-Lf
Variables	Environment of the provenance	PET Max	PET Max	PET Max	MTdjf Latitude	PET Max	PET Max
	Environment of the trial	BIO13	BIO12	BIO14	MTdjf Latitude Longitude	BIO13	BIO13
	Covariate					DBH	Lf

Note: Environmental variables selected for the provenances and the trials for the one-trait models (height, DBH, young tree survival and flushing models), and for the two-trait models (height-DBH and height-leaf flushing models). H = height; DBH = diameter at breast height; Lf = leaf flushing; PET Max = maximal monthly potential evapotranspiration; BIO12 = annual precipitation; BIO13 = precipitation of wettest month; BIO14 = precipitation of driest month; MTdjf = mean temperature of December, January and February; Covariate = trait covariate.

March, April and May (MTmam), mean temperature of June, July and August (MTjja), mean temperature of September, October and November (Mtson) and mean temperature of December, January, February, March, April and May (Mtdjfmam) in addition to latitude and longitude.

3.3 | One-trait and two-trait models

According to the best supported models (Table 1 and Supporting Information Appendix S1: Table S1.3), the most important variable related to the climate at the provenance for vertical growth, radial growth and young tree survival was maximal potential evapotranspiration (PET Max). The most important variables related to climate at the trials were precipitation of the wettest month (BIO13) for vertical growth, annual precipitation (BIO12) for radial growth, and precipitation of the driest month (BIO14) for young tree survival. In the case of leaf flushing, the mean temperature of December, January and February (MTdjf) was the most important climate variable for both the provenance and the trial site. The latitude of the provenance and the trial and the longitude of the trial were also significant in the leaf flushing model (see Supporting Information Appendix S1: Tables S1.3, S1.4 for detailed statistics on the models). We observed significant interactions between the climate of the trial and that of the provenance in all models (Table 1; Supporting Information Appendix S1: Table S1.4).

The capacity for generalization from the models (Pearson correlation coefficients) was high: between .53 for radial growth and .73 for leaf flushing. The marginal R^2 ranged from 18% for the young tree survival model to 57% for the vertical growth model, while the conditional R^2 ranged from 40% for the young tree survival model to 98% for the radial growth model (Supporting Information Appendix S1: Table S1.4).

The significance of the fixed and random effects in the one-trait models was positively affected (i.e., estimates were higher) by the addition of a second trait (Supporting Information Appendix S1: Table S1.5). Furthermore, the covariates and their interactions with the climate variables of the trials were also significant in the two-trait models (Supporting Information Appendix S1: Table S1.5). The capacity to generalize from the two-trait models was high: 0.76 for the vertical growth-radial growth model and 0.77 for the vertical growth-leaf flushing model (Supporting Information Appendix S1: Table S1.5). The marginal R^2 was 62% in the vertical growth-radial growth model and 47% in the vertical growth-leaf flushing model, while the conditional R^2 was 95% in the vertical growth-radial growth model and 99% in the vertical growth-leaf flushing model (Supporting Information Appendix S1: Table S1.5).

3.4 | Spatial patterns of phenotypic trait variation from one-trait models

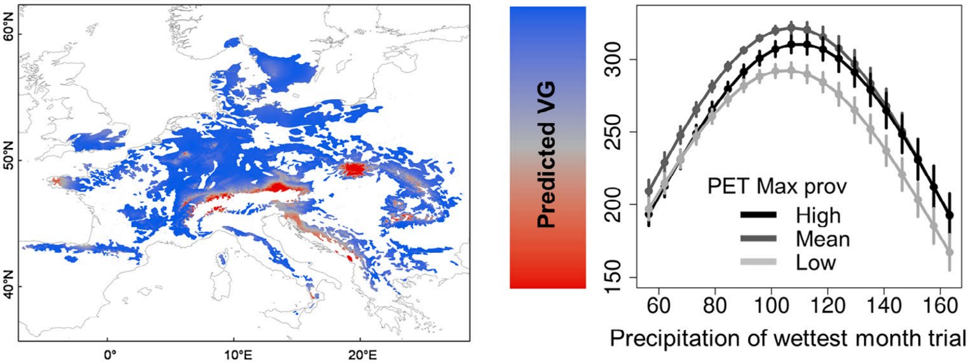
Spatial predictions showed differences in phenotypic trait variation among traits (Figure 2, maps) and the interaction graphs permitted the way that plasticity and local adaptation shape these differences to be visualized (Figure 2, interaction graphs).

Vertical growth reached its maximum value at intermediate values of precipitation of the wettest month in the trials (Figure 2a, interaction graph). These largest trees were predicted to occur mostly over the northern and western part of the species' range (Figure 2a, map). A signal of local adaptation to PET max was detected in our models and is shown by the interaction graph, where each line represents the response of provenances to high, intermediate and low levels of maximal potential evapotranspiration.

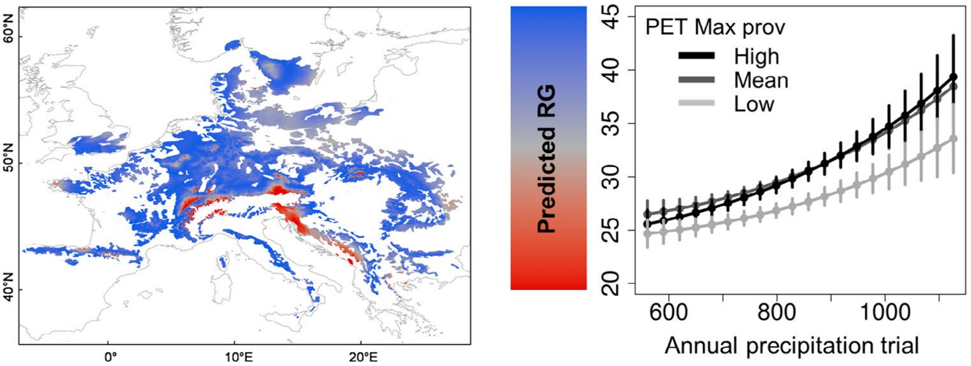
Predicted radial growth across the species' range presented a similar pattern to that of vertical growth, but with the lowest values in marginal populations, particularly at the southern margin (Figure 2b, map). High annual precipitation coincided with high growth rates (Figure 2b map), with a moderate signal of local adaptation to PET max in the form of some variation among provenances (Figure 2b, interaction graph).

The lowest young tree survival rates were predicted towards the east and at some isolated points in the southernmost part of the range (Figure 2c, map). Young tree survival increased towards those trials where precipitation is high in the driest month, with weak local adaptation to PET max indicated by very small—although statistically

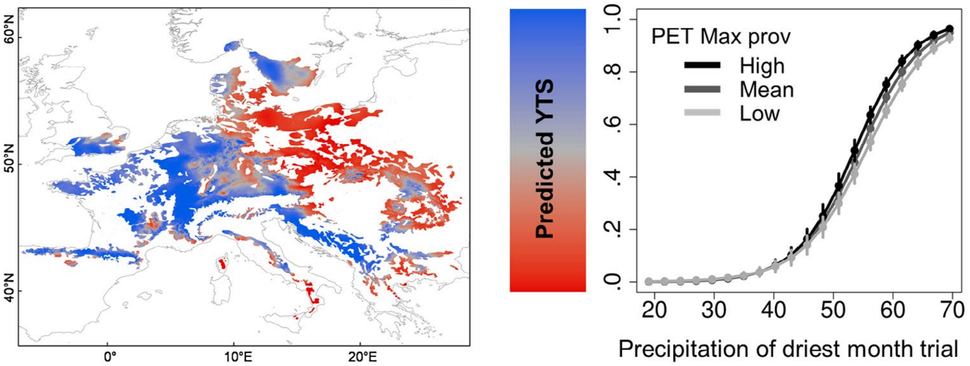
(a) Vertical growth



(b) Radial growth



(c) Young tree survival



(d) Leaf flushing

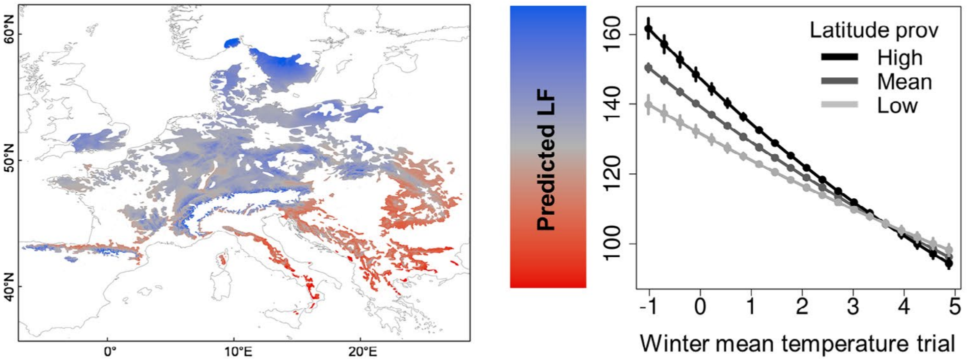


FIGURE 2 Spatial projections for (a) vertical growth (cm), (b) radial growth (mm), (c) young tree survival (probability) and (d) leaf flushing (Julian days) generated using one-trait models (maps on the left), and corresponding graphs of interactions between the best environmental predictor variable across the trials divided according to environment at the provenance for each of the four traits (graphs on the right). Interactions represent the differences in trait values that can be attributed to the provenance [interpretable as local adaptation driven by maximal potential evapotranspiration (PET max) in (a), (b) and (c) and driven by the latitude in (d)]. Interactions also represent the differences in trait values that can be attributed to the environmental conditions of the trial (interpretable as phenotypic plasticity driven by the environmental variables shown on the *x* axis). Black, dark grey and light grey lines represent high, medium and low values of the climatic variable of the provenances, respectively (as opposed to those of the trial, indicated on the *x* axis). The vertical lines represent the confidence intervals. The maps display the trait projection for contemporary climate (inferred from 2000–2014 meteorological data) across the current species' range. The colour gradient depicts the clinal variation from low (red) to high (blue) values of each trait. The values of the different traits are represented in the following way: vertical growth (cm), radial growth (mm), probability of young tree survival (0 = dead, 1 = alive) and leaf flushing (Julian days). PET max prov = maximal monthly potential evapotranspiration at the provenance; Latitude prov = latitude of the provenance; VG = vertical growth; RG = radial growth; YTS = young tree survival; LF = leaf flushing.

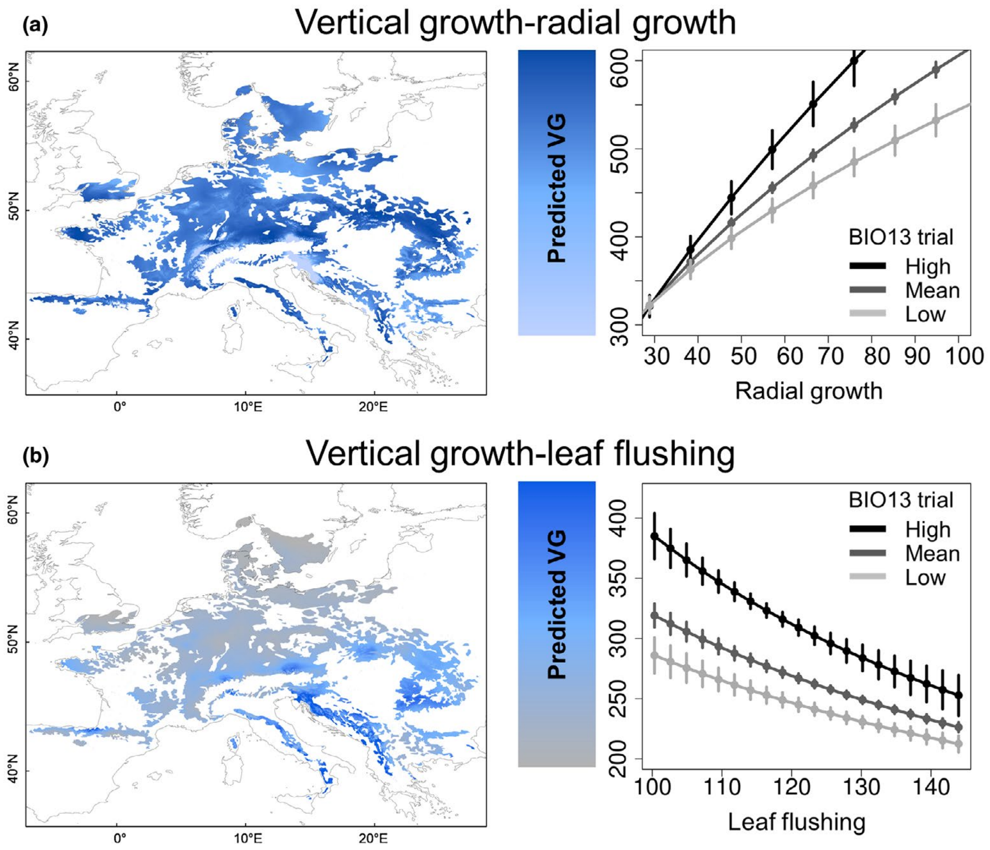


FIGURE 3 Spatial projections of vertical growth (cm) for (a) vertical-radial growth model and (b) vertical growth-leaf flushing models (maps on the left), and the corresponding graphs of covariation between vertical growth and the covariate: (a) diameter at breast height (DBH; mm) and (b) leaf flushing (Julian days). Black, dark grey and light grey lines represent high, medium and low values of the precipitation of the wettest month of the trial, respectively (BIO13). The vertical lines represent the confidence intervals. The maps display the trait projection for contemporary climate (inferred from 2000–2014 meteorological data) across the current species' range. The colour gradient depicts the clinal variation in vertical growth from 200 cm (grey) to 600 cm (blue). VG = vertical growth

significant—differences among provenances (Figure 2c, interaction graph).

Earlier flushing was predicted towards the south-eastern part of the range (Figure 1d, map), with notable local adaptation indicated by large differences among provenances depending on the latitude of origin (Figure 2d, interaction graph). Differences in flushing date among provenances were particularly large in trials where the winter temperature is low (Figure 2d, interaction graph).

3.5 | Patterns of phenotypic trait variation from two-trait models

Overall, models with a second trait as covariate produced different results to those considering a single trait only. Predicted vertical growth was higher when either radial growth (Figure 3a) or leaf flushing (Figure 3b) was included as a covariate than when no covariates were considered (Figure 2a). Vertical growth increased

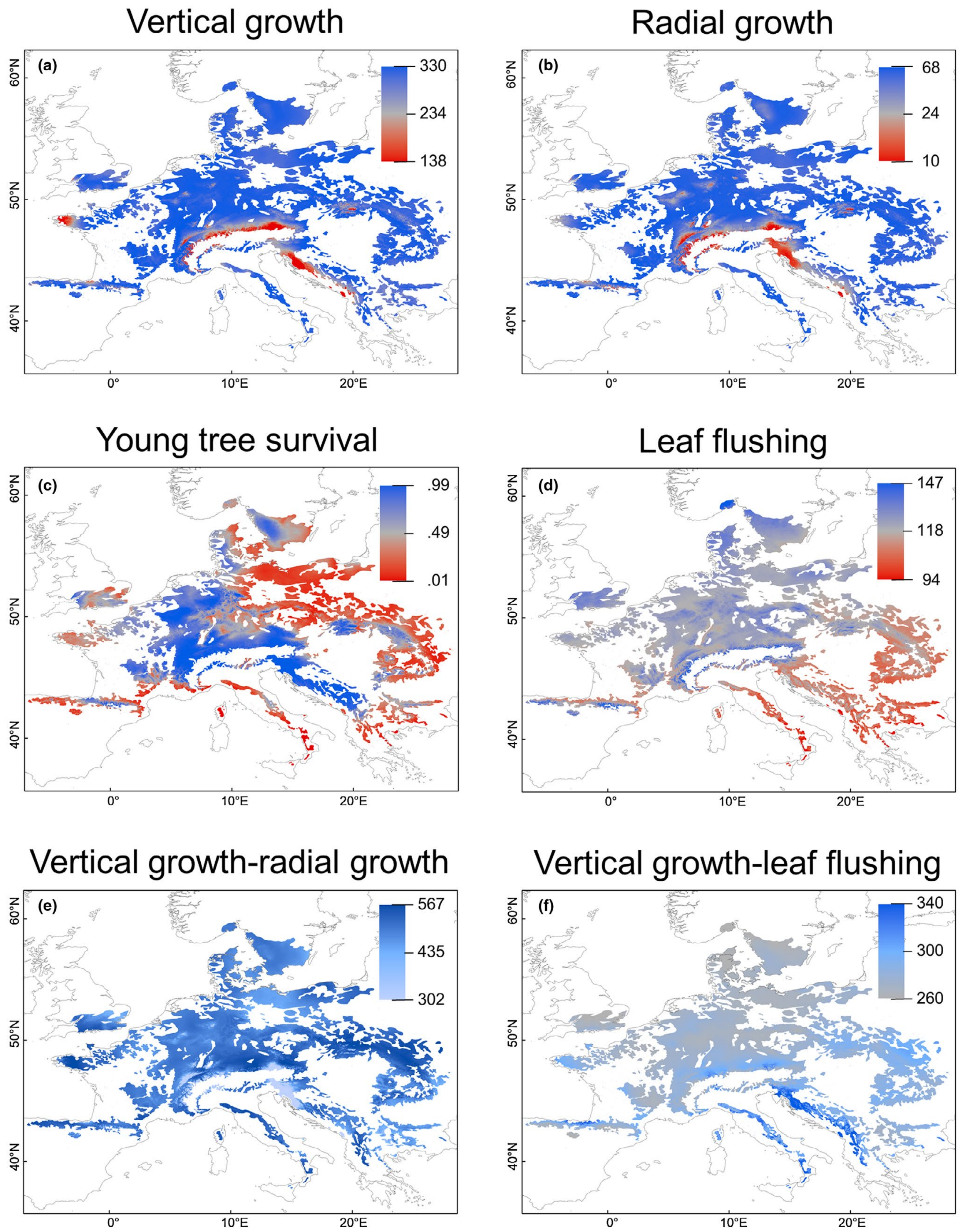


FIGURE 4 Spatial predictions for 2070 [representative concentration pathway (RCP 8.5)] across the species' range for one-trait models: (a) vertical growth (cm); (b) radial growth (mm); (c) probability of young tree survival (0 = dead; 1 = alive); (d) leaf flushing (Julian days); and for two-trait models: (e) vertical growth (cm; covariate radial growth) and (f) vertical growth (cm; covariate leaf flushing). The colour gradients depict the clinal variation from low (red) to high (blue) values

with radial growth and precipitation (Figure 3a) and decreased in those regions where leaf flushing was predicted to be late in the year (which corresponded mainly to the northern part of the range) (Figure 3b).

3.6 | Spatial predictions of traits under climate change considering one- and two-trait models

Trait projections for 2070 showed an overall increase in tree growth, particularly for radial growth (Figure 4a, b), but following similar spatial patterns to those predicted under current conditions (Figure 2a, b). Young tree survival was predicted to strongly decrease (with respect to that predicted under current conditions, Figure 2c) in the east and throughout the range periphery, while young tree survival rates remained higher in the central part (Figure 4c). Leaf flushing showed similar patterns to those predicted under current conditions (Figure 2d) but with an overall advance in flushing dates (Figure 4d).

The prediction of vertical growth, considering radial growth as a covariate, showed an overall increase across the distribution range (Figure 4e) with respect to the model projection of vertical growth without radial growth as a covariate under future conditions (Figure 4a). Nevertheless, the predictions of vertical growth considering radial growth as a covariate (Figure 4e) showed an overall decrease in vertical growth, with some increases in vertical growth in the northern and north-eastern parts of the range, compared to the same model applied to current conditions (Figure 3a; Supporting Information Appendix S1: Figure S1.3e). Predictions considering leaf flushing as a covariate tended to constrain vertical growth throughout the range (Figure 4f) compared with the same model in current conditions (Figure 3b).

3.7 | Total trait contribution to explain the species range

All traits and their interactions significantly contributed to explaining the species' occurrence (Table 2). The model explained 31% of the total deviance, with vertical growth accounting for 37%, radial growth for 33%, young tree survival for 19% and leaf flushing for 1%. Please note that the different contributions of these four traits to explaining the species' occurrence may be constrained by the nature of the data (particularly survival that is only measured in young trees). The interaction between vertical growth and young tree survival contributed 3% to the total deviance, that between radial growth and leaf flushing 2% and the remaining interactions 1% or less (Table 2).

4 | DISCUSSION

4.1 | Contribution of phenotypic plasticity and local adaptation to range-wide variation in beech growth, young tree survival and leaf flushing

Altogether, our results indicate that range-wide variation in fitness-related traits of beech is driven markedly more by phenotypic plasticity than by local adaptation (Supporting Information Appendix S1: Table S1.4), as happens in other plant species (Benito Garzón et al., 2019), and they imply that beech possesses a noteworthy capacity to respond to rapid climate change through acclimation. Although a short-term response through acclimation can be considered as positive for beech to keep pace with climate change, our results point out that the plastic component of tree growth and young tree survival is mostly related to precipitation (Table 1), which follows highly unpredictable patterns (Pflug et al., 2018), making it difficult to evaluate whether acclimation will be enough for beeches to survive (our

TABLE 2 Summary statistics for a generalized linear model (binomial family) of beech occurrence (presence/absence) as a function of trait spatial predictions and their interactions

	Estimate	*SE*	*t*	*p*	DE
(Intercept)	−5.84	1.15e-02	−509.03	2.00E-16	
VG	5.45	1.64e-02	332.93	2.00E-16	0.37
RG	0.51	7.93e-03	64.67	2.00E-16	0.33
YTS	2.11	3.75e-03	562.83	2.00E-16	0.19
LF	3.12	1.48e-02	210.94	2.00E-16	0.01
VG × YTS	0.10	4.30e-03	21.08	2.00E-16	0.03
RG × YTS	−0.60	2.04e-03	−295.94	2.00E-16	0.01
YTS × LF	−1.40	4.02e-03	−348.1	2.00E-16	0.01
VG × RG	−1.11	4.62e-03	−240.58	2.00E-16	0.01
VG × LF	−7.81	2.15e-02	−363.18	2.00E-16	0.01
RG × LF	3.43	1.09e-02	313.89	2.00E-16	0.02
Model total deviance					0.31

Note: Estimate = coefficient of the regression shown on a logarithmic scale; *SE* = standard error of fixed variables; *t* = Wald statistical test that measures the point estimate divided by the estimate of its standard error, assuming a Gaussian distribution of observations; *p* = *p*-value; DE = deviance explained; VG = vertical growth; RG = radial growth; YTS = young tree survival; LF = leaf flushing.

predictions for 2070 under RCP 8.5 show an increase of mortality in young trees at the margins of the species' range, suggesting that acclimation will not be great enough to permit the species to survive, at least at the margins of its range—Figure 4c). Local adaptation in tree growth (vertical and radial) and young tree survival are driven by adaptation to maximal potential evapotranspiration (Table 1), suggesting that populations are responding to selection factors related to drought (Volaire, in press). This is in agreement with the general consensus that beech is a drought-sensitive species (Aranda et al., 2015), although there is ongoing debate over the extent of resistance that beech has to drought (Pflug et al., 2018).

