

Phenological plasticity will not help all species adapt to climate change

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Abstract

Concerns are rising about the capacity of species to adapt quickly enough to climate change. In long-lived organisms such as trees, genetic adaptation is slow, and how much phenotypic plasticity can help them cope with climate change remains largely unknown. Here, we assess whether, where and when phenological plasticity is and will be adaptive in three major European tree species. We use a process-based species distribution model, parameterized with extensive ecological data, and manipulate plasticity to suppress phenological variations due to interannual, geographical and trend climate variability, under current and projected climatic conditions. We show that phenological plasticity is not always adaptive and mostly affects fitness at the margins of the species' distribution and climatic niche. Under current climatic conditions, phenological plasticity constrains the northern range limit of oak and beech and the southern range limit of pine. Under future climatic conditions, phenological plasticity becomes strongly adaptive towards the trailing edges of beech and oak, but severely constrains the range and niche of pine. Our results call for caution when interpreting geographical variation in trait means as adaptive, and strongly point towards species distribution models explicitly taking phenotypic plasticity into account when forecasting species distribution under climate change scenarios.

Keywords: climate change, climatic niche, European beech, phenology, Scots pine, sessile oak, species distribution model

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Introduction

Concerns are rising about the capacity of species to adapt quickly enough to global warming (Burrows *et al.*, 2011; Dawson *et al.*, 2011; Hoffmann & Sgrò, 2011). These adaptations imply genetic changes as well as nongenetic changes in trait values (Hoffmann & Sgrò, 2011; Merilä & Hendry, 2014). In long-lived organisms such as trees, genetic adaptation is slow (Savolainen *et al.*, 2004), and how much phenotypic plasticity, that is the production of several phenotypes from a single genotype in different environmental conditions, can help them cope with climate change remains largely unknown (Anderson *et al.*, 2012; Franks *et al.*, 2014; Merilä & Hendry, 2014).

Phenotypic plasticity is adaptive when the phenotype changes in a direction favoured by selection in the new environment (Conover & Schultz, 1995); that is, the phenotypic change results in higher fitness than if there was no phenotypic change. For instance, Great Tits adjust their laying date according to spring tempera-

ture, which allows matching the timing of high food demand with peaks of insect abundance, thus mitigating the impact of climate change (Charmantier *et al.*, 2008). Phenotypic plasticity can, however, result in imperfect adaptation in a changing climate, requiring further genetic changes to reduce maladaptation (Gienapp *et al.*, 2013).

As phenotypic plasticity determines fitness in spatially heterogeneous or changing environmental conditions, it is necessarily related to range size and climatic niche breadth, that is, respectively, the geographical and climatic spaces where fitness is not null. In the context of climate change, adaptive phenotypic plasticity is thus expected to mitigate fitness losses, resulting in broader range and climatic niche than in the absence of plasticity. Hence, adaptive reaction norms would result in fewer extinction rates at the trailing edge of the range and/or in wider colonizable areas at the leading edge. Theoretical models have indeed shown that adaptive phenotypic plasticity can limit range contraction under a changing climate (e.g. Valladares *et al.*, 2014) and help further genetic adaptation to stressful environment by slowing down the population decline in those environments (Chevin *et al.*, 2010). However, phenotypic plasticity can also be maladaptive (Ghalambor *et al.*, 2007),

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in particular when environments become unpredictable, thus yielding inappropriate responses and potentially important demographic costs (Reed *et al.*, 2010). Both adaptive and nonadaptive plasticity will play a role in the responses of biodiversity to climate change (Nicotra *et al.*, 2010). Distinguishing between the two thus represents an important research challenge.