The plastic response of leaf flushing to climate was mainly driven by winter temperatures (Table 1). There is a general consensus that winter temperatures will increase globally in the future (Vautard et al., 2014), and, accordingly, our projection for 2070 anticipates an advance in flushing through most of the range (Figures 2d, 3d and Supporting Information Figure S3d). However, leaf flushing can be constrained by local adaptation to photoperiod (Gauzere et al., 2017; Way & Montgomery, 2015). The fact that phenotypic plasticity and local adaptation in leaf flushing are driven by different environmental parameters implies that these two processes would interact in the long term. For instance, phenotypic plasticity concerning winter temperatures might enhance local adaptation towards new photoperiodical cues (i.e., shorter spring days), but the evolutionary timescale of local adaptation makes this interaction very unlikely in the short term.

4.2 | Trait relationships across the species range

Trait inter-dependence varied along geographical gradients as the two-trait models had higher predictive power and explained more variance than those based on a single trait (Supporting Information Appendix S1: Tables S1.4 and S1.5). The tight albeit not perfect positive interaction between tree vertical and radial growth (Figure 3a, interaction graph) is unsurprising because of allometric relationships between these two variables, particularly in a common-garden plantation that avoids competition among trees.

The biological basis of the observed covariation between vertical growth and leaf flushing is less obvious. One possible explanation is that vertical growth is greatly restricted by late flushing in northern beech populations (Kollas, Körner, & Randin, 2014). This would also explain our observation that the one-trait model predicts taller trees to occur in the north, whereas the two-trait model predicts just the opposite. Interestingly, the two-trait model thus implies that strong local adaptation of leaf flushing to photoperiod tends to constrain phenotypic plasticity for vertical growth in northern beech populations (Way & Montgomery, 2015).

4.3 | Are spatial patterns of growth, young tree survival and leaf flushing delimiting the range of beech?

Beech populations from certain eastern and southern parts of the distribution range seem most sensitive to climate, as suggested by the lowest values for all traits considered (Figure 2). In other parts of beech's range, different traits respond differently to climate, in line with the patterns found in annual plants and wood scrubs (Merow et al., 2017). Our analysis of the species' occurrence as a function of spatial trait values also suggests that each of these traits and their interactions contributed to some extent to the delimitation of the species' range (31% of the variance is explained by the four traits; Table 3). In particular: (a) young tree mortality delimits certain parts of the southern and eastern range of beech, reflecting the marginality due to climate continentality in these areas, and meaning that these populations are most threatened, thus making eastwards expansion of beech difficult (survival was exclusively measured in young trees,

TABLE 3 Summary statistics for a generalized linear model (binomial family) of beech occurrence (presence/absence) as a function of trait spatial predictions and their interactions

	Estimate	*SE*	*t*	*p*	DE
(Intercept)	−5.84	1.15e-02	−509.03	2.00E-16	
Vg	5.45	1.64e-02	332.93	2.00E-16	0.37
Rg	0.51	7.93e-03	64.67	2.00E-16	0.33
S	2.11	3.75e-03	562.83	2.00E-16	0.19
LF	3.12	1.48e-02	210.94	2.00E-16	0.01
VG × S	0.10	4.30e-03	21.08	2.00E-16	0.03
RG × S	−0.60	2.04e-03	−295.94	2.00E-16	0.01
S × LF	−1.40	4.02e-03	−348.1	2.00E-16	0.01
VG × RG	−1.11	4.62e-03	−240.58	2.00E-16	0.01
VG × LF	−7.81	2.15e-02	−363.18	2.00E-16	0.01
RG × LF	3.43	1.09e-02	313.89	2.00E-16	0.02
Model total deviance					0.31

Note: Estimate = coefficient of the regression shown on a logarithmic scale; *SE* = standard error of fixed variables; *t* = Wald statistical test that measures the point estimate divided by the estimate of its standard error, assuming a Gaussian distribution of observations; *p* = *p*-value; DE = deviance explained; VG = vertical growth; RG = radial growth; S = survival; LF = leaf flushing.

reflecting recruitment processes that are largely limited to climatically favourable years, indicating that more studies on regeneration and mortality are needed to confirm this result); this is the case for many species whose highest mortality is in the driest part of their range (Anderegg et al., 2015; Benito-Garzón et al., 2013; Camarero, Gazol, Sancho-Benages, & Sangüesa-Barreda, 2015); (b) the smallest girths are predicted in the southern part of the distribution and the eastern part of the range, suggesting that radial growth is mostly restricted by drought (interaction graph and map, Figure 2b), as has already been pointed out (Farahat & Linderholm, 2018); (c) with very little variation across climatic gradients, vertical growth alone will not delimit beech's range. This is not the case for other tree species in which tree height is clearly delimiting their range (Chakraborty, Schueler, Lexer, & Wang, 2018), highlighting the fact that no single best trait delimits tree species ranges; (d) projections of trees growing in southern and south-eastern regions that flush early also have higher mortality and lower growth predictions than elsewhere within the species' range. However, when tree height and leaf flushing are pooled together in the two-trait model, this leads to an decrease in vertical growth in the north; (e) it seems that in beech, and likely in other species with local adaptation to photoperiod, phenology could restrict the northern expansion of ranges (Duputié et al., 2015; Saltré, Duputié, Gaucherel, & Chuine, 2015). However, the link between phenology, young tree survival and fitness is still unclear, and more experiments would provide a better understanding the interaction between photoperiod and phenology.

4.4 | Implications of using trait approaches based on phenotypic variation to forecast beech sensitivity to climate change

Overall, spatial patterns of vertical and radial growth, young tree survival and leaf flushing predicted for the future (Figure 4) are relatively similar to those predicted by the models under current conditions (Figures 2 and 3). This might be due to the high plasticity of these traits that allows populations to respond to short-term changes in their environment, but other factors such as dispersal capacity, geographical or human barriers, and adjustment of climatic scenarios for the future would change our predictions. Our results, based on the study of phenotypic variation, predict the species' persistence in the future [if the occurrence of the species can be linked to high trait values (Merow et al., 2017)] rather than extinction and migration northwards as predicted by species distribution models based on the occurrence of the species (Kramer et al., 2010; Stojnic et al., 2018).

Nevertheless, the direct comparison of our trait predictions for current and future conditions allows us to detect some differences in their spatial patterns and total trait values (Supporting Information Appendix S1: Figure S1.3), and gives us a better understanding of the temporal dynamics of traits and their relative importance for beech persistence in the future. For instance, our models of leaf flushing predict reduced geographical variability in phenology in the future (from days 94 to 160—Figure 2d; and from days 94 to 147—Figure 4d), as has been reported worldwide (Ma, Huang, Hänninen, & Berninger, 2018). This is mostly explained by larger advances in the phenology of populations at colder sites than those at warmer sites, likely as a consequence of the larger increases in winter temperatures that happen in the north (Kjellström et al., 2018). Survival of young trees is predicted to decrease at the margins of the distribution, but less markedly than is predicted by species distribution models (Kramer et al., 2010; Stojnic et al., 2018). Although our spatial trait predictions do not perfectly match the species' occurrence, they explain the adaptive and plastic responses of populations' fitness-related traits to climate (Benito Garzón et al., 2019).

Including more than one trait related to growth likely reflects a conserved allometric relationship between vertical and radial growth in the future (Figure 4e), but this may be a direct consequence of the lack of competition among trees in our experimental design. Including phenology in two-trait models seems to be detrimental for vertical growth, at least for northern populations where growth is likely constrained by phenology (Figure 4f). However, our trait covariation approaches are limited to vertical growth as response variables, limiting our understanding of the interplay that other traits may have across the species' range in the future.

4.5 | Limitations, perspectives and future research

Although this study relied on the largest network of common gardens for a forest tree in Europe, the resulting inferences suffer from a number of limitations. Our models are based on a limited set of ages (from 2 to 15 years old). However, the expression of phenotypic plasticity changes with age (Mitchell & Bakker, 2014), which may restrict the scope of our results to those ages that we considered. This limitation is particularly pronounced for the case of survival (age range 2 to 6 years), for which data only reflect early recruit survival. Our models of young tree mortality may also reflect the quality of the data from common gardens, where recruit survival was measured over a short study period and did not necessarily faithfully capture the regeneration potential of forest tree populations.

Tree growth and phenology are directly related to fitness (Chuine, 2010; Delpierre et al., 2017; Younginger et al., 2017). However, other relevant proxies for tree fitness such as fecundity and reproduction have not been considered in our approach. In beech, climate warming tends to increase seed production in northern populations (Drobyshev et al., 2010) and to cause a decline in seedling density in southern ones (Barbeta, Peñuelas, Ogaya, & Jump, 2011), which would be expected to continue under climate change.

Our approach includes the plastic and adaptive components of traits to determine species ranges. Important elements of spatial ecology, such as geographical barriers and trees' dispersal capacity (Svenning & Skov, 2005), competition and other biotic interactions across large geographical gradients (Archambeau et al., 2019) and those aspects related to the uncertainty of future climate (Nazarenko et al., 2015), are not considered in our approach. Adding these processes to our models would open up a new perspective that would extend understanding of the realized niche of species ranges. The genetic effect attributed to the provenances in our models includes both the genetic structure and the potential of populations to adapt. As more genomic information on adaptive traits becomes available, models could incorporate the genomic basis of climate adaptation to help separate these different genetic effects (Bay et al., 2018).

Our predictions should help to shape future controlled experiments on those populations most sensitive to climate (in the south-east of the range), and others designed to test those trait relationships that are still unclear (phenology—growth—mortality) at the northernmost distribution edge. Although both for beech, and for tree species in general, plasticity is thought to help populations to persist under climate change (Benito Garzon et al. 2019), evolutionary processes can play an crucial role for annual plants and those organisms with short generation cycles, permitting them to adapt to new climate conditions (Fox et al., 2019; Scheepens et al., 2018). Both theoretical and empirical studies on the interplay between phenotypic plasticity and local adaptation across organisms with different life-history strategies are needed to fully understand how these two processes modify populations' responses to climate change.

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AUTHOR CONTRIBUTIONS

MBG and AH designed the study. HGE analysed the data with the help of NVM and MBG. TMB analysed the original data of leaf flushing. MBG and HGE wrote the first draft and all co-authors contributed to the writing of the final version of the manuscript.

DATA ACCESSIBILITY

All phenotypic data used in this study are available at https://zenodo.org/record/1240931#.XBuSa81CeUk (Robson et al., 2018). All the maps generated in this study are available from the authors.

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BIOSKETCH

The authors' research is focused on plant ecology and global change. The authors use multidisciplinary approaches including ecophysiology, genetics and ecological modelling to understand complex processes in ecology at large geographical scales.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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CHAPTER 2

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

Homero Gárate-Escamilla, Craig C. Brelsford, Arndt Hampe, T. Matthew Robson & Marta Benito Garzón. *Agricultural and Forest Meteorology*. Under review.

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 by BB and 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.

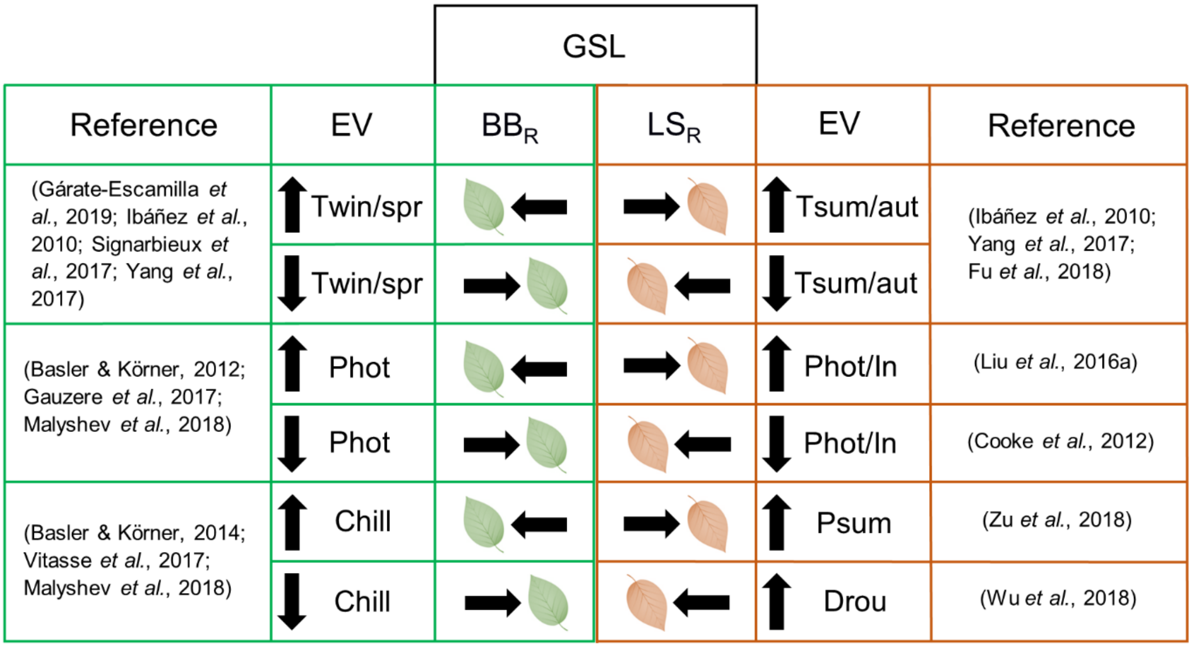
Key words: *Fagus sylvatica*, spring phenology, autumn phenology, environmental factors, provenance effect, climate change

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; sometimes coupled with photoperiod (Basler and Körner 2014; Fu et al. 2015) (Fig. 1). The major drivers of LS have been more difficult to identify (Gallinat et al. 2015; Brelsford et al. 2019). A recent meta-analysis showed that summer and autumn temperatures, precipitation and photoperiod can all affect LS (Gill et al. 2015). Generally, temperature tends to be predominant at lower latitudes

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



		GSL			
Reference	EV	BB_R	LS_R	EV	Reference
(Gárate-Escamilla *et al.*, 2019; Ibáñez *et al.*, 2010; Signarbieux *et al.*, 2017; Yang *et al.*, 2017)	↑ Twin/spr	🍃 ←	→ 🍂	↑ Tsum/aut	(Ibáñez *et al.*, 2010; Yang *et al.*, 2017; Fu *et al.*, 2018)
	↓ Twin/spr	→ 🍃	🍂 ←	↓ Tsum/aut	
(Basler & Körner, 2012; Gauzere *et al.*, 2017; Malyshev *et al.*, 2018)	↑ Phot	🍃 ←	→ 🍂	↑ Phot/In	(Liu *et al.*, 2016a)
	↓ Phot	→ 🍃	🍂 ←	↓ Phot/In	(Cooke *et al.*, 2012)
(Basler & Körner, 2014; Vitasse *et al.*, 2017; Malyshev *et al.*, 2018)	↑ Chill	🍃 ←	→ 🍂	↑ Psum	(Zu *et al.*, 2018)
	↓ Chill	→ 🍃	🍂 ←	↑ Drou	(Wu *et al.*, 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 color and green leaf: Reference, EV related to bud burst and BB_R; Orange color 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.

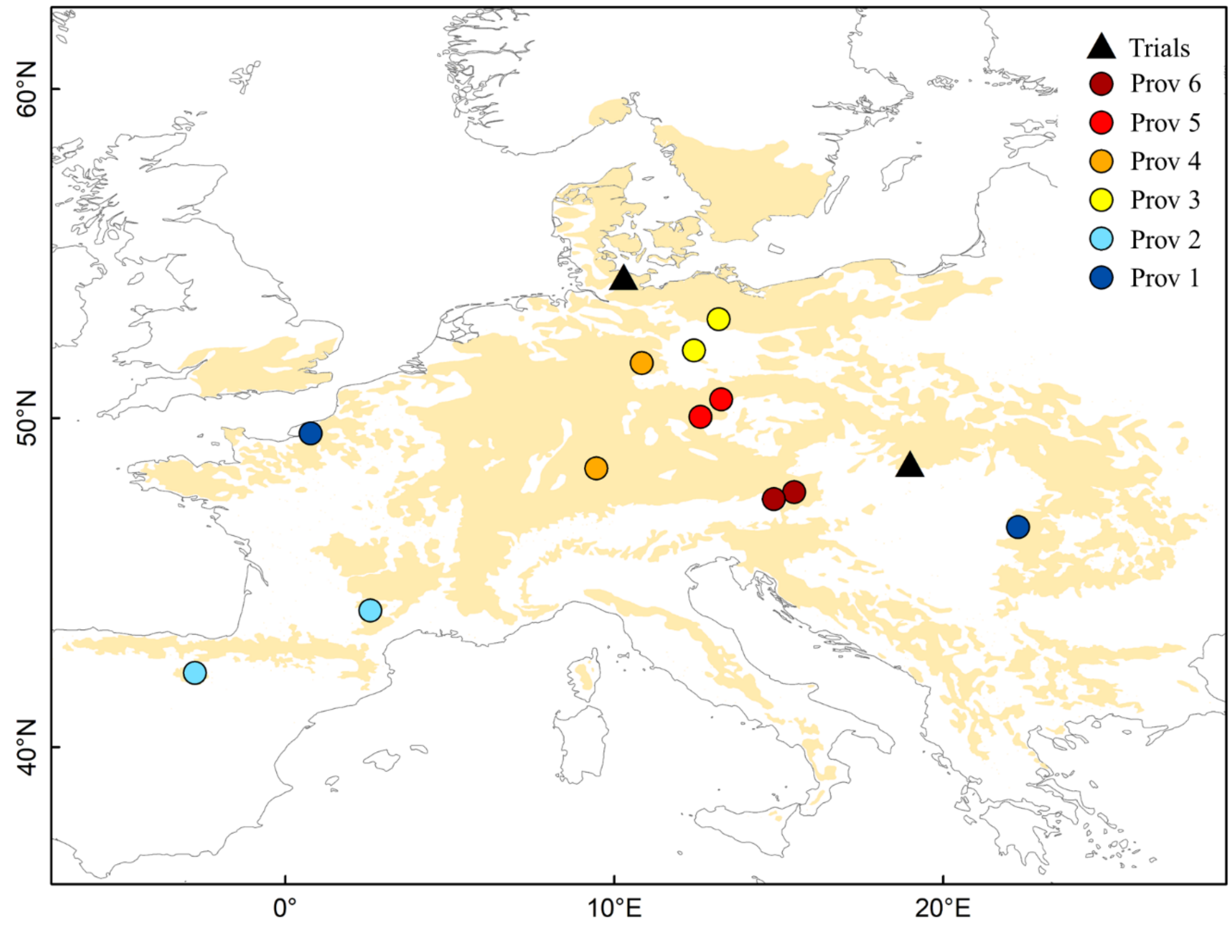
Fagus sylvatica L. (European beech, henceforth "beech") is one of the most dominant and widespread broadleaf forest trees in Europe (Preston and Hill 1997), and it is of high ecological and economic importance (Packham et al. 2012). In beech, BB responds to a combination of chilling and forcing temperature 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 populations, and by chilling requirements in warmer populations (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 color 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 populations (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 populations; (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 populations

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



Trial	Prov	Long	Lat	M	Trees	Age	BIO14	Ppet Min	P jja	TM jja	TM son	I jja	I son	r
Germany	**1**	15.47	47.75	99	76	12 & 13	62.74	39.08	145.31	10.96	2.94	4.77	2.34	0.99
Slovakia		14.85	47.53	199	124	11 & 12	66.97	45.39	159.62	11.37	3.32	4.77	2.34	
Germany	**2**	12.62	50.03	97	55	12 & 13	53.93	-15.57	96.22	13.09	5.00	4.44	1.87	0.99
Slovakia		13.25	50.57	94	66	11 & 12	50.19	-5.59	91.98	13.22	5.23	4.44	1.87	
Germany	**3**	10.83	51.67	109	94	12 & 13	55.73	-23.51	86.16	14.72	7.14	4.31	1.77	0.99
Slovakia		9.45	48.47	180	109	11 & 12	50.58	-20.54	105.49	15.42	7.56	5.00	2.21	
Germany	**4**	13.17	53.00	78	58	12 & 13	30.00	-58.73	64.89	16.96	8.67	4.29	1.67	0.99
Slovakia		12.42	52.05	116	81	11 & 12	31.85	-69.49	64.42	17.08	8.77	4.36	1.71	
Germany	**5**	-2.75	42.25	80	66	12 & 13	42.96	-140.38	47.96	16.83	9.56	5.83	3.02	0.99
Slovakia		2.58	44.15	79	52	11 & 12	52.14	-111.58	65.79	18.05	11.35	5.79	2.88	
Germany	**6**	22.27	46.68	73	57	12 & 13	39.27	-104.09	69.63	20.76	11.45	5.14	2.52	0.98
Slovakia		0.77	49.53	104	67	11 & 12	44.52	-86.53	50.84	16.97	11.04	5.04	2.09	

Figure 2. Map: Geographical distribution of beech populations (colored circles) and trials (triangles) underlying this study. Beige shading indicates the distribution range of beech. Each different color of circle indicates a pair of similar populations from each trail (the color gradient depicts the clinal variation from cold [blue] to warm [red] populations, as defined in Table S1). Table: Climatic and geographic data used for merging populations of similar origin for modeling purposes. As the populations were not shared between the two sites, we selected provenances of similar geographical origin (latitude and longitude) and climatic characteristics. Prov: number of the populations as shown in Figure 1; N: total number of trait measurements (including repeated measurements over years); Trees: total number of individual trees; Trial: trial where the trees were measured; Year M: year in which the trees were measured, BIO14: precipitation of driest month; Ppet Min: minimal annual water balance; P jja: precipitation of January, July and August; Tm JJA: mean temperature of January, July and August; Tm SON: mean temperature of September, October and November; Dim JJA: mean daily insolation of June, July and August; Dim SON: mean daily insolation of September, October and November; *r*: Pearson correlations per pair of populations accommodated under the same number.

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

We transformed the observational stages (phenophases), and score data (qualitative measurements) for BB and LS to Julian days by fitting the phenophases (Fig. 3 and S1; Table S1 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 hava changed color 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 population (genetic effects) from those of the trial (environmental effects), we used the average climate from 1901 to 1990 for each population 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 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). 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 populations (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 population effects. Our model allowed us to: (i) estimate the date of LS for each of the six pairs of populations; (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 population; 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 modeling 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 populations, with BB as a co-variable (Equation 1). Each model included one environmental variable from the population, one environmental variable from the trial site and BB as fixed effects. The trial, blocks nested within the trial, individual trees and populations 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} population in the k^{th} trial; EP = environmental variable that characterized the population site of the i^{th} individual of the j^{th} population; ET = environmental variable that characterized 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 × ET, EP × BB, and ET × BB. EP × ET, interactions represent differences in LS values that can be attributed to the interactions between genetic (population) and environmental (site) effects. EP × BB and ET × BB interactions represent the effects of the population 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 collinearly 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 using the AIC criterion; (iii) we retained the best environmental variable related to the population comparing the models that included one environmental variable from the population, 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 generalization 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 analyzed the significant interactions (EP × ET, EP × BB, ET × 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 populations showing early, mean and late BB. We also inspected gradients of GSL for the six populations by plotting GSL against the environmental variable of the trial selected in the model (ET) and population 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 populations, achieved using our BB model (Gárate-Escamilla et al. 2019), and plotted the predicted future GSL against ET, for each of the populations.

2.4.4 Spatial predictions

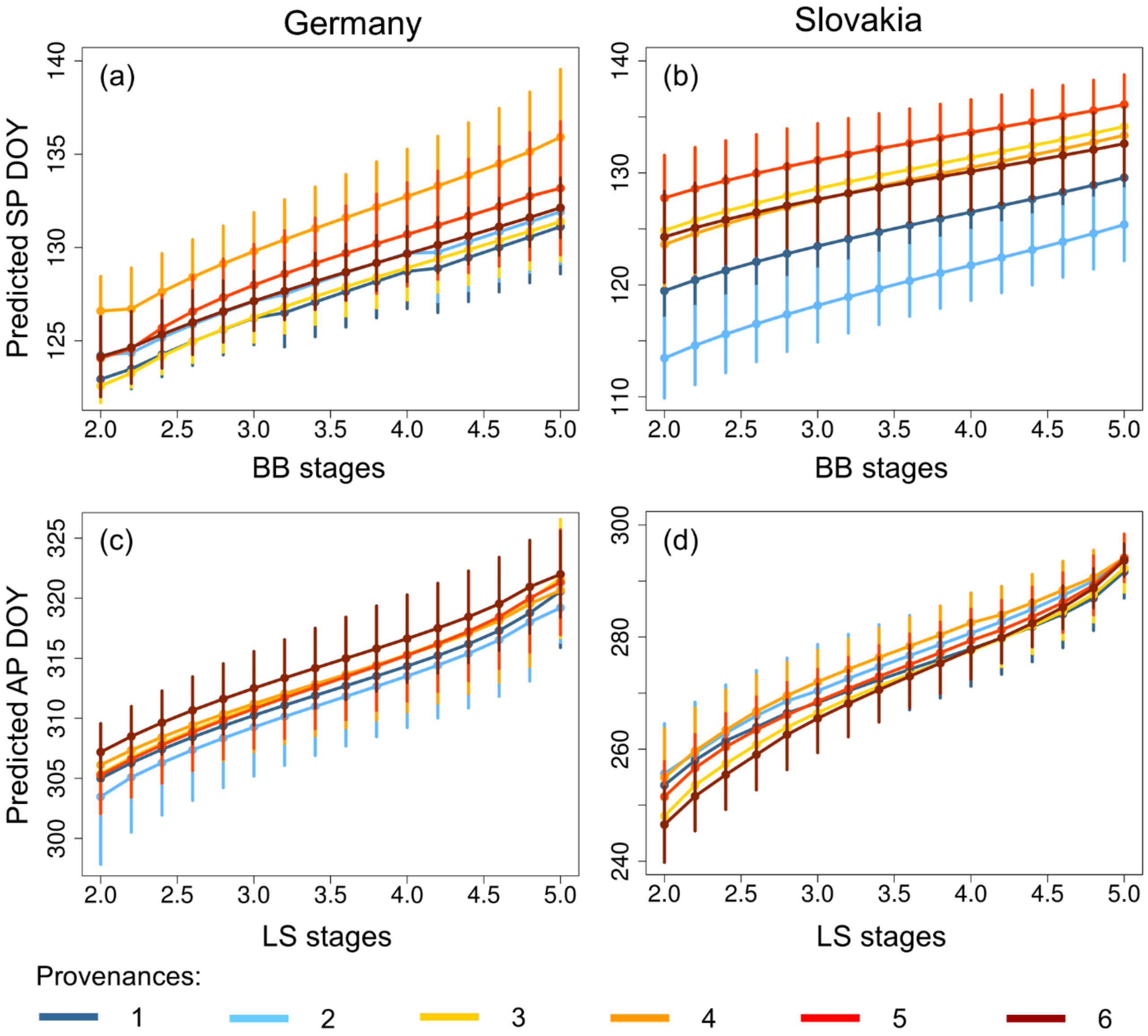
Spatial projections of LS were calculated using our LS model for current and future climatic conditions and predictions of BB were taken from Gárate Escamilla et al. (2019). Predictions of GSL were calculated by substracting the predicted BB from LS for both current and future climatic conditions across the species range. For the current and future predictions, the climate for populations 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 (predictions including exclusively the climatic range of the two trials, 7.5 to 10°C) and an extrapolated area (including 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 populations 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 bigger 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 population (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.

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. Population colors range from dark blue (cold origin) to dark red (warm origin) for the populations 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) population and trial variables were not correlated with each other; (ii) temperature (TmJJA and TmSON)- and precipitation (BIO14, PpetMin and PrecJJA)-related variables for the populations were correlated, whilst daily insolation (DIMJJA and DIMSON) variables for the populations were only correlated with the latitude (Lat) of the populations; (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 (DIMJJA and DIMSON) and temperature (TmJJA and TmSON)-related variables for the populations, 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 population, 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 population. 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).

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

3.3 Leaf senescence model

LS differed among the populations and between the two trials. These differences were explained by the Tm SON of the trial and population, as well as by BB (Table 1). Interactions between BB and Tm SON of the trial and population were also significant (Table 1). Late LS timing was related to higher Tm SON of the trial and populations (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 generalization from the model was $r = 0.92$ (Table 1).

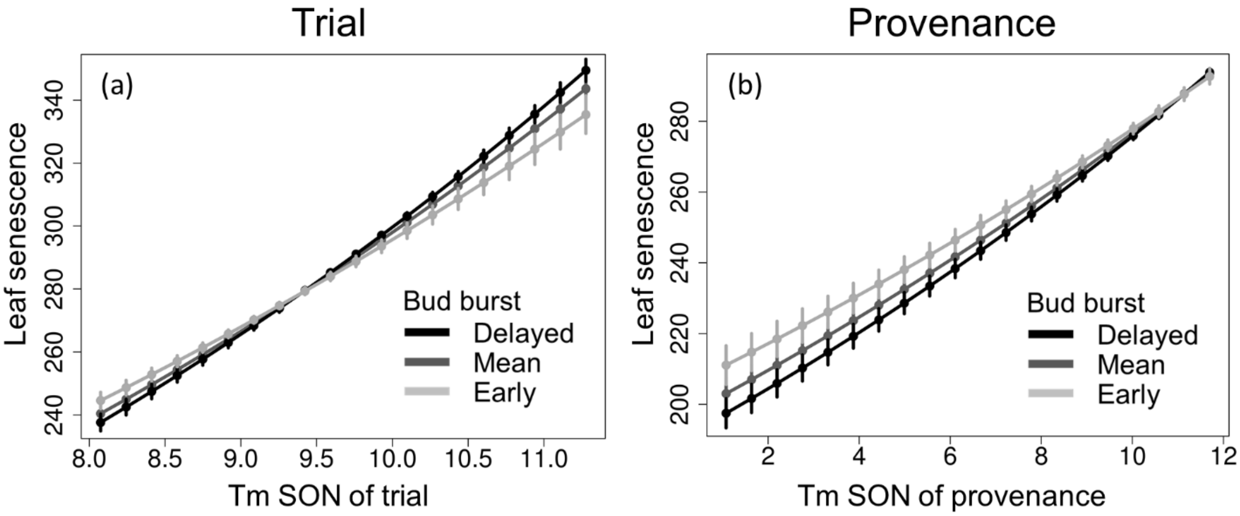


Figure 4. Interaction between leaf senescence and the mean temperature in September, October and November (Tm SON) for the trial (a) and for the population (b). Leaf senescence is given in Julian days, and Tm SON in °C. The black line represents delayed bud burst, the dark-gray mean bud-burst and the light-gray 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 populations (Fig. 5). The increase in GSL was greatest for cold populations (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 populations 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°) populations, 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).

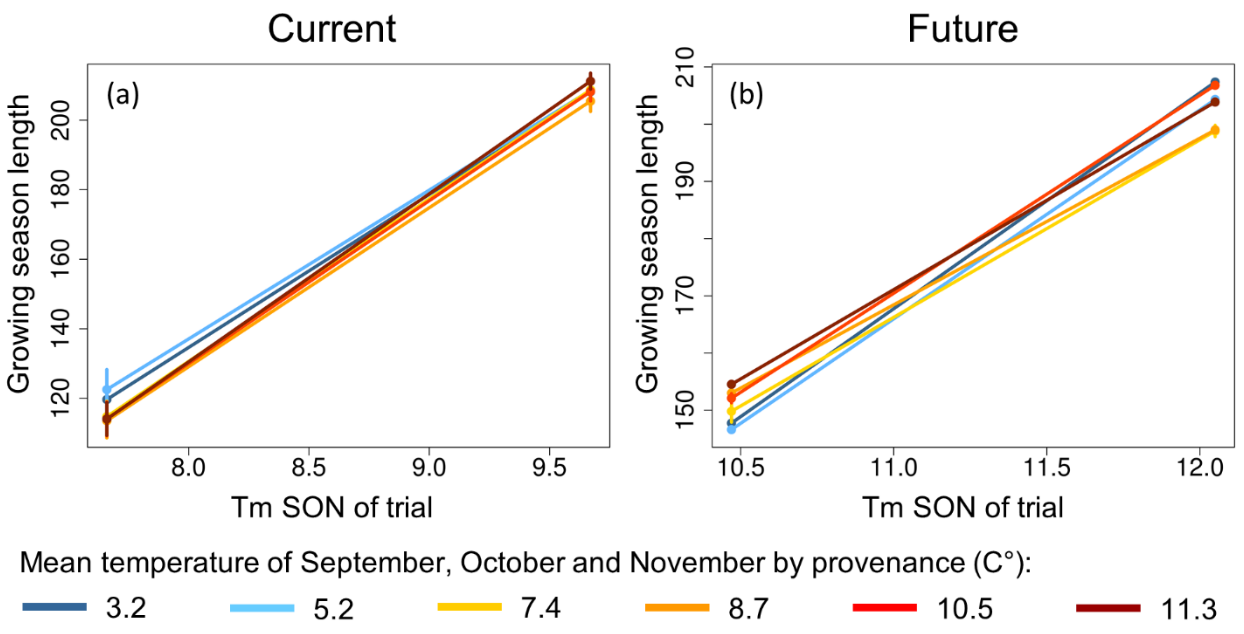


Figure 5. Interaction between growing season length and the mean temperature of September, October and November (Tm SON) of the trial, for (a) current climatic conditions (year of measurement minus year of plantation) and (b) the future climate scenario (RCP 8.5 for 2070). The color gradient depicts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

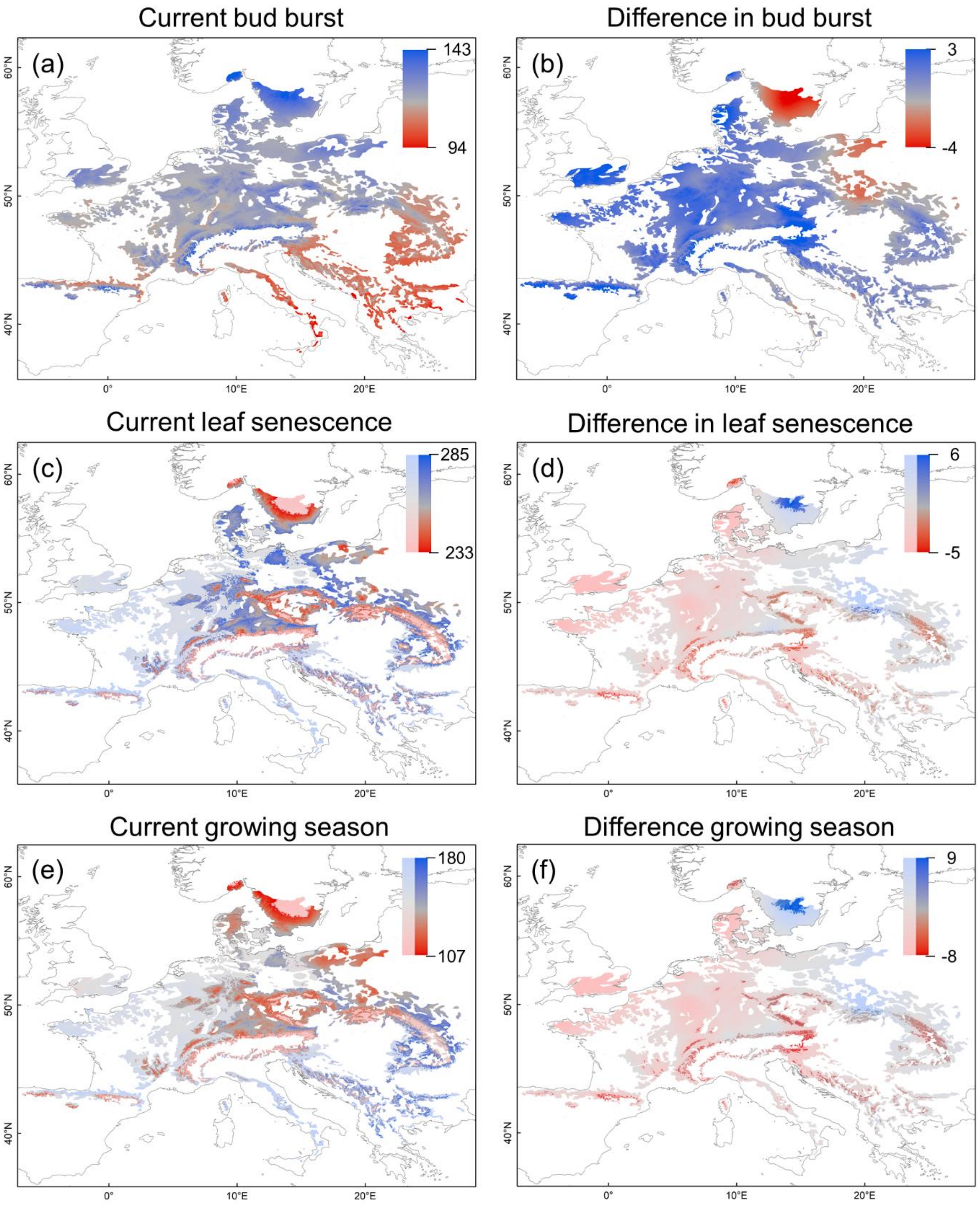

Current bud burst
(a)
143
94
Difference in bud burst
(b)
3
-4
Current leaf senescence
(c)
285
233
Difference in leaf senescence
(d)
6
-5
Current growing season
(e)
180
107
Difference growing season
(f)
9
-8
60°N
50°N
40°N
0°
10°E
20°E

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 color 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 colors represent the predicted geographic area without extrapolation from the climatic area covered by the trials (TmSON = 7.5 to 10°C), the soft colors 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 Population differences in bud burst and autumn leaf senescence

The origin of beech populations 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 populations (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 populations 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), 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 temperature, because this parameter covaried with daily insolation, latitude and precipitation (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; 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). This benefit feeds back, potentially producing a delay in LS 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 carry-over effect of BB on LS timing that we found 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). This interdependency makes disentangling the effects of temperature on both

BB and LS difficult. In this respect, the significant interaction effect of BB and the autumn temperature of the populations on LS is notable (Table 1; Fig. 4), as it suggests that the relationship between BB and LS is moderated by the temperature at the site of population origin in a population-specific manner. The relationship between BB and LS is complex and various different mechanisms that 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 populations 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 populations (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 tease apart 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 populations 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 we spatially predict our models within the climatic range of the trials, only trees in northern regions are predicted to increase their GSL up-to 9 days, a trend that continues in the north-eastern regions when we extrapolate 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). While 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 coincident with cold beech populations, there have been no recorded increases in the GSL for southern populations of four temperate European tree species (*Quercus robur*, *Fagus sylvatica*, *Betula pendula* and *Aesculus hippocastanum*) over the last two decades (Chen et al. 2018). 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 those 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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CHAPTER 3

The legacy of the 20th century inter-annual climate variation in European beech populations' phenotypic plasticity

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1 Introduction

The pace of climate change imposes high pressure on organisms to persist *in-situ* (Carroll et al. 2018). Organisms rely on evolutive processes as local adaptation and phenotypic plasticity to respond to rapid climate change (Pulido & Berthold 2004, Valladares et al. 2014b). Local adaptation requires several generations to change the frequency of alleles in response to changes in the environment (Savolainen et al. 2007), whilst phenotypic plasticity is a faster mechanism that relies on the ability of a genotype to render different phenotypes across different environments (Nicotra et al. 2010). In long-lived organisms such as trees it implies that local adaptation is carried out at long time scales (Savolainen et al. 2007), whilst plasticity is the main mechanism to respond to rapid climate change (Benito Garzón et al. 2019).

The extent of phenotypic plasticity that tree populations present is trait-dependent (Peterson et al. 2018, Benito Garzón et al. 2019, Gárate-Escamilla et al. 2019, Gárate-Escamilla et al. Under review). In the case of life-history traits, growth shows typically higher plasticity than survival and phenological traits (Vitasse et al. 2010, Duputié et al. 2015, Richardson et al. 2017, Gárate-Escamilla et al. 2019, Fréjaville et al. 2020) Life-history traits show generally lower plasticity than functional traits (Drake et al. 2017, Patterson et al. 2018), probably owe to trade-offs between those functional traits that contribute to life-history traits (e.g. the contribution of photosynthesis and wood density to tree growth). Although the origin of plasticity has been generally attributed to environmental variation, only few examples exist (Valladares et al. 2014a, Schmid et al. 2019). For instance, populations from higher latitudes show greater plasticity than populations from lower latitudes (Molina-Montenegro & Naya 2012). Likewise, climatic variability over time can also drive phenotypic plasticity suggesting that some populations may evolve towards more plastic genotypes under high variability (Vizcaíno-Palomar et al. In revision).

Phenotypic plasticity can change along the developmental stages of organism (Mitchell & Bakker 2014) which can be adaptive at an early age. Yet, understanding phenotypic plasticity across time and space is a major challenge in evolutionary ecology (Fox et al. 2019).

Fagus sylvatica L. (European beech, henceforth "beech"), is an economically important and widespread broadleaf tree in Europe (Preston & Hill 1997, Packham et al. 2012). Here we show the importance of inter-annual climate variation during the 20th century shaping populations' phenotypic plasticity in growth, survival and spring and autumn leaf phenology across beech distribution range. To this aim, we study five life-history traits (vertical growth (VG), radial growth (RG), budburst (BB), leaf senescence (LS) and young tree survival (YS)), measured in common gardens across the beech distribution range (Robson et al. 2018). The objectives of this study are to: (i) quantify populations' plasticity indexes; (ii) evaluate phenotypic plasticity changes along development stages; (iii) determine the extent to which inter-annual climate variation during the 20th century is related to differences in populations' phenotypic plasticity variation; and (iv) predict populations' plasticity across the beech range.

2. Materials and methods

Here we used the previously populations' reaction norms of life-history traits (Gárate-Escamilla et al. 2019, Gárate-Escamilla et al. in review) to estimate populations' plasticity indexes (PPI) for all the traits (VG, RG, BB, LS and YS) and developmental stages of beech (seedlings, saplings, and young adults).

2.1 Life-history traits

We used vertical growth (VG), radial growth (RG), budburst (BB), leaf senescence (LS) and young tree survival (YS) recorded in the largest network of common gardens for forest trees in Europe, covering the entire distribution range of beech. Trials were established in 1995 and 1998 with plants germinated in greenhouses and planted in the trials at two-years old (details given in Robson et al. 2018). We used 108,415 measurements of VG from 205 provenances planted in 36 trials, 31,339 measurements of RG from 187 provenances planted in 19 trials, 41,309 measurements of BB from 167 provenances planted in 14 trials, 7,863 measurements of LS from 12 provenances planted in 2 trials , 925 measurements of YS from 114 provenances planted in 7 trials (Table 1).

Table 1. The extent of data used for modelling the phenotypic plasticity index. Stage= age category; Age= the age at what the trees where measured; Prov= total number of provenances; Trees: total number of individual trees; Trial= total number of sites; PPI= average population' phenotypic plasticity index; SD= standard deviation of the phenotypic plasticity index.

Trait	Stage	Age	Prov	Trees	Trial	PPI	SD
Vertical growth	Seedling	4	205	108 415	36	0.480	0.010
Vertical growth	Sapling	9	205	108 415	36	0.510	0.010
Vertical growth	Early adult	14	205	108 415	36	0.540	0.010
Radial growth	Sapling	9	187	31 339	19	0.813	0.003
Radial growth	Early adult	14	187	31 339	19	0.935	0.001
Young tree survival	Seedling	3	114	41 309	7	0.980	0.006
Young tree survival	Sapling	6	114	41 390	7	0.999	1.23E-05
Budburst	Early adult	12	62	7 863	14	0.372	0.021
Leaf senescence	Early adult	12	12	925	2	0.305	0.001

2.2 Developmental stages

Traits were measured in trees between 2 and 15-year-old. To analyse the effect of age on populations' phenotypic plasticity, three classes of developmental stages were defined: seedlings (SEEDL), saplings (SAPL), and young adults (ADUL). The seedling class was formed by 4 and 3 year-old trees in VG and YS, respectively; sapling class by trees of 9, 9 and 6 year-old in VG, RG and YS, respectively; and young adult class composed by trees of 14, 14, 12 and 12 year-old in VG, RG, BB and LS respectively (Table 1).