Because trees are long lived, they experience variable environmental conditions throughout their lifetime and are likely to show high levels of plasticity. Because of their long generation time, trees are also likely to cope with environmental changes more rapidly through plastic responses than through microevolution (Savolainen *et al.*, 2004; Chevin *et al.*, 2013; Franks *et al.*, 2014). Phenological traits, that is the timing of occurrence of phases of the life cycle, are highly plastic. They vary among places and years, depending mostly on temperature (Schwartz, 2003). The reaction norms of phenology to temperature in plant species result from natural selection, optimizing growing period and reproduction under given environmental conditions. This optimization has to cope with several trade-offs. For example, in boreal and temperate regions, there is a trade-off between maximizing annual carbon assimilation – which favours early leaf unfolding – and reducing the risk of damage caused by frost on vegetative organs – which favours late leaf unfolding (Chaine, 2010). In addition, in ectotherms such as plants, temperature also affects phenology directly by influencing the rates of biochemical processes, which complicates the interpretation of phenotypic plasticity, as it may reflect both physiological constraints and adaptive strategies. Inadequacy of phenology to local climates, leading to failure of mature seed production or bud dormancy release, often explains the position of the northern and southern range limits of trees (Morin *et al.*, 2007). More generally, plant phenology is a major component of fitness and contributes to shape plant species' ecological niches and geographical distributions (reviewed in Chaine, 2010).

By far, most observations of climate change responses have involved alterations of species' phenology (Parmesan, 2006). Reported changes in phenology are mainly advanced spring events, but also delayed fall events. A large part of these shifts in phenology is due to phenotypic plasticity (Franks *et al.*, 2014). Whether these plastic shifts in phenology are adaptive in the context of climate change is, however, open to debate (Chaine, 2010). For instance, earlier growing season in warmer climate could expose populations to drought stress in Mediterranean regions (Misson *et al.*, 2011). In a recent study, Amano *et al.* (2014) found that species showing the weakest changes in flowering dates showed the largest extinction rates at the trailing edge and/or fastest poleward shifts of their range. The

contribution of phenological plasticity to fitness is not easy to measure empirically, especially for long-lived species such as trees; the spatial and temporal scales at which it is adaptive is still unclear. These empirical difficulties are even more acute when trying to predict the adaptive value of current phenological plasticity in future climatic conditions.

Here, we assess whether and where the plasticity of phenological traits is adaptive in three common European trees (European beech *Fagus sylvatica* L., sessile oak *Quercus petraea* (Matt.) Liebl. and Scots pine *Pinus sylvestris* L.) using a process-based species distribution model that describes precisely the phenology of the entire annual cycle. The process-based submodels that describe the reaction norms of each species' phenology to temperature are parameterized using phenological observations in natural populations across the species distribution. These reaction norms generate both interannual and geographical variations of phenological traits and long-term trends under warming climatic conditions (e.g. earlier spring phenology; Parmesan, 2006). For each species, we generated virtual populations with altered levels of plasticity, suppressing the expression of either (i) interannual variation alone, or (ii) both interannual and spatial variations, or (iii) interannual, spatial and trend variations in phenological traits in response to temperature variation. We compared these virtual populations to normally plastic populations to assess how interannual, spatial and trend variation in phenology due to plasticity impacted fitness, and therefore niche breadth and geographical range, in current and future climatic conditions.

Materials and methods

The process-based species distribution model PHENOFT

PHENOFT (Chaine & Beaubien, 2001) is a process-based species distribution model developed for temperate trees. It assumes that the reproductive output and survival of an average individual depend on the dates of occurrence of key phenological events (leaf unfolding, flowering, fruit maturation and leaf senescence) and on its ability to resist temperature and water stresses. Figure 1 gives insight into the submodels determining survival and reproductive output from phenology and abiotic stresses, depending on daily temperature, precipitation and photoperiod.