2.3 Climate variables

We used the EuMedClim (Fréjaville & Benito Garzón 2018) database to: (i) characterize the effect of the provenance (average climate from 1901 to 1990) with the annual mean temperature (TMP, °C) of each population; and (ii) calculate the inter-annual climate variation indices (CVI) during the 20th century, computing the standard deviation (SD) of climate variables between 1901 and 1990, to reflect the past climate variation faced by each population. We calculated de SD of the following climatic variables: mean annual temperature (BIO1.SD, °C), mean diurnal temperature range (BIO2.SD, °C), maximum temperature of the warmest month (BIO5.SD, °C), minimum temperature of the coldest month (BIO6.SD, °C), annual precipitation (BIO12.SD, mm), precipitation of the wettest month (BIO13.SD, mm) and precipitation of the driest month (BIO14.SD, mm). Climate variables were standardized for modelling analyses.

2.4 Previously calibrated linear mixed-effect models of phenotypic traits

We used previous reaction norms estimated from linear mixed-effect models for VG, RG, YS and BB (Gárate-Escamilla et al. 2019), and LS (Gárate-Escamilla et al. In revision). We performed a series of linear mixed-effects models for each phenotypic trait as a function of environmental variables from the trial and the provenances. Each model included the climatic variable at the provenance and the trial, the age of trees, and the quadratic effect. For the BB model also latitude and longitude as fixed effects, and for LS model 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 phenotypic traits model took the form:

$$log(TR_{ijk}) = \alpha_0 + \alpha_1(Age_{ik}) + \alpha_2(CP_{ij}) + \alpha_3(CT_{ik}) + \alpha_4(CP_{ij}{}^2) + \alpha_5(CT_{ik}{}^2) \\ + \alpha_6(Age_{ik} \times CP_{ij}) + \alpha_7(Age_{ik} \times CT_{ik}) + \alpha_8(CP_{ij} \times CT_{ik}) + \beta + \varepsilon$$

Eq. 1

Where TR = trait response of the i^{th} individual of the j^{th} provenance in the k^{th} trial; Age = tree age of the i^{th} individual in the k^{th} trial; CP = climate at the provenance site of the i^{th} individual of the j^{th} provenance; CT = climate at the trial site 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: Age and CP, Age and CT, and CP and CT.

2.5 Populations' Plasticity Index

Using the populations' phenotypic responses curves (i.e. populations' reaction norms) of all the traits of each population and each developmental stages (SEEDL, SAPL and ADUL) we computed populations' phenotypic plasticity index (PPI; (Valladares et al. 2006) adapted to reaction norms from common gardens (Vizcaíno-Palomar et al. In revision). PPI index is computed as follows:

$$PPI = \frac{(PRM - PRm)}{PRM}$$

Eq. 2

where PRM is the highest phenotypic value for each population reaction norm, and PRm is the lowest phenotypic value observed in the reaction norm. Values equal 1 mean maximum plasticity whilst values equal to 0 means absence of plasticity.

2.6 Analysis of populations' phenotypic plasticity across developmental stages

To test if PPI changed along the developmental stages, we performed analyses of variance (ANOVA) for VG, RG and YS.

2.7 Linear regression of populations' phenotypic plasticity index and the inter-annual climate variability recorded in the 20th century

To avoid co-linearity and reduce the number of variables to test in the models, we made a correlation matrix between all the CVI for each trait (Figure S1), and we performed a variance inflator factors (VIF) of all CVI for each trait analysed (Table S2). We only used weakly correlated CVI (-0.5 < R < 0.5), and CVI with VIF lower than 5 for modelling purposes.

We regressed the populations' plasticity indexes (PPI) against the inter-annual climate variability index (CVI) of each population from 1900 to 2014 (SD: BIO1.SD, BIO2.SD, BIO5.SD, BIO6.SD, BIO12.SD, BIO13.SD, BIO14.SD and their interactions, as explanatory variables) at ADUL stage for VG, RG, BB and LS, and at SAPL stage for YS.

$$PCV = \alpha_0 + \sum_{i=1}^{p} \alpha_i X_i + e$$

Eq. 3

where PCV is the plasticity climate variation, α_0 is the intercept, α_i is the set of p parameters associated with the effects of X_i(BIO$_i$.SD) and their interactions, and $\varepsilon$is the residual error. The best model for each trait was selected using the "step" function of the package "stats" in R (R

Development Core Team 2015). The suitability of the models was shown plotting the residuals vs fitted values and with qq-plots (Figure S2). The goodness of fit of the final models was assessed using the the variance explained by the model (R^2) and the generalization capacity (Pearson correlation) of the model using cross-validation (64% of the data used for calibration and the remaining 34% for validation).

2.8 Spatial predictions of PPI

Spatial predictions of PPI for each trait were calculated using our PCV models across the species range. The inter-annual climate variation during the 20th century was represented by the SD of the period from 1901 to 1990 of the climatic variables selected. We calculated the average phenotypic plasticity of all the traits by adding the PPI of each trait and diving the final result by five. All spatial predictions were delimited within the beech distribution range (EUFORGEN 2009). Spatial analyses were performed with the ‘raster’ package in R (Hijmans et al. 2017).

3. Results and discussion

3.1. Populations’ phenotypic plasticity index

Our PPI derived from populations’ reaction norms resulting from linear mixed-effect models (Gárate-Escamilla et al. 2019, Gárate-Escamilla et al. in revision) showed different plastic responses (Table 1 and Figure 1a). YS and RG had the highest values of plasticity (PPI = 0.99 and 0.9 respectively), VG showed medium values (PPI = 0.5), and leaf phenology traits (budburst and senescence) showed the lowest plastic values (PPI = 0.30 and 0.37 respectively; Table 1 and Figure 1a); These large differences in phenotypic plasticity indices have been found in the functional traits of numerous temperate and other tree species (Matzek 2012, Bongers et al. 2017, Chmura et al.

2017).

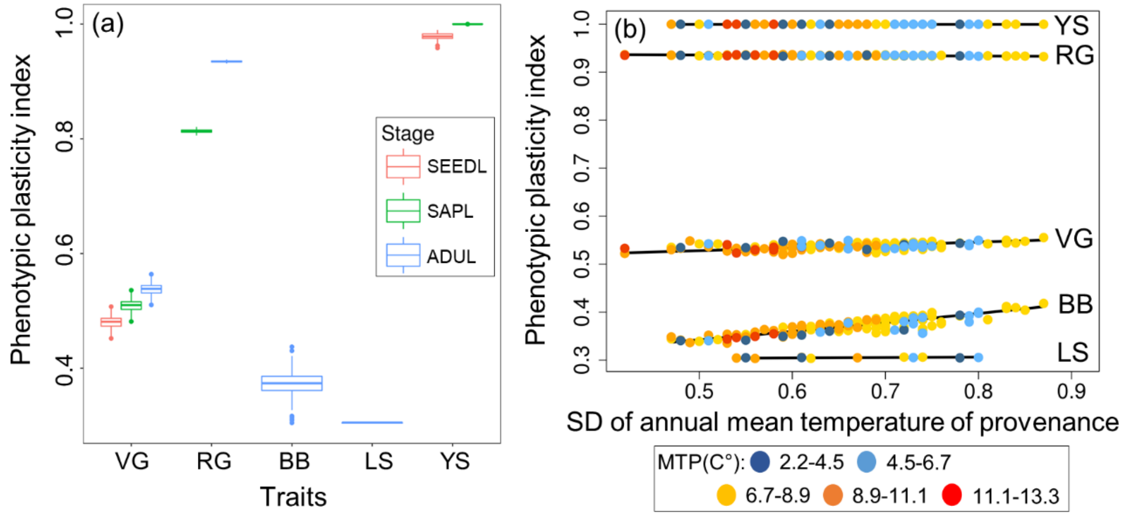


Figure 1. (a) Phenotypic plasticity values for the five traits (VG= vertical growth, RG: radial growth, BB: budburst, LS: leaf senescence, YS: young tree survival) for the three age stages(SEEDL: seedlings (red), SAPL: saplings (green), ADUL: young adults (blue)). (b) Phenotypic plasticity predicted values across the coefficients of inter-annual past climate variation (SD) for ADUL trees. The annual mean temperature of each population (MTP) is represented in each trait prediction by the colored circles (blue and light blue = cold populations, yellow = mean populations, orange and red = warm populations).

3.2. Populations' phenotypic plasticity index along developmental stages

According to the analysis of variance to test phenotypic plasticity variation across developmental stages, there were significant difference between the developmental stages for VG, RG and YS (Table S1). Phenotypic plasticity increased in older trees for VG, RG and YS (Figure 1a), which is in line with results that reported variation in plasticity between developmental stages from other tree species (Vizcaino-Palomar et al., in revision; Bradshaw, 2006; Valladares et al., 2002).

3.3. Populations' phenotypic plasticity index and inter-annual climatic variability

The inter-annual climate variation indexes (CVI) selected for our models were BIO1.SD, BIO2.SD, BIO5.SD and BIO13.SD (Figure S1 and Table S2). According to the best supported models of each trait, BIO1.SD, BIO2.SD, BIO5.SD and BIO13.SD were significant for VG, RG and BB, explaining 0.38, 0.37 and 0.53 of the variance, and 0.59, 0.52 and 0.72 of the generalization capacity respectively (Table 2). BIO1.SD and, BIO5.SD were the significant variables of LS, explaining 0.40 of the variance and 0.53 of the generalization capacity (Table 2). BIO1.SD and BIO2.SD were the significant variables of YS, explaining 0.32 of the variance and 0.52 of the generalization capacity (Table 2).

The phenotypic plasticity in YS, RG and LS sowed very small-although statistically significant-differences among provenances (Figure 1b). These results are in agreement with previous studies where plastic responses were associated with climate variation in Mediterranean pine species (Vizcaino-Palomar et al., in revision) and in the shrub species *Convolvulus chilensis* and *Senna candolleana* (Gianoli & González-Teuber 2005, Lázaro-Nogal et al. 2015). Higher changes of phenotypic plasticity among provenances were found in VG and BB (Figure 1b). The provenances with higher inter-annual climate variation and with mean (6.7-8.9 °C) and cold (2.2-6.7 °C) annual mean temperature at the provenance were more plastic in BB and VG (Figure 1b).

Table 2. Results from the linear fixed-effect models between the phenotypic plasticity index (PPI) and the set of coefficients of inter-annual past climate variation (SD). Results are presented for the five traits: vertical growth, radial growth, budburst, leaf senescence and young tree survival. Each sub-table contains the results from the models fitted for the PPI by trait. Estimate = coefficient of the regression shown on a logarithmic scale; SE= standard error; p= p-value; R^2= adjusted R-squared; BIO1.SD= annual mean temperature; BIO13.SD= precipitation of the wettest month; BIO2.SD= mean diurnal range; BIO5.SD= maximum temperature of the warmest month.

Vertical growth					
Variable	Estimate	SE	p-value	R2	r
Intercept	-6.20E-01	1.01E-03	***		
BIO1.SD	9.43E-03	1.12E-03	***		
BIO13.SD	8.14E-03	1.25E-03	***		
BIO2.SD	-1.18E-02	1.21E-03	***		
BIO5.SD	8.85E-03	1.27E-03	***	0.40	0.59

Radial growth					
Variable	Estimate	SE	p-value	R2	r
Intercept	-6.75E-02	7.71E-05	***		
BIO1.SD	-6.74E-04	8.50E-05	***		
BIO13.SD	-5.79E-04	9.62E-05	***		
BIO2.SD	8.47E-04	9.33E-05	***		
BIO5.SD	-6.32E-04	9.80E-05	***	0.39	0.52

Budburst					
Variable	Estimate	SE	p-value	R2	r
Intercept	-1.00E+00	4.55E-03	***		
BIO1.SD	3.93E-02	4.66E-03	***		
BIO13.SD	-2.63E-02	6.13E-03	***		
BIO2.SD	-1.31E-02	5.40E-03	*		
BIO5.SD	1.74E-02	4.94E-03	***		
BIO1.SD:BIO13.SD	-1.81E-02	5.36E-03	***		
BIO1.SD:BIO2.SD	1.47E-02	5.12E-03	**		
BIO13.SD:BIO2.SD	1.16E-02	3.94E-03	**		
BIO1.SD: BIO5.SD	-1.19E-02	5.60E-03	*		
BIO13.SD:BIO5.SD	-1.21E-02	5.83E-03	*	0.56	0.72

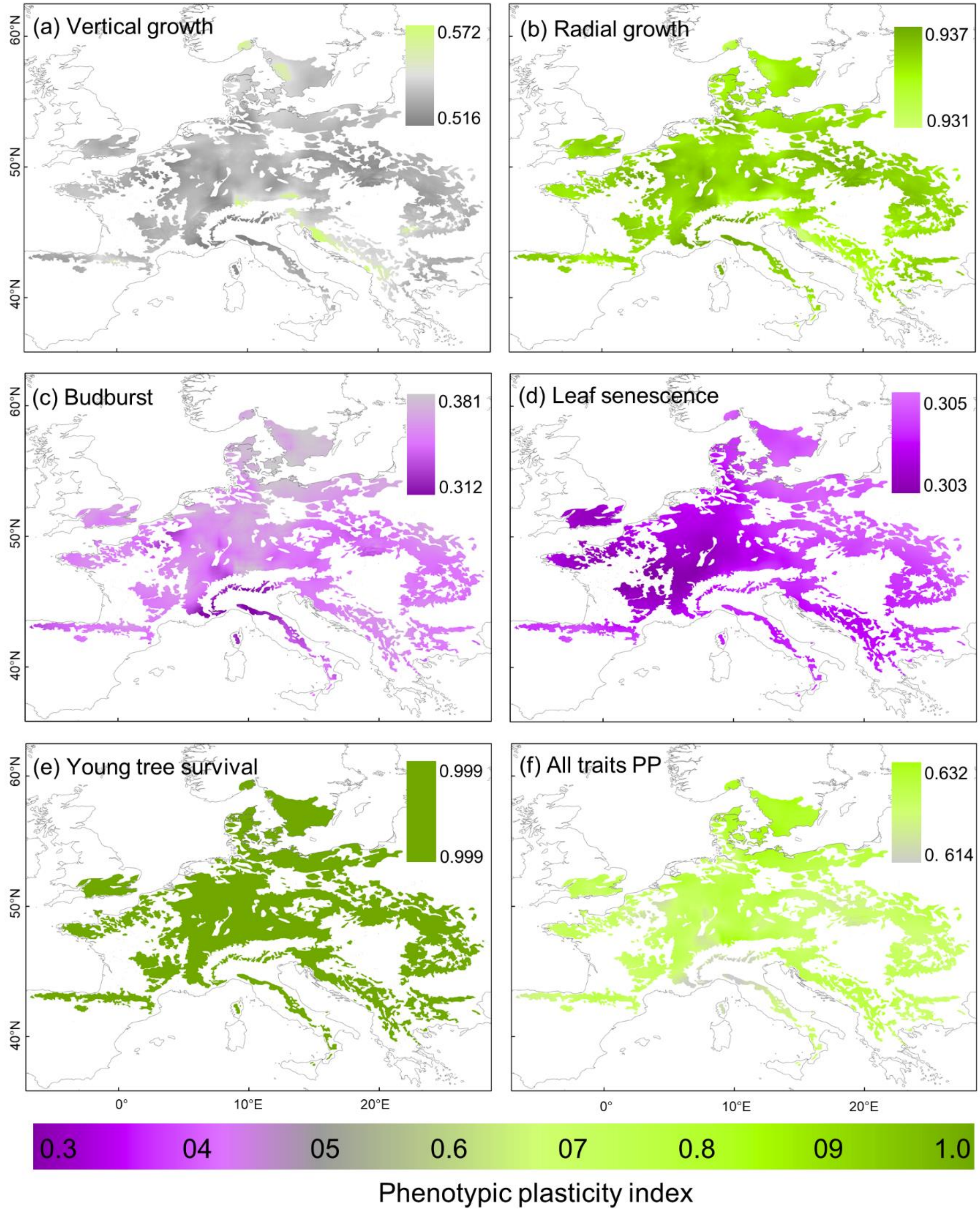
Leaf senescence					
Variable	Estimate	SE	p-value	R2	r
Intercept	-1.19E+00	8.13E-04	***		
BIO1.SD	2.17E-03	8.94E-04	*		
BIO5.SD	-2.27E-03	8.94E-04	*	0.51	0.53

Young tree survival					
Variable	Estimate	SE	p-value	R2	r
Intercept	-4.17E-05	9.51E-07	***		
BIO1.SD	-5.36E-06	9.89E-07	***		
BIO2.SD	4.55E-06	1.13E-06	***		
BIO1.SD:BIO13.SD	2.41E-06	9.81E-07	*	0.34	0.52

3.4. Spatial predictions of phenotypic plasticity

According to the PCV spatial predictions across species ranges: (i) YS showed no changes (Figure 2e); (ii) RG and LS sowed small changes (Figure 2b and d); and VG and BB showed greater changes (Figure 2a and c). The greater values of phenotypic plasticity were located at higher latitudes and altitudes in the range. The sum of phenotypic plasticity in all the traits showed 0.6 of plasticity and small changes across the beech ranges (Figure 2f). The regions more plastic within the beech range according to the individual trait response and the sum of phenotypic plasticity in all traits were at northern latitudes and higher elevations (Figure 2). This tendency was recently also confirmed for phenotypic plasticity of vertical growth in *Quercus petraea* (Fréjaville et al. 2019).

Figure 2. Spatial prediction of phenotypic plasticity (PP) for (a) tree height, (b) radial growth, (c), budburst, (d) leaf senescence and (e) young tree survival and (f) beech mean according to the sum of the five traits across beech ranges. The color gradient depicts the clinal variation of PP from low (purple) to high (green) values of each trait.


(a) Vertical growth
0.572
0.516
(b) Radial growth
0.937
0.931
(c) Budburst
0.381
0.312
(d) Leaf senescence
0.305
0.303
(e) Young tree survival
0.999
0.999
(f) All traits PP
0.632
0. 614
60°N
50°N
40°N
0°
10°E
20°E
0.3
04
05
0.6
07
0.8
09
1.0
Phenotypic plasticity index

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DISUSSION

This thesis uses a modelling approach to better understand the formation of the distribution range of European beech based on phenotypic plasticity and local adaptation of fitness-related traits measured in common gardens spread across a large geographical gradient. The results can be used to evaluate the potential impact of future climates on fitness-related traits across the species range. In particular, they provide important insights into: i) the spatial patterns of local adaptation and phenotypic plasticity; ii) relationships between traits and patterns of trait co-variation; iii) the relation of trait variation with fitness and its implications for the delimitation of the species range; and iv) our understanding of the sensitivity of beech under future climates.

1 ΔTraitSDMs

1.1 Phenotypic plasticity and local adaptation

Phenotypic variation may influence community structure and ecosystem function (Des Roches et al., 2018; Whitham et al., 2006) . When phenotypic variation is generated by local adaptation, intraspecific trait variation can reflect microgeographic adaptation, divergent selection and even incipient speciation, whilst when it is generated by plasticity, traits can change rapidly within generations and differ drastically across populations in dissimilar habitats (Des Roches et al., 2018). In beech, phenotypic plasticity had the greatest contribution to total intra-specific trait variation in vertical and radial growth, young tree survival, budburst and leaf senescence (Table Ch1-S1.4 and Ch2-1). A similar phenomenon has been shown for vertical and radial growth, survival, leaf and flower phenology, biomass, leaf width and chlorophyll content in various tree (*Abies alba*, *Picea mariana*, *Pinus pinaster*, *Pinus ponderosa*, *Pinus strobus*, *Pinus sylvestris*, *Pseudotsuga menziesii*, *Quercus petraea*, *Quercus robur*), shrub (*Artemisia tridentata*) and herbaceous (*Andropogon gerardii*) species in the northern hemisphere (Benito Garzón et al., 2019). Extensive phenotypic plasticity is often considered favorable in long-lived organisms for the persistence of populations under rapid climate change (Valladares et al., 2014), although it can delay evolutionary adaption to new environments in the long term (Fox et al., 2019).

Even though plasticity had the highest contribution to phenotypic variation, I also found that the effects of local adaptation and the interaction between environment and population provenance (i.e., differences in plasticity among populations) were always significant (Table Ch1-S1.4 and Ch2-1). This finding suggests that: (i) climatic optima of provenances covary with their climate of origin; and (ii) plasticity differs significantly among populations. Similar signals of local adaptation and environment –provenance interactions has been observed in trees (*Abies alba*, *Pinus contorta*, *Pseudotsuga menziesii*, *Quercus petraea*) and herbaceous species (*Festuca rubra*) (Fréjaville et al., 2019; Leites et al., 2012; Münzbergová et al., 2017; Sáenz-Romero et al., 2017; Wang et al., 2006)

1.2. Drivers of phenotypic plasticity and local adaptation

Tree growth and survival - Plastic responses in vertical and radial growth and young tree survival were mainly driven by precipitation-related variables (Table Ch1-S1.4). These can strongly fluctuate under new climates (Pflug et al., 2018), making it difficult to reliably predict to which extent plasticity would maintain population persistence in the near future. Local adaptation of provenances for vertical and radial growth and young tree survival were primarily driven by maximum evapotranspiration (Table Ch1-S1.4). This result suggests that beech populations are responding to selection related to drought (Volaire, 2018), which is in agreement with the general consideration of beech as a drought sensitive species (Aranda et al., 2015), although, there is ongoing debate over the extent of resistance that beech has to drought (Pflug et al., 2018). My results showed differences in resistance to drought among populations, an observation that underscores the existence of a combined effect of local adaptation and plasticity (see also Aranda et al., 2015; Stojnic et al., 2018).

Phenology - Plasticity and local adaptation in leaf phenology were primarily associated with temperature related variables (Table Ch1-S1.4 and Ch2-1). Budburst was driven by a combination of winter temperature, latitude and longitude (Table Ch1-S1.4). Although climate models predict an overall increase of winter temperature in the future (e.g. IPCC, 2014), this does not necessary imply that leaf flushing will start earlier because this trait can also be constrained by local adaptation to photoperiod, especially in northern populations (Figure Ch1-2; Way and Montgomery, 2015). Leaf senescence was driven mostly by autumn temperatures, with high autumn temperatures delaying leaf senescence (Delpierre et al., 2009; Vitasse et al., 2011). However, autumn temperatures covaried with daily insolation, latitude and precipitation (Fig. Ch2-S2 and Table Ch2-S3), suggesting that they may also have affected leaf senescence timing to some extent: (i) in low latitudes, warmer temperatures accompanied by moderate drought appear to delay leaf senescence until a certain threshold in deciduous forest (Xie et al., 2015); but beyond this drought threshold LS is accelerated (Estiarte and Peñuelas, 2015); and (ii) in high latitudes, longer photoperiod and higher insolation significantly delayed the timing leaf senescence in deciduous forest (Liu et al., 2016a, 2016b).

2 Analysis of the phenotypic plasticity index

2.1 Phenotypic plasticity across traits

Plasticity was trait-dependent: Large differences were found in the values of the phenotypic plasticity index between the traits (Table Ch3-1, Figure Ch3-1a). Large differences in phenotypic plasticity indices have been found in the functional traits of numerous temperate and other tree species (Bongers et al., 2017; Chmura et al., 2017; Matzek, 2012). In beech, young tree survival and radial growth had the highest values of plasticity (PPI = 0.99 and 0.9 respectively), while vertical growth showed medium values (PPI = 0.5). Plasticity in young tree survival and growth traits is strongly species-dependent, large differences in plasticity indices have been found in the survival of seedlings of *Quercus* and *Pinus* species (Sánchez-Gómez et al., 2006) and in growth traits in *Pinus* (Vizcaíno-Palomar et al., in revision) and tropical trees species (Harja et al., 2012). Finally, the leaf phenology traits budburst and senescence showed the lowest plastic values (PPI = 0.30 and 0.37 respectively; Table Ch3-1a, Figure Ch3-1); similarly low values have been found in phenology traits in *Quercus spp* (Castro-Díez et al., 2006) and perennial herbaceous species (Gugger et al., 2015), suggesting that plasticity in phenology is trait-dependent.

2.2. Phenotypic plasticity and tree developmental stage

For the traits considered (i.e., young tree survival and growth traits), phenotypic plasticity increased with age (Figure Ch3-1a), which is in line with results that reported variation in plasticity between developmental stages from other tree species (Vizcaino-Palomar et al., in revision; Bradshaw, 2006; Valladares et al., 2002). The most likely explanation is that the effect of plastic growth rates accumulates through time (Weiner, 2004), resulting in a successive increase in (absolute) size differences. Curiously, Mediterranean pines show the opposite pattern in their plasticity across the developmental stages in vertical growth (Vizcaino-Palomar et al., in revision), this difference may have been observed to some extent, since Mediterranean pines show higher plasticity at the seedlings stage than broadleaf species (*Quercus spp.*; Sánchez-Gómez et al., 2006). This can be due to trade-offs among functional traits that are hidden when only consider structural traits as growth.

2.3 Explaining populations' phenotypic plasticity with climate variation over time

Those populations subjected to a more variable climate (see standard deviations of bio1, bio 5, bio15 and bio13 in Table Ch3-2) during the 20th century showed a greater capacity to respond plastically to changes in climate (e.g. long-term trends; Figure Ch3-1b). These results are in agreement with previous studies where plastic responses were associated with climate variation in Mediterranean pine species (Vizcaino-Palomar et al., in revision) and in the shrub species *Convolvulus chilensis* and *Senna candolleana* (Gianoli and González-Teuber, 2005; Lázaro-Nogal et al., 2015).

The spatial predictions of the phenotypic plasticity index showed that all fitness related traits in beech exhibit higher phenotypic plasticity in populations located at higher latitude and higher elevation within the species range (Figure Ch3-2). This finding implies that northern and high-elevation beech populations would be more plastic than those growing further south or in lowland areas. This tendency was recently also confirmed for phenotypic plasticity of vertical growth in *Quercus petraea* (Fréjaville et al., 2019). One possible explanation would be populations growing far away from species' glacial refugia have been selected for low levels of specialization

(Dynesius and Jansson, 2000). Alternatively, northern and high-latitude populations are likely to be the ones that arrived latest at their growing sites (Magri et al., 2006); the time since their establishment could simply have been too short to allow for extensive local adaptation.

3 Fitness-related traits across the range

3.1 Using trait variation to delimit species ranges

Previous approaches attempting to predict the geographical range limits of species from their functional traits have used species-level mean values (Stahl et al., 2014; Violle and Jiang, 2009). In contrast, the modeling approach used in this thesis considers intraspecific trait variation since it is based on different trees from the same provenance distributed in the blocks of the same trial site.

Although I observed great variation in the spatial patterns of phenotypic variation in different traits, all traits showed their lowest values in the eastern and southern range parts, suggesting that these parts of the distribution range seem most sensitive to climate (Fig. Ch1-2 and Ch2-6). This consistency could imply that these combined traits are likely to delimit the species range in these regions. Many species have shown higher mortality risk in the driest part of their range (Anderegg et al., 2015; Benito-Garzón et al., 2013; Camarero et al., 2015; Ruiz-Benito et al., 2017). In the particular case of beech, it has been reported that growth is more sensitive to drought and precipitation than to temperature (Farahat and Linderholm, 2018) and that it is susceptible to growth reduction during drought events (Granier et al., 2007). In turn, the evidence for traits as determinants of the northern range limit is less clear. Photoperiod might constrain the northern range limits of beech through its effect on the timing of budburst (not allowing the species to properly complete its reproductive cycle); this effect might be exacerbated by the fact that beech shows relatively strong local adaptation concerning photoperiod (Duputié et al., 2015).

3.2 Trait interactions across the range

The two-trait models including the trait combinations vertical growth-radial growth, vertical growth-budburst and leaf senescence-budburst suggested a certain amount of trait co-variation, since they had higher predictive power and explained more variance than when traits were modeled separately (Table Ch1-S1.5).

In the case of vertical growth, predictions tended to increase when considering a second trait as co-variate (one-trait model: 150 to 300 cm; model with radial growth as co-variate: 300 to 600 cm; model with budburst as co-variate: 200 to 400 cm; Figure Ch1-2a and Ch1-3). The vertical growth-radial growth relationship (Fig. Ch1-3a) probably just reflects tree allometry (Weiner, 2004). The observed co-variation of vertical growth and budburst suggested that budburst could confer an advantage on tree growth at lower latitudes by increasing vertical growth, likely because of the increase in the number of growing days in spring before growing ceases in response to drought in summer, as already shown at regional scale (Fig. Ch1-3b; Delpierre et al., 2017; Gömöry and Paule, 2011; Robson et al., 2013). In northern latitudes vertical growth decreases when co-variating with budburst suggesting that vertical growth is strongly limited by budburst in northern populations (Fig. Ch1-3b; Kollas et al., 2014; Menzel et al., 2015). This finding implies hence that local adaptation of budburst to photoperiod can effectively constrain the phenotypic plasticity of vertical growth in northern beech populations (Way and Montgomery, 2015).

The significant co-variation observed between budburst and leaf senescence (known as “carry-over effect”) is consistent with other recent studies on beech (Table Ch2- 1; Chen et al., 2018; Fu et al., 2014; Signarbieux et al., 2017; Zohner and Renner, 2019), and other deciduous trees across the northern hemisphere (Keenan and Richardson, 2015; Liu et al., 2016b). This carry-over effect correlates early budburst with early leaf senescence (Chen et al., 2018; Fu et al., 2014; Zohner and Renner, 2019). The use of multiple provenances with different climatic origin in the study presented in chapter 2 allows to isolate the genetic component of the carry-over effect of budburst on leaf senescence from the temperature response, founding that early budburst was related with early leaf senescence only among cold provenances (3.2-5.2 C°; Fig. Ch2S3) and in regions with high autumn temperature (11.5-12 C°; Fig. Ch24a).

3.3 Perspective: frost damage*

This thesis relied only on structural traits (growth and phenology traits). The study of ecophysiological traits is important because trade-offs between structural and ecophysiological traits can eclipse or exacerbate the effect of structural traits (Cooper et al., 2019; Zohner et al., 2019). For example, photosynthesis can be very active but if plants suffer cold damage at the same time, its effect in terms of growth is probably null (Ma et al., 2019). Late frosts in spring, once leaf budburst has occurred, cause ecological and economic damage (Ma et al., 2019). Previous studies have used budburst records, and freezing temperatures taken from large-scale climate data, to forecast frost risk (Ma et al., 2019; Xie et al., 2015). Frost damage derived from satellite image data has been analyzed using penalized regression methods (Xie et al., 2015), and frost damage derived from observational data were analyzed using linear mixed-effect models (Ma et al., 2019).

*Collaboration: Brelsford C.C., Gárate-Escamilla H., Robson T.M., Benito Garzón M. Fear of the frost: predicting risk of late spring frost in *Fagus sylvatica* across Europe under climate change. In prep.

In beech, a recent study performed in Italy using satellite image data found that frost damage is strongly related to site-specific conditions (i.e. minimum temperatures as well as the phenological stage of the trees) involving both altitude and exposure (Allevato et al., 2019). Another dendrochronological study on a beech population in Southwest France revealed that early budburst trees were most negatively affected in their radial stem growth by two years with late frosts (Ouayjan, 2017). Recently, we started a modeling approach using linear mixed-effect models to achieve the following objectives: 1) to model frost damage incorporating phenotypic plasticity of budburst, to better predict frost risk under climate change, and 2) to assess the main climatic drivers of late spring frosts, and 3) to predict late spring frosts. We used budburst data and frost damage records from the BeechCOSTe52 database, consisting of 166 provenances of beech, across 6 trial sites in a common garden experiment. Large-scale climate data predicted which sites were affected, but not which trees within each site were damaged by frost, suggesting a need to increase our understanding of microclimates. In beech, frost damage was found in the southeastern areas of the range, which is in agreement with previous work (Allevato et al., 2019). Predicting frost damage under future climate change scenarios suggests that the risk of spring frost to beech will remain in the southeastern areas of beech distribution (Figure D1).

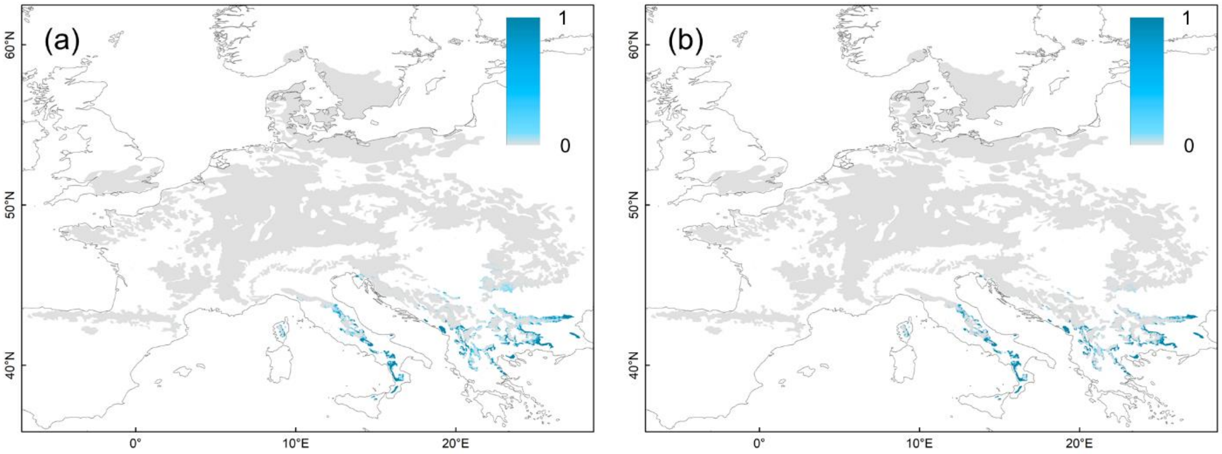

Figure D1. Spatial projections for (a) frost damage risk under current climatic conditions, and (b) frost damage risk under future conditions. The color gradient depicts the clinal variation from low (gray) to high (blue) values of frost damage risk. Current climate refers to the average climate calculated from 2000-2014, and future climate refers to the average climate calculated to 2070, using the RCP 8.5.

4 The future of beech in Europe

4.1 Beech under future conditions

Spatial patterns of vertical and radial growth, young tree survival, budburst and leaf senescence predicted for the future are similar to those predicted under current predictions (Fig. Ch1-2, Ch-4 and Ch2-6), which is likely due to the high plasticity found for these traits that allow population to respond at short-term changes (relative to the species' generation time) in the environment. My results, based on the study of phenotypic variation, predict that beech will persist in much of its range by 2070 (through high trait values), rather than experiencing significant northward range sifts as predicted by species distribution models based only on the occurrence of the species (Figure D2; Cheaib et al., 2012; Duputié et al., 2015; Gritti et al., 2013; Kramer et al., 2010; Maiorano et al., 2013; Meier et al., 2012; Rickebusch et al., 2008; Saltré et al., 2015; Stojnic et al., 2018). In other words, the modeling approach used here draws a less alarming picture of the species future than more traditional ones (Benito Garzón et al., 2019).

The differences between trait predictions for current and future climate conditions allow to detect some differences in the total values of traits throughout their distribution (Fig. Ch1-S1.3 and Ch2-6). The most commonly observed difference concerned a reduction of trait values in the periphery, especially in the south, and an increase of traits values in the north of the distribution. This pattern of trait values can be compared to spatial distribution models: low trait values would correspond to low habitat suitability and high trait values would be attributed to areas with high habitat suitability (Figure D2; Cheaib et al., 2012; Duputié et al., 2015; Gritti et al., 2013; Kramer et al., 2010; Maiorano et al., 2013; Meier et al., 2012; Rickebusch et al., 2008; Saltré et al., 2015; Stojnic et al., 2018).

Although ΔTraitSDMs share similarities with more classical species distribution models, the latter generally only provide information on the occurrence of the species, while ΔTraitSDMs provide information on the performance of the trait and its amount of plasticity and genetic adaptation across the species distribution (Fig. D2). There are significant differences between ΔTraitSDMs (Fig. D2a, b, c, d and e; Gárate-Escamilla et al., 2019; Gárate-Escamilla et al., under revision), species distribution models (SDMs) and process-based models (PBMs) in predicting the future distribution of beech: (a) classical-SDM overestimate the presence of beech in the south and east regions of Europe (Fig. D2f; Maiorano et al., 2013); (b) migration-SDMs limit beech distribution all over Europe (Fig. D2g; Meier et al., 2012); (c) ecophysiological SDMs underestimate beech occurrence through western and overestimate in eastern Europe (Fig. D2h; Gritti et al., 2013); (d) phenological PBMs limit beech distribution to northeastern Europe (Fig. D2i; Gritti et al., 2013); and (e) however when phenological PBMs are applied regionally in France they overestimate the occurrence of beech (Fig. D2j; Cheaib et al., 2012). Dynamic vegetation models (DGVMs) using physiological and biochemical parameters predict future beech distribution more similarly to ΔTraitSDMs (Fig. D2hk and l; Cheaib et al., 2012; Gritti et al., 2013), although DGVMs may be limited to low survival in the east and south of the range, low growth in the south of the range or earlier budburst and later leaf senescence in the south of the distribution.

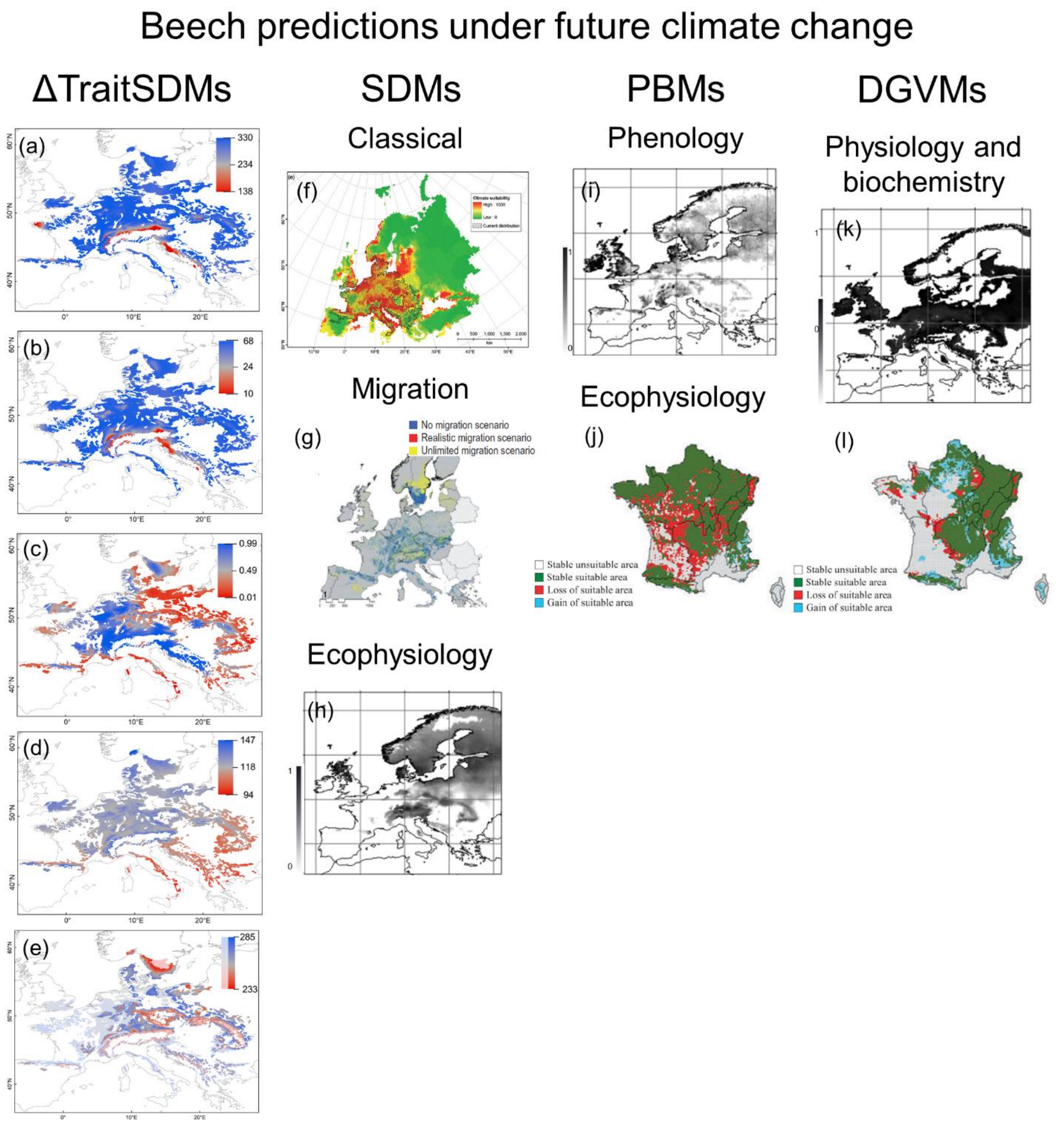

Fig. D2 Spatial predictions of beech distribution under climate change scenarios. First column shows the predictions for 2070 using ΔTraitSDMs in species range for (a) vertical growth, (b) radial growth, (c) young tree survival, (d) budburst and (e) leaf senescence (Figures taken from Gárate-Escamilla et al., 2019; Gárate-Escamilla et al., under revision). Second column shows the predictions in Europe using spatial distribution models (SDMs) for (f) climate suitability (average years 2071-2100; Maiorano et al., 2013), (g) migration (year 2050; Meier et al., 2012), and (h) ecophysiological parameters (average years 2080-2100; Gritti et al., 2013). Third column shows the predictions using process-based models (PBMs) for (i) phenological parameters in Europe (average years 2080-2100; Gritti et al., 2013) and (j) ecophysiological parameters in France (year 2055; Cheaib et al., 2012). Fourth column shows the predictions using dynamic vegetation models (DGVMs) for (k) physiological and biochemical parameters in Europe (average years 2080-2100; Gritti et al., 2013), and (p) physiological and biochemical parameters in France (year 2055; Cheaib et al., 2012).

4.2 Limitations, perspectives, and future research

Beech ΔTraitSDMs are based in a limited set of ages, mostly including seedlings (from 2 to 15 years old). However, the expression of phenotypic plasticity changes over years (Mitchell and Bakker, 2014; Valladares et al., 2007), which can restrict the broad scope of our results to the ages that we considered. This is particularly limiting for the case of mortality, where ages considered are only between 2 to 6, hence only reflect early survival rather than the mortality of adult trees.

In beech mixed forests (usually *Fagus sylvatica* in combination with *Picea abies*, *Pinus sylvestris*, and/or *Quercus petraea*), beech has presumably the highest chances to persist under new climates if it would only depend on its plastic response at the short-term and its capacity to evolve at medium- long-term. (Sáenz-Romero et al., 2019). However, more empirical studies in multi-community dynamics across species ranges are needed to confirm these hypothesis (Ovaskainen et al., 2019). The use of Joint Species Distribution Models (JSDM) may shed light on this question as JSDM consider multiple interrelated species simultaneously, allowing inferences to be drawn at both species and community levels (Thorson et al., 2016).

Although all the traits that we have considered are to some extent related to the survival component of the fitness, including the other component of fitness, reproduction, may change our model results (Hacket-Pain et al., 2018; Pearse et al., 2016). Climate warming tends to increase seed production in northern populations (Drobyshev et al., 2010; Övergaard et al., 2007) and cause a decline in seedling density in southern ones (Barbeta et al., 2011), which would be expected to continue under climate change. Unfortunately, reproduction remains poorly studied across species ranges (Vacchiano et al., 2017), which limits our capacity to test how it may shape their dynamics in response to a change climate.

Likewise, resistance to pathogens can condition population fitness as happened in some colder populations in *Populus fremontii* that were more resistant to pathogenic fungi than warmer populations (Grady et al., 2015), in some warmer populations in *Pinus pinaster* that were less susceptible to pathogenic fungi than cold populations (Hurel et al., in revision), and in *Quercus suber* that populations with earlier budburst were more exposed to insect herbivory (Sampaio et al., 2016), suggesting that resistance to pathogens has a provenance effect. More studies of this nature are needed in beech to know the role that the provenance influences in the relationship plant-pathogen.

In-situ and *ex-situ* conservation programs aim generally to preserve the genetic diversity of beech (von Wühlisch, 2008; Westergren et al., 2015). This thesis may open a new perspective to include in those programs. The great plasticity in all the traits analyzed suggests that future beech seed choice should consider those genotypes presenting high plasticity as an option to mitigate climate change impacts on beech populations, in addition to the genetic diversity that has been considered so far.