Each phenological model implemented in PHENOFT assumes a different reaction norm of tissues to temperature. In this study, leaf unfolding and flowering dates are determined using a sequential model that describes an endodormancy phase (bud development is stopped even in optimal meteorological conditions) and a subsequent ecodormancy phase (bud development is stopped only in adverse meteorological conditions). While the endodormancy requires exposure to

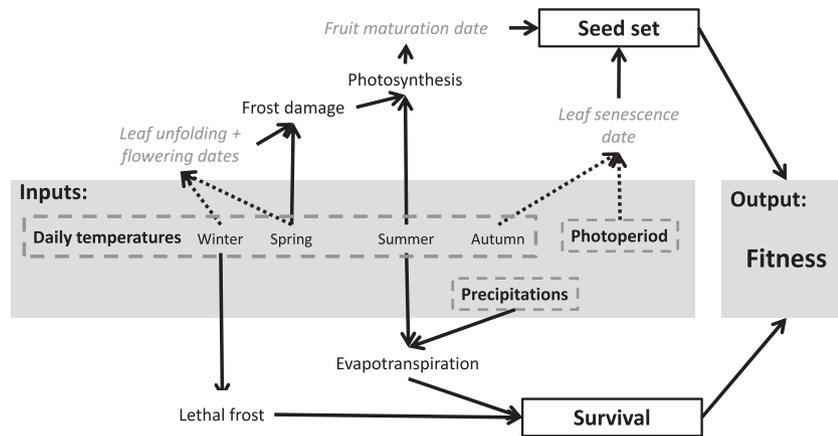


Fig. 1 The model PHENOFIT determines the fitness of an average individual (as the product of seed set and survival) as a function of environmental variables (daily temperatures, photoperiod and precipitation). Arrows show the dependency of each process to environmental drivers or phenological events (grey italics). Each arrow thus represents a reaction norm, calibrated either on time series observations or on experiments. Dotted arrows show the reaction norms that were suppressed in the virtual species with altered levels of plasticity.

cool temperatures for several days to be broken (i.e. chilling), the ecodormancy phase requires warmer temperatures to finish. During each phase (endodormancy and ecodormancy), each species shows a specific reaction norm to temperature. The date of fruit maturation depends on photosynthetic ability, which itself depends on temperature, available water in the soil and the proportion of leaves not destroyed by frost. Leaf senescence is modelled as a function of photoperiod and temperature following the study of Delpierre *et al.* (2009). For each event and each species, reaction norms to temperature, photoperiod and water availability are inferred statistically (see below) using time series data from different sites and different years, that is under a wide range of climatic conditions. These reaction norms are responsible for the temporal and geographical variations of the dates of leaf unfolding, flowering, fruit maturation and leaf senescence (deciduous) or bud set (evergreen) observed in natural populations. In this study, we used the local 20-year average of the product of survival and reproductive output as a proxy for fitness (ranging from 0 to 1). Details on the model are available in the online Supplementary Information file (Section S1).

Climatic data

For each species, the model PHENOFIT was used to compute the yearly phenology, reproductive success and survival of the species over Europe (11°W, 34°N to 32°E, 72°N) over 1981–2000 and 2081–2100 following two climatic scenarios, A1Fi ('business-as-usual') and B2 (lower greenhouse gas emissions; IPCC, 2000). The model was driven by daily climatic data obtained from the general circulation model HadCM3 (Hadley Centre Coupled Model 3, MetOffice Hadley Centre for Climate Change, Exeter, UK, Gordon *et al.*, 2000) downscaled by the ATEAM project at 10' resolution (Mitchell *et al.*, 2004). These data are monthly mean values corrected by their anomalies on the benchmark period (1961–1990, 30 years of mean

climate data). Because daily climate data are needed to run PHENOFIT, we used a stochastic weather generator to create daily temperatures (Nicks *et al.*, 1995; Morin & Chuine, 2005).

Parameterization of observed and altered phenological plasticity

Using a simulated annealing algorithm, we parameterized the different phenological models using time series observations of the different phenological events in natural populations and corresponding daily temperatures, for three common European tree species: European beech *Fagus sylvatica*, sessile oak *Quercus petraea* and Scots pine *Pinus sylvestris*. Although reaction norms of phenology to climatic cues may vary across the range of a species, we deliberately fitted a single phenological model per event (leaf unfolding, flowering, fruit maturation and leaf senescence) and per species for two reasons. First, our objective here was to disentangle the effects of plasticity on fitness and to decompose the interannual, spatial and trend effects of the reaction norms. We here assess the fitness effect of the spatial variation in phenological traits due to spatial variation in climates only, excluding variation due to potential local adaptation of the reaction norms of phenology to climate. Second, accounting for local adaptation throughout species' ranges requires long-term accurate phenological records from many populations scattered across the range. Data currently available do not meet this requirement.