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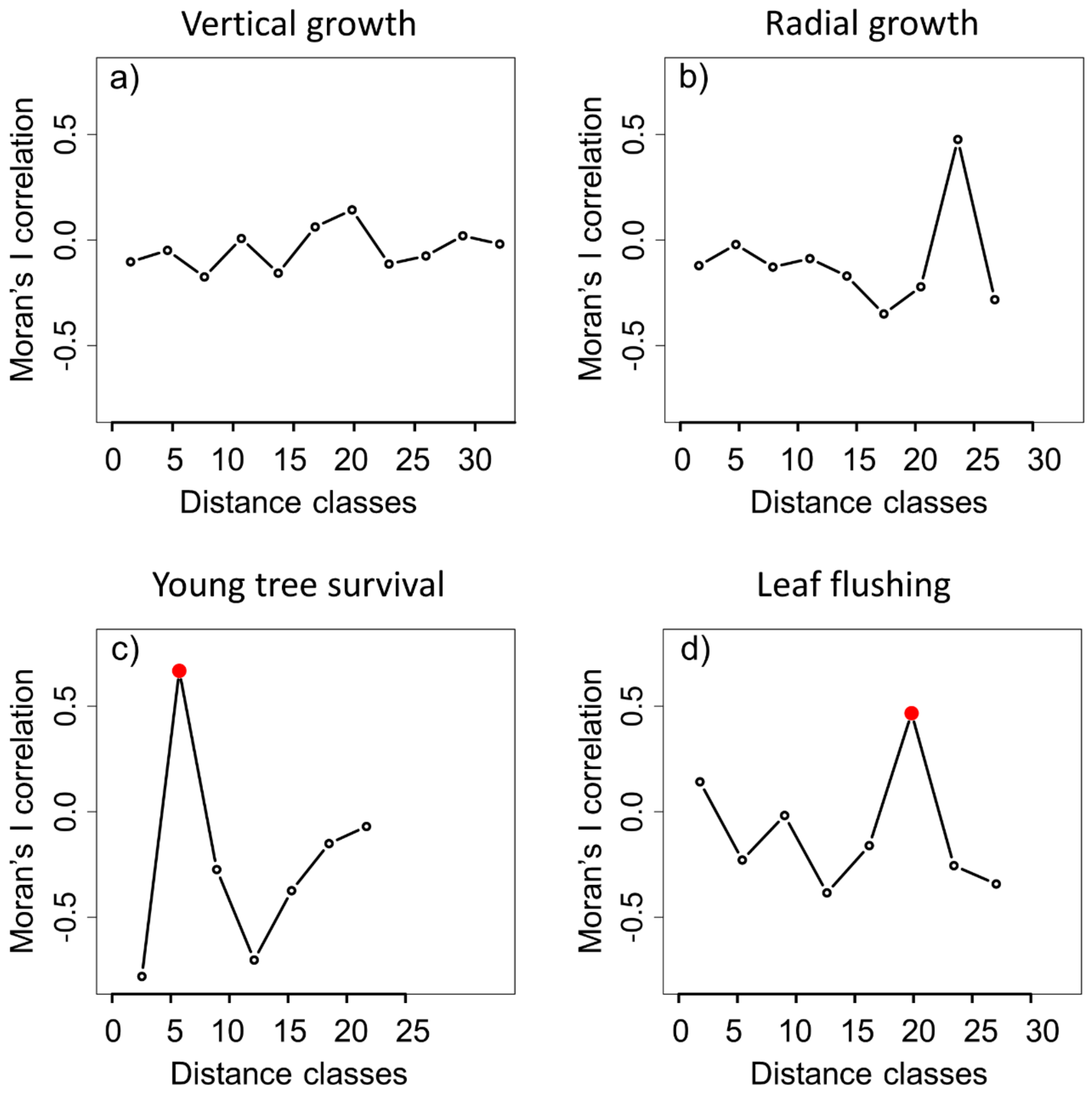
SUPPORTING INFORMATION: CHAPTER 1

1. Moran's I correlation coefficient

Supporting Information Table S1.1. Statistics of the spatial autocorrelation of vertical growth (VG), radial growth (RG), young tree survival (YTS) and leaf flushing (LF). Ob: observed computed Moran's I; Ex: expected value of I under the null hypothesis; Sd: standard deviation of I under the null hypothesis; p-value: p-value of the test of the null hypothesis against the alternative hypothesis; Null hypothesis: the data does not have spatial correlation.

	VG	**RG**	**YTS**	**LF**
Ob	-0.04	-0.09	-0.17	-0.10
Ex	-0.03	-0.05	-0.13	-0.08
Sd	0.06	0.06	0.17	0.08
p-value	0.81	0.47	0.78	0.74

2. Moran’s I correlograms



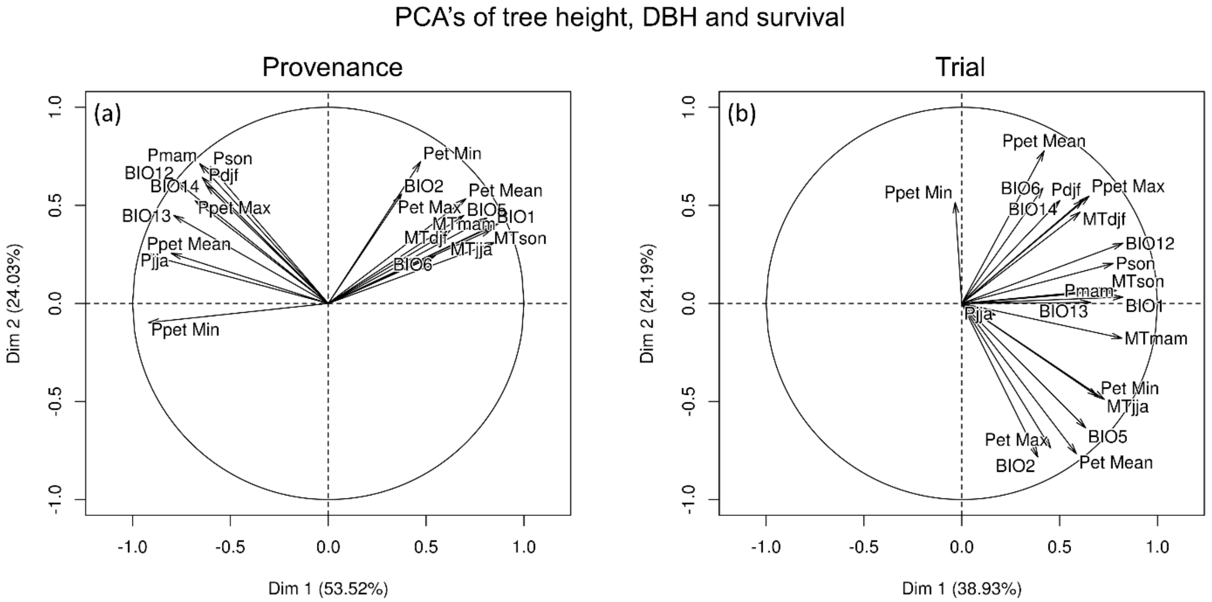
Supporting Information Figure S1.1. Correlograms of Moran’s I correlation coefficient (y-axis) and the distance classes (x-axis) for vertical (a) and radial (b) growth, young tree survival (c), and leaf flushing (d). Moran’s correlation coefficient ranges between 1 and -1. Distance classes are Euclidian and in degrees. Distances of significant spatial dependence are shown in red (significant values $p < 0.05$).

3. Climatic variables

Supporting Information Table S1.2. List of yearly climatic variables provided by EuMedClim. °C: Celsius degree; mm: millimeters; water balance: precipitation minus potential evapotranspiration.

Climatic variables	Definition	Unit
BIO1	Annual mean temperature	°C
BIO2	Mean diurnal temperature range	°C
BIO5	Maximal temperature of the warmest month	°C
BIO6	Minimal temperature of the coldest month	°C
BIO12	Annual precipitation	mm
BIO13	Precipitation of the wettest month	mm
BIO14	Precipitation of the driest month	mm
MTdjf	Mean temperature of December, January and February	°C
MTmam	Mean temperature of March, April and May	°C
MTjaj	Mean temperature of June, July and August	°C
MTson	Mean temperature of September, October and November	°C
Pdjf	Precipitation of December, January and February	mm
Pmam	Precipitation of March, April and May	mm
Pjaj	Precipitation of June, July and August	mm
Pson	Precipitation of September, October and November	mm
PET Mean	Annual potential evapotranspiration	mm
PET Max	Maximal monthly potential evapotranspiration	mm
PET Min	Minimal monthly potential evapotranspiration	mm
PPET Mean	Annual water balance	mm
PPET Max	Maximal monthly water balance	mm
PPET Min	Minimal monthly water balance	mm

4. Principal Components Analysis (PCA) of the climate variables



Supporting Information Figure S1.2. Results of PCA for checking for co-linearity and reducing the climatic space to select the final climate variables for the stepwise procedure used in the models on traits vertical and radial growth, and young tree survival, conducted by provenance (a) and by trial (b). When two variables are strongly correlated, only one of them was used in models. The variance explained by the first two axes is indicated in the figures.

5. AIC analysis

We performed a total of 64 one-trait models and selected the best model based on AIC.

Supporting Information Table S1.3. AIC values obtained for vertical growth, radial growth, young tree survival and leaf flushing one-trait models. AIC: Akaike information criterion; CP: climate of the provenance; CT: climate of the trial; BIO1: annual mean temperature; BIO5: max temperature of warmest month; BIO6: min temperature of coldest month; BIO12: annual precipitation; BIO13: precipitation of wettest month; BIO14: precipitation of driest month; PET Max: maximal monthly potential evapotranspiration; PET Mean: annual potential evapotranspiration; MTdjf: mean temperature of December, January and February; MTmam: mean temperature of March, April and May; MTjja: mean temperature of June, July and August; MTson: mean temperature of September, October and November; MTdjfmam: mean temperature of December, January, February March, April and May.

Vertical growth			**Radial growth**			**Young tree survival**			**Leaf flushing**		
CP	**CT**	**AIC**	**CP**	**CT**	**AIC**	**CP**	**CT**	**AIC**	**CP**	**CT**	**AIC**
PET Max	BIO13	102495.10	PET Max	BIO12	23099.69	PET Max	BIO14	39299.61	MTdjf	MTdjf	-32835.88
BIO13	BIO13	102498.40	BIO12	BIO12	23099.77	BIO5	PET Max	39299.75	MTdjfmam	BIO5	-32835.2
BIO1	BIO13	102509.20	PET Mean	BIO12	23100.00	BIO5	BIO13	39300.20	MTdjfmam	MTdjf	-32835.01
BIO5	BIO13	102509.70	BIO5	BIO12	23100.17	BIO14	BIO14	39300.57	MTdjf	BIO5	-32834.71
PET Mean	BIO13	102515.30	BIO13	BIO12	23105.95	PET Mean	PET Max	39301.21	BIO1	MTdjf	-32833.53
BIO12	BIO13	102538.90	BIO14	BIO12	23107.76	PET Mean	BIO14	39303.74	MTson	MTdjf	-32833.2
BIO6	BIO13	102647.10	BIO1	BIO12	23109.40	PET Max	PET Max	39307.04	BIO1	BIO5	-32832.97
BIO14	BIO13	102694.40	BIO14	PET Max	23112.39	BIO12	BIO14	39307.83	MTdjfmam	MTjja	-32832.95
BIO5	BIO12	102827.20	BIO6	BIO12	23113.15	BIO5	BIO12	39308.26	BIO6	MTdjf	-32832.8
BIO1	BIO12	102836.50	PET Max	PET Max	23119.66	BIO13	BIO13	39308.30	MTdjf	MTjja	-32832.59
PET Max	BIO12	102849.60	BIO12	PET Max	23119.73	PET Mean	BIO1	39308.32	MTson	BIO5	-32832.53
PET Mean	BIO12	102849.80	PET Mean	PET Max	23123.73	BIO5	BIO14	39308.80	BIO6	BIO5	-32831.78
BIO13	BIO12	102856.00	BIO13	PET Max	23124.58	PET Mean	PET Mean	39308.84	BIO1	MTjja	-32830.75
BIO12	BIO12	102924.80	BIO5	PET Max	23127.81	BIO5	BIO1	39308.93	MTson	MTjja	-32830.39
BIO6	BIO12	103000.30	BIO6	PET Max	23129.06	BIO5	PET Mean	39309.13	MTmam	MTdjf	-32829.82
BIO14	BIO12	103035.00	BIO1	PET Max	23131.01	BIO13	PET Max	39310.60	MTmam	BIO5	-32829.69
BIO13	BIO14	104366.60	PET Mean	BIO13	23155.46	PET Mean	BIO5	39310.84	BIO6	MTjja	-32829.67
BIO12	BIO14	104433.70	BIO1	BIO13	23158.17	BIO13	BIO14	39311.05	MTdjfmam	MTson	-32828.93
BIO5	BIO5	104479.60	BIO5	BIO13	23158.45	PET Mean	BIO13	39311.74	MTdjf	MTson	-32828.49
BIO1	BIO5	104486.20	PET Max	BIO13	23160.20	PET Max	BIO13	39312.16	MTmam	MTjja	-32827.31

BIO13	BIO5	104486.40	BIO6	BIO13	23161.55	BIO13	BIO12	39312.17	BIO1	MTson	-32826.31
PET Max	BIO5	104498.00	BIO12	BIO13	23170.84	BIO6	BIO13	39312.88	BIO5	BIO5	-32826.25
PET Mean	BIO5	104502.00	BIO14	BIO13	23170.94	PET Max	BIO1	39313.22	MTson	MTson	-32825.79
BIO12	BIO5	104531.00	BIO13	BIO13	23172.87	BIO14	BIO13	39313.52	BIO6	MTson	-32825.65
BIO1	BIO14	104548.20	BIO12	BIO14	23213.00	BIO5	BIO6	39313.96	BIO5	MTdjf	-32825.32
BIO6	BIO5	104551.90	BIO13	BIO14	23214.59	BIO12	PET Max	39314.37	BIO5	MTjja	-32824.01
PET Max	BIO14	104554.10	BIO14	BIO14	23221.30	BIO12	BIO13	39314.57	MTmam	MTson	-32823.39
PET Mean	BIO14	104561.80	PET Max	BIO14	23228.03	BIO13	BIO1	39314.63	MTdjfmam	BIO1	-32821.39
BIO5	BIO14	104568.60	BIO12	BIO6	23228.43	BIO5	BIO5	39315.15	MTdjf	BIO1	-32821.3
BIO14	BIO5	104595.80	PET Mean	BIO14	23229.18	PET Max	PET Mean	39315.57	BIO5	MTson	-32819.16
BIO14	BIO14	104632.90	BIO13	BIO6	23230.85	BIO1	BIO13	39315.98	BIO1	BIO1	-32818.88
BIO6	BIO14	104662.10	BIO5	BIO14	23231.28	BIO1	BIO14	39316.04	MTson	BIO1	-32818.63
BIO5	BIO1	104948.50	BIO6	BIO14	23231.86	BIO6	BIO14	39316.50	MTjja	BIO5	-32818.54
PET Max	BIO1	104951.50	BIO1	BIO14	23235.69	BIO12	BIO1	39316.56	BIO6	BIO1	-32818.38
PET Mean	BIO1	104953.40	BIO14	BIO6	23236.45	PET Mean	BIO12	39316.71	MTjja	MTdjf	-32817.94
BIO13	BIO1	104958.20	BIO6	BIO6	23240.51	BIO6	BIO12	39316.72	MTjja	MTjja	-32816.41
BIO1	BIO1	104990.00	PET Max	BIO6	23247.34	BIO6	PET Max	39316.79	MTmam	BIO1	-32815.09
BIO12	BIO1	105034.80	PET Mean	BIO6	23248.79	PET Max	BIO12	39316.82	MTdjfmam	BIO6	-32813.73
BIO6	BIO1	105103.40	BIO5	BIO6	23251.22	BIO13	PET Mean	39317.10	MTdjf	BIO6	-32813.64
BIO14	BIO1	105134.00	BIO1	BIO6	23251.39	PET Max	BIO6	39317.35	MTson	BIO6	-32811.78
BIO13	PET Mean	105607.20	PET Max	BIO5	23326.60	BIO1	PET Max	39317.45	BIO1	BIO6	-32811.7
BIO13	BIO6	105655.60	PET Mean	BIO5	23330.74	PET Max	BIO5	39317.56	MTjja	MTson	-32811.33
BIO12	PET Mean	105700.20	BIO5	BIO5	23333.80	BIO13	BIO6	39317.60	BIO6	BIO6	-32810.51
BIO12	BIO6	105740.90	BIO14	BIO5	23336.46	PET Mean	BIO6	39317.70	BIO5	BIO1	-32810.39
BIO5	PET Mean	105752.70	BIO12	BIO5	23337.86	BIO1	BIO1	39317.71	MTmam	BIO6	-32807.09
BIO1	PET Mean	105753.10	BIO13	BIO5	23342.73	BIO14	PET Max	39317.82	MTjja	BIO1	-32803.17
PET Max	PET Mean	105762.50	BIO1	BIO5	23343.08	BIO14	BIO1	39317.95	BIO5	BIO6	-32803.03
PET Mean	PET Mean	105769.40	BIO12	BIO1	23344.66	BIO14	BIO12	39318.04	MTdjfmam	MTdjfmam	-32798.69
PET Max	BIO6	105777.20	PET Max	BIO1	23345.37	BIO12	BIO12	39318.24	MTdjf	MTdjfmam	-32798.47
PET Mean	BIO6	105777.90	BIO6	BIO5	23345.84	BIO6	BIO1	39318.36	MTson	MTdjfmam	-32796.38
BIO5	BIO6	105782.20	BIO5	BIO1	23349.97	BIO13	BIO5	39318.74	BIO1	MTdjfmam	-32796.37
BIO1	BIO6	105790.00	PET Mean	BIO1	23350.61	BIO12	BIO6	39320.02	MTjja	BIO6	-32795.95
BIO6	PET Mean	105851.70	BIO14	BIO1	23353.91	BIO12	PET Mean	39320.05	BIO6	MTdjfmam	-32795.67
BIO14	PET Mean	105867.10	BIO13	BIO1	23354.27	BIO14	BIO6	39320.34	MTmam	MTdjfmam	-32792.13
BIO6	BIO6	105898.10	BIO6	BIO1	23363.77	BIO6	BIO6	39320.41	BIO5	MTdjfmam	-32787
BIO14	BIO6	105901.40	BIO1	BIO1	23367.18	BIO12	BIO5	39320.73	MTdjfmam	MTmam	-32786.71
BIO13	PET Max	106062.80	BIO14	PET mean	23417.15	BIO1	BIO6	39321.01	MTdjf	MTmam	-32785.98
BIO12	PET Max	106132.40	PET Max	PET mean	23420.69	BIO1	BIO12	39321.06	BIO1	MTmam	-32784.65
BIO1	PET Max	106176.20	BIO12	PET mean	23423.00	BIO1	PET Mean	39321.28	MTson	MTmam	-32784.57
BIO5	PET Max	106179.00	PET Mean	PET mean	23423.23	BIO6	PET Mean	39321.81	BIO6	MTmam	-32783.62
PET Max	PET Max	106187.20	BIO5	PET mean	23426.95	BIO14	PET Mean	39321.88	MTmam	MTmam	-32780.58
PET Mean	PET Max	106194.00	BIO13	PET mean	23427.90	BIO14	BIO5	39322.35	MTjja	MTdjfmam	-32780.05
BIO14	PET Max	106256.90	BIO6	PET mean	23431.24	BIO1	BIO5	39323.48	BIO5	MTmam	-32775.52
BIO6	PET Max	106268.70	BIO1	PET mean	23432.28	BIO6	BIO5	39323.84	MTjja	MTmam	-32768.2

6. Summary statistics of one-trait models

Supporting Information Table S1.4. Statistics of random and fixed effects from generalized linear mixed-effect models of vertical growth, radial growth, young tree survival and leaf flushing. 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 for vertical growth, radial growth and leaf flushing; 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; *z*: Wald statistical test that measures the point estimate divided by the estimate of its SE, assuming a binomial distribution of observations conditional on fixed and random effects. Fixed effects: Coefficients of the fixed effects of the model; CP: climate of the provenance origin; CT: climate of the trial; LatP: latitude of the provenance origin; LatT: latitude of the trial; LongT: longitude of the trial; CP^2: quadratic effect of the climate of the provenance; CT^2: quadratic effect of the climate of the trial. Coefficients of the interactions: Age x CP, Age x CT, CP x CT, LatP x CT, LatP x LatT, LatP x LongT, CP x LongT. 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); r: Pearson correlation. The climate variable of the provenance (CP) for vertical growth, radial growth and young tree survival is maximal potential evapotranspiration; CP for leaf flushing is mean temperature of December, January and February. The climate variable of the trial (CT) for vertical growth is precipitation of the wettest month, for radial growth is annual precipitation, for young tree survival is precipitation of the driest month and for leaf flushing is mean temperature of December, January and February.

	Vertical growth			**Radial growth**			**Young tree survival**			**Leaf flushing**		
Model	Linear Mixed Effect			Linear Mixed Effect			Generalized Linear Mixed Effect (Family: binomial)			Linear Mixed Effect		
	Random Effects			Random Effects			Random Effects			Random Effects		
	Obs	Variance	SD	Obs	Variance	SD	Obs	Variance	SD	Obs	Variance	SD
Provenance	205	1.00e-02	9.00e-02	187	9.31e-03	9.65e-02	114	2.98e-01	5.46e-01	62	4.60e-04	2.20e-02
Trial	36	9.00e-02	3.00e-01	19	3.81e-01	6.17e-01	7	6.31e-01	7.94e-01	7	3.60e-05	6.00e-03
Trial:Block	107	9.00e-02	1.00e-01	56	6.97e-03	8.35e-02	21	1.48e-01	3.84e-01			
Trial:Block:Tree	108415	8.00e-02	2.80e-01	31339	1.10e-01	3.32e-01	37433	1.16e-02	1.08e-01			
Residuals		5.00e-02	2.20e-01		1.66e-02	1.29e-01		1.54e-01	3.92e-01		8.56e-04	2.92e-02
	Fixed Effects			Fixed Effects			Fixed Effects			Fixed Effects		
	Estimate	SE	*t*	Estimate	SE	*t*	Estimate	SE	*z*	Estimate	SE	*t*
Intercept	4.84e+00	5.22e-02	92.7	2.82e+00	1.56e-01	18.1	1.08e+00	3.38e-01	3.2	4.76e+00	5.16e-03	921.9
Age	6.45e-01	1.14e-03	563.6	7.17e-01	8.74e-03	82	-1.72e+00	9.29e-02	-18.5			
CP	2.58e-02	6.93e-03	3.7	2.94e-02	8.81e-03	3.3	2.83e-02	5.30e-02	0.1	1.07e-02	2.63e-03	4.1
CT	9.70e-02	4.63e-03	20.9	2.54e-01	7.02e-02	3.6	1.54e-01	2.78e-01	0.6	-1.28e-01	9.77e-03	-13.1
LatP										5.43e-03	2.63e-03	2.1
LatT										4.38e-02	4.77e-03	9.2
LongT										-1.12e-01	9.87e-03	-11.4
CP^2	-1.27e-02	4.84e-03	-2.6									
CT^2	-1.50e-01	2.45e-03	-61.2	-4.30e-01	5.89e-02	-7.3						
Age x CP	-1.07e-02	7.86e-04	-13.6	-1.09e-02	3.58e-03	3						
Age x CT	-1.92e-02	1.50e-03	-12.8	3.33e-01	1.44e-02	23.1	1.59e+00	1.21e-01	13.1			
CP x CT	9.58e-03	1.29e-03	7.4	7.45e-03	3.01e-03	2.5	8.11e-02	2.52e-02	3.2			
LatP x CT										-1.08e-02	1.74e-03	-6.2
LatP x LatT										4.15e-03	7.95e-04	5.2
LatP x LongT										-1.09e-02	1.61e-03	-5.3
CP x LongT										-2.63e-03	4.98e-04	-6.8
	r	R^2 M	R^2 C	r	R^2 M	R^2 C	r	R^2 M	R^2 C	r	R^2 M	R^2 C
	0.69	0.57	0.91	0.53	0.51	0.98	0.59	0.18	0.40	0.73	0.49	0.68

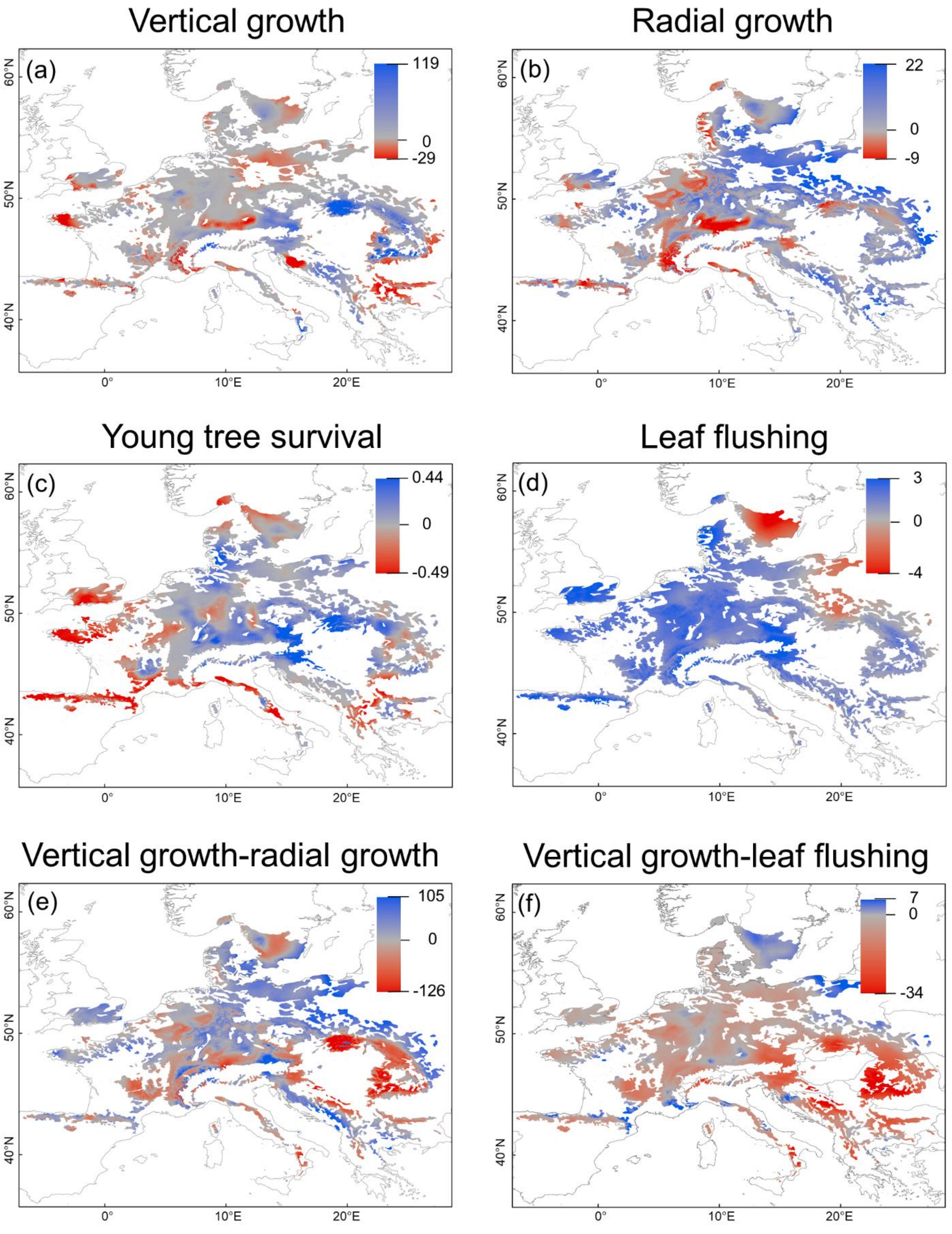
7. Summary statistics of two-trait models

Supporting Information Table S1.5. Statistics of random and fixed effects from linear mixed-effect models of the vertical growth-radial growth and vertical growth-leaf flushing two-trait models. 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 in 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. Coefficients of the fixed effects of the model: Cov: trait covariate; CP: climate of the provenance origin; CT: climate of the trial; CP^2: quadratic effect of the climate of the provenance. Coefficients of the interactions: Age x CP, CP x CT, Cov x Age and Cov x CT. 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); *r*: Pearson correlation. The trait co-variate (Cov) for growth-radial growth is radial growth and for vertical growth-leaf flushing is leaf flushing. The climate variable of the trial (CT) for the two-trait models is precipitation of the wettest month (BIO13). The climate variable of the provenance (CP) for the two-trait model is maximal potential evapotranspiration.

	Vertical growth-Radial growth			**Vertical growth-Leaf flushing**		
Model	Linear Mixed Effect			Linear Mixed Effect		
	Random Effects			Random Effects		
	Obs	Variance	SD	Obs	Variance	SD
Provenance	187	1.70e-03	4.21e-02	150	2.33e-02	1.53e-01
Trial	19	3.26e-02	1.81e-01	6	1.05e-01	3.24e-01
Trial:Block	56	2.20e-03	4.60e-02	17	1.00e-03	3.24e-02
Trial:Block:Tree	31339	9.50e-03	9.70e-02	10634	9.82e-02	3.13e-01
Residuals		1.50e-02	1.23e-01		2.70e-03	5.21e-02
	Fixed Effects			Fixed Effects		
	Estimate	SE	*t*	Estimate	SE	*t*
Intercept	4.38E+00	4.51e-02	97.18	4.94e+00	4.23e-01	11.68
Cov	3.50E-01	5.02e-03	69.72	6.24e-02	8.40e-02	0.74
Age	-1.97E-01	1.26e-02	-15.66	7.40e+00	5.28e-01	14.01
CP	5.04E-03	3.47e-03	1.45	2.59e-02	1.38e-02	1.87
CT	-1.33E-01	3.47e-02	-3.84	1.91e+00	3.89e-01	4.92
CP^2	-5.26E-03	2.43e-03	-2.17			
Age x CP				-1.96e-02	5.33e-03	-3.68
CP x CT	-3.47E-02	9.66e-03	-3.59	1.78e-02	5.72e-03	3.11
Cov x Age	1.05E-01	3.44e-03	30.57	-1.43e+00	1.09e-01	-13.08
Cov x CT	8.02E-02	3.82e-03	21	-3.84e-01	7.84e-02	-4.89
	r	R^2 M	R^2 C	*r*	R^2 M	R^2 C
	0.76	0.62	0.95	0.77	0.47	0.99

8. Differences in spatial predictions between future and current climate for one- and two-trait models

Vertical growth prediction for 12 year-old trees showed small changes in the core of the species range, and moderate decrease in growth in some areas of southern, eastern, western and northern Europe. Increases in vertical growth were mainly expected in the eastern region of the distribution (Supporting Information Figure S1.3a, Appendix S1). Radial growth of 12 year-old trees was predicted to increase in the eastern regions and to decrease across the rest of the range (Supporting Information Figure S1.3b, Appendix S1). Survival of 6 year-old trees was expected to strongly decrease in the western and southern parts of the distribution. Increases in young tree survival were mainly expected in central and some eastern regions of the species range (Supporting Information Figure S1.3c, Appendix S1). The model predicted later leaf flushing in the future than at present for almost all central and western parts of the species distribution. Earlier leaf flushing in the future than today was particularly expected in Sweden (Supporting Information Figure S1.3d, Appendix S1). Differences in vertical growth predictions between future and present climatic conditions for the vertical growth-radial growth model showed an overall increase in vertical growth in some regions of the eastern and southern range; the largest decrease was expected in the southeastern region (Supporting Information Figure S1.3e, Appendix S1). Differences in vertical-growth predictions between the future and present conditions for the vertical growth-leaf flushing model anticipated a decrease in the southeastern and the southern range. A small increase in the northeast was predicted by this model (Supporting Information Figure S1.3f, Appendix S1).


Vertical growth

Radial growth

Young tree survival

Leaf flushing

Vertical growth-radial growth

Vertical growth-leaf flushing

Supporting Information Figure S1.3. Differences in predictions between future (2070) and contemporary (2000-2014) climate for one-trait models in beech range: (a) vertical growth of 12 year-old trees (in cm); (b) radial growth of 12 year-old trees (in mm); (c) probability of young tree survival of 6 year-old trees; (d) leaf flushing of 12 year-old trees (difference in Julian days); and for two-trait models: (e) vertical growth (in cm; co-variate radial growth) and (f) vertical growth (in cm; co-variate leaf flushing). The color gradient depicts the clinal variation from low (red) to high (blue) values.

SUPPORTING INFORMATION: CHAPTER 2

1 Predicted DOY for spring leaf flushing phenology stages

Table S1 Predicted DOY for spring leaf flushing phenology stages. The predicted mean DOY and standard error of each spring phenology stage is given for each provenance at every trial. Trial: trial where the trees were measured; Prov Num: number of the provenances as shown in Figure 1; Stage 2: buds swollen and elongated; Stage 2.5: bud burst; Stage 3: first green becomes visible between bud scales, bud adopts a silver-grey sheen; Stage 4: first folded hairy leaves become visible but remain partially held by the bud; Stage 5: entire leaves cascade from the bud but are still largely folded and flaccid.

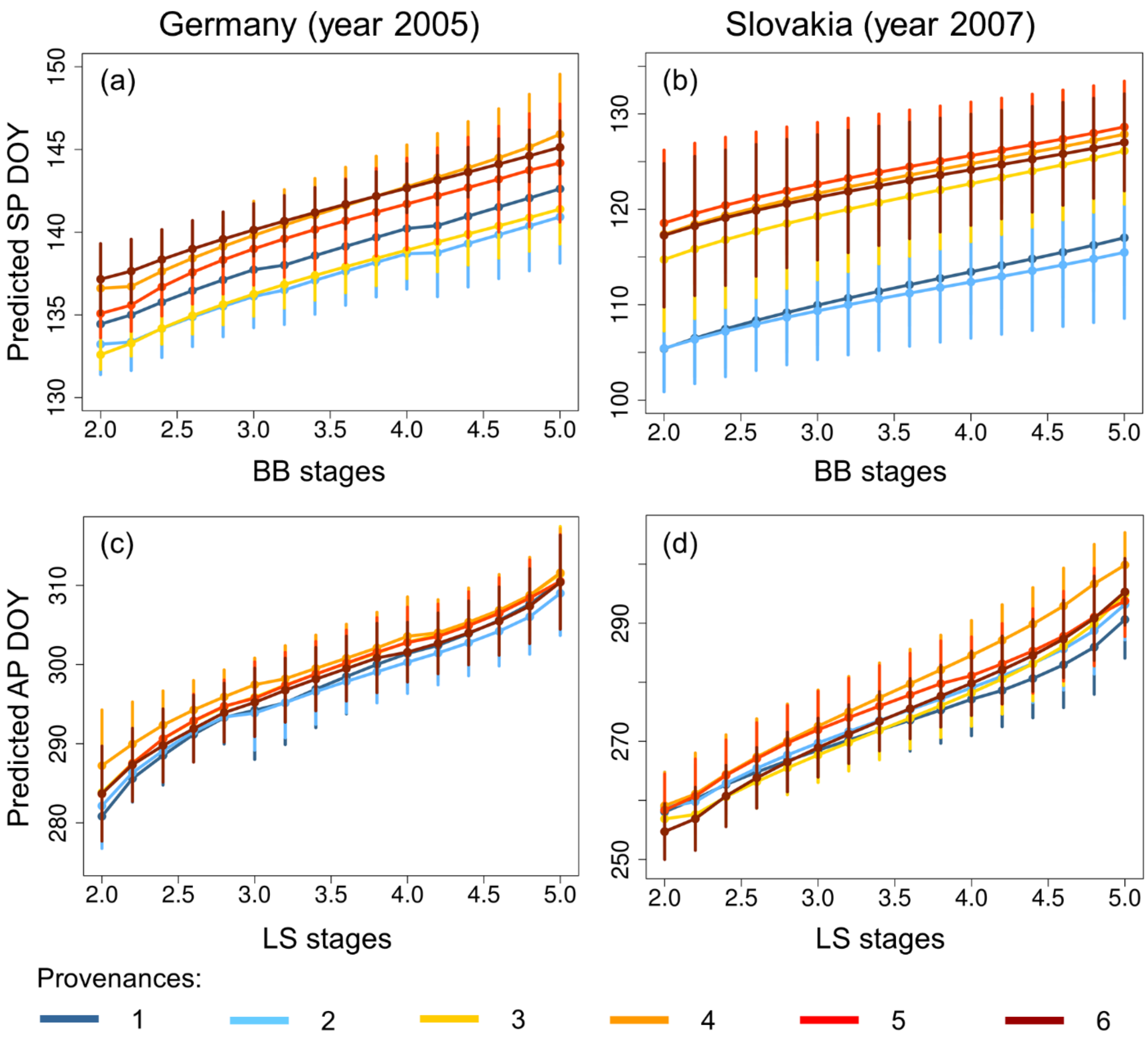
Trial	Prov Num	Stages				
		2	2.5	3	4	5
Germany	1	122.94 ± 1.03	124.62 ± 1.24	126.23 ± 1.44	128.72 ± 2.00	131.12 ± 2.53
Germany	2	124.22 ± 1.83	125.53 ± 1.77	127.11 ± 1.87	129.70 ± 2.14	131.92 ± 2.80
Germany	3	122.59 ± 0.90	124.58 ± 1.05	126.26 ± 1.34	128.91 ± 1.72	131.40 ± 2.11
Germany	4	126.60 ± 1.85	128.04 ± 2.02	129.80 ± 2.07	132.74 ± 2.53	135.92 ± 3.63
Germany	5	124.07 ± 1.46	126.15 ± 1.84	127.99 ± 2.19	130.71 ± 2.77	133.18 ± 3.57
Germany	6	124.16 ± 2.15	125.67 ± 1.76	127.13 ± 1.59	129.70 ± 1.49	132.13 ± 1.60
Slovakia	1	119.46 ± 4.03	121.68 ± 4.01	123.46 ± 4.04	126.49 ± 4.23	129.58 ± 4.59
Slovakia	2	113.46 ± 3.58	116.07 ± 3.41	118.16 ± 3.27	121.75 ± 3.14	125.38 ± 3.22
Slovakia	3	124.86 ± 3.36	126.95 ± 3.18	128.60 ± 3.07	131.38 ± 2.96	134.14 ± 3.00
Slovakia	4	123.61 ± 3.69	125.84 ± 3.48	127.58 ± 3.32	130.48 ± 3.12	133.35 ± 3.03
Slovakia	5	127.76 ± 3.81	129.64 ± 3.52	131.12 ± 3.29	133.62 ± 2.93	136.11 ± 2.66
Slovakia	6	124.28 ± 4.08	126.15 ± 3.88	127.64 ± 3.72	130.13 ± 3.46	132.61 ± 3.24

2 Predicted DOY for autumn leaf senescence stages

Table S2 Predicted DOY for autumn leaf senescence stages. The predicted mean day and standard error for each stage of autumn leaf senescence is given for each provenance and trial. Trial: trial where the trees were measured; Prov Num: number of the provenance as shown in Figure 1; Stage 2: <5% of leaves yellow; Stage 3: <50% of leaves yellow; Stage 4: <100% of leaves yellow; Stage 5: winter state.

Trial	Prov Num	Stages			
		2	3	4	5
Germany	1	305.00 ± 2.65	310.24 ± 3.07	314.35 ± 3.86	320.57 ± 4.68
Germany	2	303.47 ± 5.63	309.26± 4.08	313.51 ± 4.28	319.20 ± 2.88
Germany	3	305.40 ± 2.69	310.94 ± 3.34	315.31 ± 4.11	321.64 ± 4.92
Germany	4	306.11 ± 3.27	311.21 ± 4.02	315.27± 4.72	320.66 ± 0.31
Germany	5	305.27 ± 3.20	310.80 ± 3.30	315.25 ± 3.81	321.33 ± 4.37
Germany	6	307.19 ± 2.37	312.50 ± 3.07	316.63 ± 3.65	321.99 ± 3.59
Slovakia	1	253.57 ± 10.06	268.27 ± 8.32	277.90 ± 6.68	291.63 ± 4.67
Slovakia	2	255.64 ± 8.91	270.40 ± 8.27	280.68 ± 6.49	293.47 ± 2.81
Slovakia	3	248.06 ± 7.66	266.50 ± 6.17	277.57 ± 5.10	292.26 ± 4.25
Slovakia	4	254.94 ± 8.76	272.01 ± 5.67	282.54± 5.33	294.13 ± 3.80
Slovakia	5	251.51 ± 6.33	268.52 ± 5.70	279.38 ± 5.61	294.14 ± 4.25
Slovakia	6	246.53 ± 6.75	265.49 ± 6.12	277.74 ± 5.25	293.73 ± 2.92

3 Predicted bud burst and leaf senescence stages in Germany (year 2005) and Slovakia (year 2007)

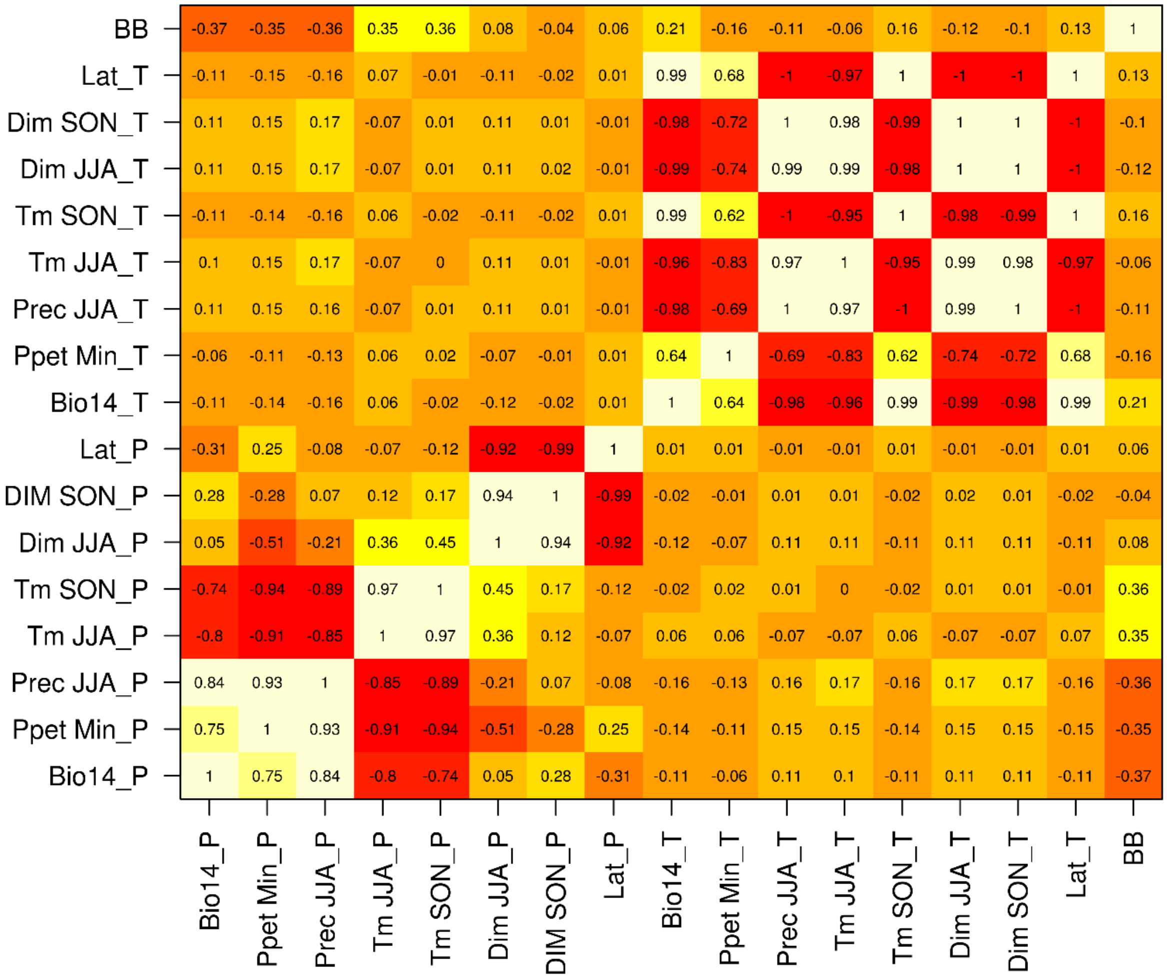


Spring leaf flushing phenology stages	
2	Buds swollen and elongated.
2.5	Bud burst.
3	First green becomes visible between bud scales, bud adopts a silver-grey sheen.
4	First folded hairy leaves become visible but remain partially held by the bud.
5	Entire leaves cascade from the bud, but are still largely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

Figure S1. 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 colors 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 2005 in Germany and 2007 in Slovakia.

4 Correlation Matrix



	Bio14_P	Ppet Min_P	Prec JJA_P	Tm JJA_P	Tm SON_P	Dim JJA_P	DIM SON_P	Lat_P	Bio14_T	Ppet Min_T	Prec JJA_T	Tm JJA_T	Tm SON_T	Dim JJA_T	Dim SON_T	Lat_T	BB
BB	-0.37	-0.35	-0.36	0.35	0.36	0.08	-0.04	0.06	0.21	-0.16	-0.11	-0.06	0.16	-0.12	-0.1	0.13	1
Lat_T	-0.11	-0.15	-0.16	0.07	-0.01	-0.11	-0.02	0.01	0.99	0.68	-1	-0.97	1	-1	-1	1	0.13
Dim SON_T	0.11	0.15	0.17	-0.07	0.01	0.11	0.01	-0.01	-0.98	-0.72	1	0.98	-0.99	1	1	-1	-0.1
Dim JJA_T	0.11	0.15	0.17	-0.07	0.01	0.11	0.02	-0.01	-0.99	-0.74	0.99	0.99	-0.98	1	1	-1	-0.12
Tm SON_T	-0.11	-0.14	-0.16	0.06	-0.02	-0.11	-0.02	0.01	0.99	0.62	-1	-0.95	1	-0.98	-0.99	1	0.16
Tm JJA_T	0.1	0.15	0.17	-0.07	0	0.11	0.01	-0.01	-0.96	-0.83	0.97	1	-0.95	0.99	0.98	-0.97	-0.06
Prec JJA_T	0.11	0.15	0.16	-0.07	0.01	0.11	0.01	-0.01	-0.98	-0.69	1	0.97	-1	0.99	1	-1	-0.11
Ppet Min_T	-0.06	-0.11	-0.13	0.06	0.02	-0.07	-0.01	0.01	0.64	1	-0.69	-0.83	0.62	-0.74	-0.72	0.68	-0.16
Bio14_T	-0.11	-0.14	-0.16	0.06	-0.02	-0.12	-0.02	0.01	1	0.64	-0.98	-0.96	0.99	-0.99	-0.98	0.99	0.21
Lat_P	-0.31	0.25	-0.08	-0.07	-0.12	-0.92	-0.99	1	0.01	0.01	-0.01	-0.01	0.01	-0.01	-0.01	0.01	0.06
DIM SON_P	0.28	-0.28	0.07	0.12	0.17	0.94	1	-0.99	-0.02	-0.01	0.01	0.01	-0.02	0.02	0.01	-0.02	-0.04
Dim JJA_P	0.05	-0.51	-0.21	0.36	0.45	1	0.94	-0.92	-0.12	-0.07	0.11	0.11	-0.11	0.11	0.11	-0.11	0.08
Tm SON_P	-0.74	-0.94	-0.89	0.97	1	0.45	0.17	-0.12	-0.02	0.02	0.01	0	-0.02	0.01	0.01	-0.01	0.36
Tm JJA_P	-0.8	-0.91	-0.85	1	0.97	0.36	0.12	-0.07	0.06	0.06	-0.07	-0.07	0.06	-0.07	-0.07	0.07	0.35
Prec JJA_P	0.84	0.93	1	-0.85	-0.89	-0.21	0.07	-0.08	-0.16	-0.13	0.16	0.17	-0.16	0.17	0.17	-0.16	-0.36
Ppet Min_P	0.75	1	0.93	-0.91	-0.94	-0.51	-0.28	0.25	-0.14	-0.11	0.15	0.15	-0.14	0.15	0.15	-0.15	-0.35
Bio14_P	1	0.75	0.84	-0.8	-0.74	0.05	0.28	-0.31	-0.11	-0.06	0.11	0.1	-0.11	0.11	0.11	-0.11	-0.37

Figure S2 Correlation matrix between all the variables (provenance and trial variables) tested in the leaf senescence models.

5 Trial environmental variable selection

Table S3 Selection of the most important variables of leaf senescence related to the trial. AIC: Akaike information criterion; *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); BIO14: precipitation of driest month; Ppet Min: minimal annual water balance; P jja: precipitation of January, July and August; Tm JJA: mean temperature of January, July and August; Tm SON: mean temperature of September, October and November; DIM JJA: mean daily insolation of June, July and August; DIM SON: mean daily insolation of September, October and November.

Mean Temperature				
	AIC	R^2M	R^2C	Effect
Tm SON	-6356.71	0.52	0.99	+
TM JJA	-6329.15	0.12	0.98	+

Mean daily insolation				
	AIC	R^2M	R^2C	Effect
DIM JJA	-6517.52	0.22	0.99	+
DIM SON	-5899.99	0.15	0.99	+

Photoperiod				
Latitude	-5841.32	0.54	0.89	+

Precipitation				
	AIC	R^2M	R^2C	Effect
Ppet Min	-6280.78	0.03	0.96	-
P JJA	-5919.31	0.58	0.98	-
BIO14	-5840.82	0.01	0.94	-

6 Final model selection

Table S4 AIC values obtained for the series of leaf senescence models. BB: bud burst; ET: environmental variable of the trial; EP: environmental variable of the provenance; AIC: Akaike information criterion; Tm SON: mean temperature of September, October and November; Tm JJA: mean temperature of June, July and August; Dim SON: mean daily insolation of September, October and November; Dim JJA: mean daily insolation of June, July and August.

BB	**Trial**	**Prov**	**AIC**
BB	Tm SON	Tm SON	-6386.39
BB	Tm SON	Tm JJA	-6386.09
BB	Tm SON	DIM SON	-6375.72
BB	Tm SON	Dim JJA	-6377.44

7 Leaf senescence and bud burst interactions (growing season length)

Leaf senescence was later in those trees with early bud burst in warm populations, whilst for colder populations, later leaf senescence was expected in those trees with later bud burst (Figure S2a). Under future conditions, our results predict a change in leaf senescence patterns for cold populations: leaf senescence started later in those trees with earlier bud burst (Figure S2b). As a consequence, colder populations are predicted to increase their growing season length (Figure S2b).

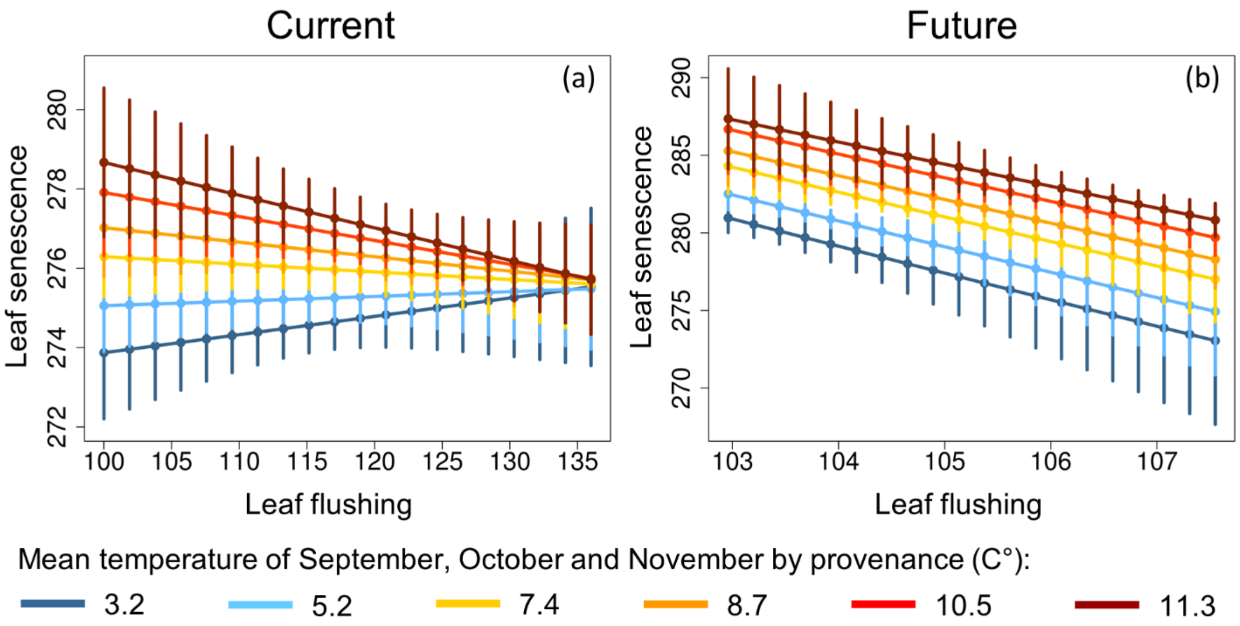


Figure S3 Interactions between leaf senescence and bud burst (i.e. growing season length; represented as day of the year) for (a) provenance climate (1900-1990) and (b) future climate (2070, RCP 8.5) according to mean temperatures in September, October and November (Tm SON) of the provenance. The color gradient depicts the clinal variation from cold (blue) to warm (red) populations (Tm SON). The vertical lines represent the confidence intervals.

SUPPORTING INFORMATION: CHAPTER 3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1. Analysis of variance

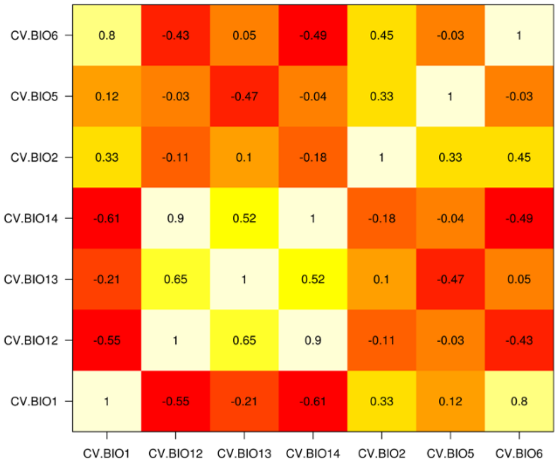
Table S1. Results from the analysis of variance to test phenotypic plasticity variation across developmental stages and for vertical growth, radial growth and young tree survival. df= degrees of freedom; Sum sq= Sum of squares; F= F-value; p= p-value; PPI= phenotypic plasticity index.

	df	Sum Sq	F	p	
Vertical growth					
PPI	2	0.33937	1694.5	< 2.2e-16	***
Residuals	612	0.06128			
Radial growth					
PPI	1	1.37785	297581	< 2.2e-16	***
Residuals	372	0.00172			
Young tree survival					
PPI	1	0.02647	1366.5	< 2.2e-16	***
Residuals	226	0.00438			

2. Correlation matrix

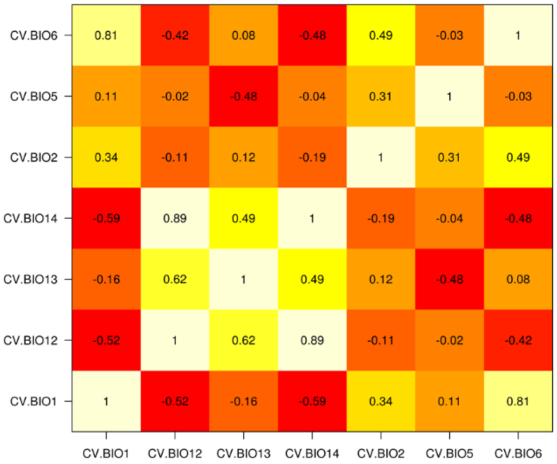
Figure S1. Correlation matrix between all climatic variables selected for each trait analyzed. SD = coefficients of inter-annual past climate variation; BIO1.SD= annual mean temperature; BIO13.SD= precipitation of the wettest month; BIO2.SD= mean diurnal range; BIO5.SD= maximum temperature of the warmest month.

(a) Vertical growth



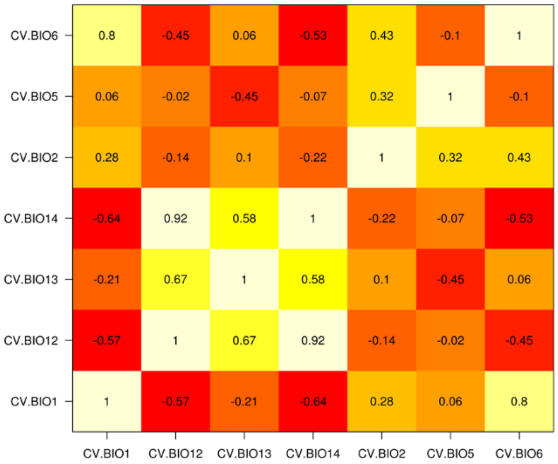
	CV.BIO1	CV.BIO12	CV.BIO13	CV.BIO14	CV.BIO2	CV.BIO5	CV.BIO6
CV.BIO6	0.8	-0.43	0.05	-0.49	0.45	-0.03	1
CV.BIO5	0.12	-0.03	-0.47	-0.04	0.33	1	-0.03
CV.BIO2	0.33	-0.11	0.1	-0.18	1	0.33	0.45
CV.BIO14	-0.61	0.9	0.52	1	-0.18	-0.04	-0.49
CV.BIO13	-0.21	0.65	1	0.52	0.1	-0.47	0.05
CV.BIO12	-0.55	1	0.65	0.9	-0.11	-0.03	-0.43
CV.BIO1	1	-0.55	-0.21	-0.61	0.33	0.12	0.8

(b) Radial growth



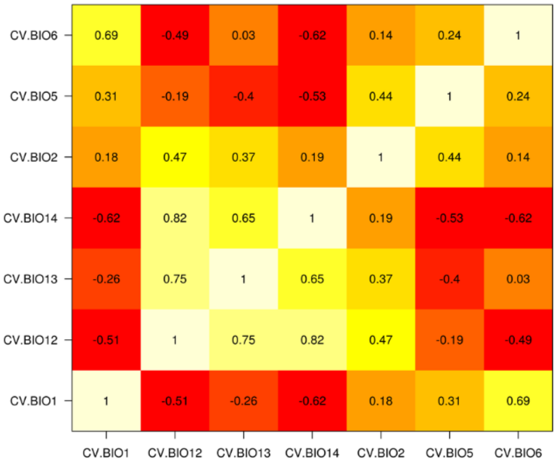
	CV.BIO1	CV.BIO12	CV.BIO13	CV.BIO14	CV.BIO2	CV.BIO5	CV.BIO6
CV.BIO6	0.81	-0.42	0.08	-0.48	0.49	-0.03	1
CV.BIO5	0.11	-0.02	-0.48	-0.04	0.31	1	-0.03
CV.BIO2	0.34	-0.11	0.12	-0.19	1	0.31	0.49
CV.BIO14	-0.59	0.89	0.49	1	-0.19	-0.04	-0.48
CV.BIO13	-0.16	0.62	1	0.49	0.12	-0.48	0.08
CV.BIO12	-0.52	1	0.62	0.89	-0.11	-0.02	-0.42
CV.BIO1	1	-0.52	-0.16	-0.59	0.34	0.11	0.81

(c) Budburst



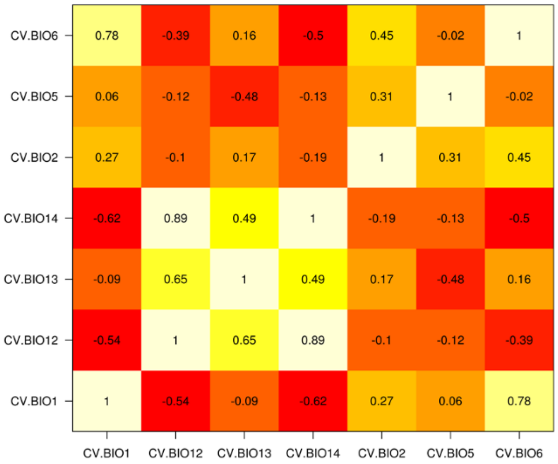
	CV.BIO1	CV.BIO12	CV.BIO13	CV.BIO14	CV.BIO2	CV.BIO5	CV.BIO6
CV.BIO6	0.8	-0.45	0.06	-0.53	0.43	-0.1	1
CV.BIO5	0.06	-0.02	-0.45	-0.07	0.32	1	-0.1
CV.BIO2	0.28	-0.14	0.1	-0.22	1	0.32	0.43
CV.BIO14	-0.64	0.92	0.58	1	-0.22	-0.07	-0.53
CV.BIO13	-0.21	0.67	1	0.58	0.1	-0.45	0.06
CV.BIO12	-0.57	1	0.67	0.92	-0.14	-0.02	-0.45
CV.BIO1	1	-0.57	-0.21	-0.64	0.28	0.06	0.8

(d) Leaf senescence



	CV.BIO1	CV.BIO12	CV.BIO13	CV.BIO14	CV.BIO2	CV.BIO5	CV.BIO6
CV.BIO6	0.69	-0.49	0.03	-0.62	0.14	0.24	1
CV.BIO5	0.31	-0.19	-0.4	-0.53	0.44	1	0.24
CV.BIO2	0.18	0.47	0.37	0.19	1	0.44	0.14
CV.BIO14	-0.62	0.82	0.65	1	0.19	-0.53	-0.62
CV.BIO13	-0.26	0.75	1	0.65	0.37	-0.4	0.03
CV.BIO12	-0.51	1	0.75	0.82	0.47	-0.19	-0.49
CV.BIO1	1	-0.51	-0.26	-0.62	0.18	0.31	0.69

(d) Young tree survival



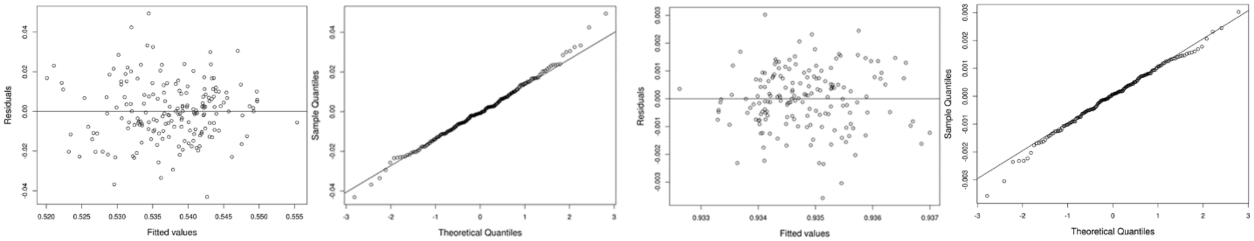
	CV.BIO1	CV.BIO12	CV.BIO13	CV.BIO14	CV.BIO2	CV.BIO5	CV.BIO6
CV.BIO6	0.78	-0.39	0.16	-0.5	0.45	-0.02	1
CV.BIO5	0.06	-0.12	-0.48	-0.13	0.31	1	-0.02
CV.BIO2	0.27	-0.1	0.17	-0.19	1	0.31	0.45
CV.BIO14	-0.62	0.89	0.49	1	-0.19	-0.13	-0.5
CV.BIO13	-0.09	0.65	1	0.49	0.17	-0.48	0.16
CV.BIO12	-0.54	1	0.65	0.89	-0.1	-0.12	-0.39
CV.BIO1	1	-0.54	-0.09	-0.62	0.27	0.06	0.78

3. Variance inflator factors for each trait

Table S2. Variance inflator factors (VIF) of all climatic variables selected for each trait analyzed. SD = coefficients of inter-annual past climate variation; BIO1.SD= annual mean temperature; BIO13.SD= precipitation of the wettest month; BIO2.SD= mean diurnal range; BIO5.SD= maximum temperature of the warmest month.

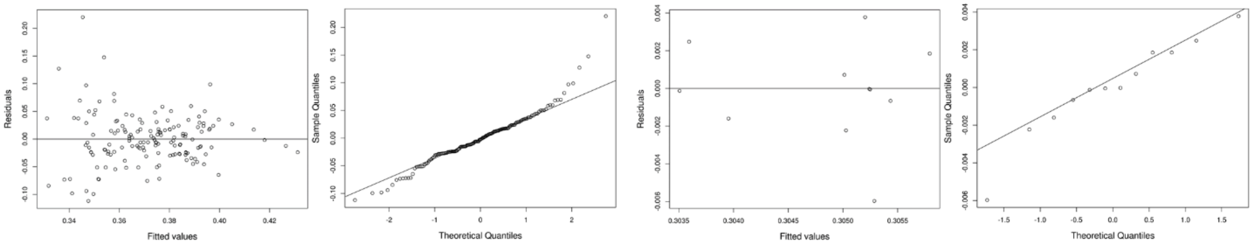
Vertical growth		**Radial growth**		**Budburst**		**Leaf senescence**		**Young tree survival**	
Variables	**VIF**	**Variables**	**VIF**	**Variables**	**VIF**	**Variables**	**VIF**	**Variables**	**VIF**
BIO1.SD	3.697894	BIO1.SD	3.817353	BIO1.SD	3.658544	BIO1.SD	2.682016	BIO1.SD	3.270998
BIO12.SD	8.912565	BIO12.SD	7.851618	BIO12.SD	10.258549	BIO12.SD	14.384663	BIO12.SD	8.457002
BIO13.SD	4.483871	BIO13.SD	4.303327	BIO13.SD	5.204505	BIO13.SD	12.06235	BIO13.SD	4.963156
BIO14.SD	6.047725	BIO14.SD	5.371728	BIO14.SD	7.292655	BIO14.SD	8.383299	BIO14.SD	5.686521
BIO2.SD	1.769878	BIO2.SD	1.894231	BIO2.SD	1.902997	BIO2.SD	3.682287	BIO2.SD	1.775625
BIO5.SD	2.430031	BIO5.SD	2.49365	BIO5.SD	2.580604	BIO5.SD	4.30043	BIO5.SD	2.252453
BIO6.SD	4.024126	BIO6.SD	4.261285	BIO6.SD	4.15897	BIO6.SD	8.627436	BIO6.SD	3.808057

4. Residuals of best-supported models



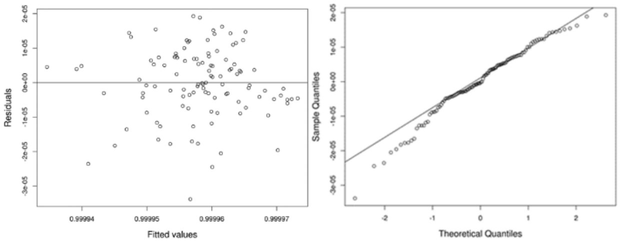
(a) Vertical growth

(b) Radial growth



(c) Budburst

(d) Leaf senescence



(e) Young tree survival

Figure S2. Plots of residuals of the best-supported models for (a) vertical growth, (b) radial growth, (c) budburst, (d) leaf senescence and (f) young tree survival. Figures show for each trait the fitted values against residuals in left panel, and the theoretical quantiles against sample quantiles in right panel.