We assessed the validity of model projections (without altering plasticity) over the historical time period by comparing modelled fitness to the known distribution of the species, using consensual observed distribution maps (see Supplementary Information Section S2; Duputié *et al.*, 2014). The discriminatory power of the model was fair to good, with areas under the receiver operating curves (Swets, 1988) varying from 0.645 to 0.875 depending on the species (Section S2). This shows that the model can produce a fair representation of observed distri-

butions, even when local adaptation in phenological reaction norms is not taken into account.

Phenological observations of natural populations were obtained from the French and European Phenological Databases (Observatoire des Saisons, <http://www.gdr2968.cnrs.fr/> and PEP 725, <http://www.pep725.eu/>). For *Fagus sylvatica*, leaf unfolding, leaf senescence and flowering date observations were obtained at the European scale (models were calibrated with 575, 560 and 23 observations, respectively), but fruit maturation observations were only collected from French sites (23 observations). For *Quercus petraea*, all event dates were obtained from French sites (522 observations of leaf unfolding, 202 for flowering, 296 for fruit maturation and 228 for leaf senescence). For *Pinus sylvestris*, we did not calibrate phenological models, but used those prescribed by Kramer (1994), which were obtained on a German provenance. Detailed information on the data used is provided in the Supplementary Information file (Section S1).

For each species, PHENOFIT was run using the same climatic data sets but with four nested degrees of phenological plasticity (hereafter called 'Models') (Table 1). In model 0, plasticity was not altered: the empirically determined reaction norms determined the date of occurrence of each phenological event, each year and at each location. In models 1, interannual variation in phenological dates was suppressed. Event dates were imposed at their local 20-year average, and fitness was computed given that constraint. In models 2, phenological dates were set to their 20-year rangewide average according to model 0 for the period considered. Models 2 thus additionally remove geographical variation in phenology due to plasticity. Models 0, 1, 2 were run under historical and future climatic conditions. Models 3 were run under future climatic conditions only. In these models, phenological dates were held at their 1981–2000 rangewide mean, while PHENOFIT was run with future climatic conditions. Models 3 thus further removed the trend variation in phenological traits, due to the expression of phenological plasticity under warmer climates. Our treatments thus progressively remove the spatiotemporal variation of spring and fall event dates due to phenotypic plasticity,

around their mean values. Different predictions about the adaptive value of plasticity would be obtained if different values were used as a nonplastic reference (e.g. earliest or latest recorded date for an event). Exploring such alternative contrasts could inform us on the adaptive value of delaying or accelerating phenology in different locations and years but is out of the scope of this study.

Note that models 0–3 are nested. Comparing models 0 and 3 (or 2 for historical conditions) provides the total contribution of phenological plasticity to fitness. Comparing models 0 and 1 provides the contribution of interannual variation in phenology to fitness. Comparing models 2 and 1 provides the additional contribution of spatial variation in plasticity to fitness. Comparing models 3 and 2 provides the additional contribution of the trend variation in phenology due to global warming (Table 1). Here, phenological plasticity will be considered adaptive when and where fitness is higher in a plastic treatment than in a nonplastic one (e.g. when fitness is higher in model 0 than in models 1, 2 or 3).

The four models were applied to the following traits: (i) spring events (i.e. leaf unfolding and flowering dates – models 1a, 2a and 3a), (ii) fall events (i.e. leaf senescence date – models 1b, 2b and 3b) and (iii) spring and fall events dates (models 1c, 2c and 3c; Table 1). Note that only spring events were manipulated in the evergreen *Pinus sylvestris*. Dates of leaf unfolding and flowering were always set jointly because they are determined largely by the same cues and are highly correlated. The plasticity of the fruit maturation date, which is tightly linked to reproductive success, was not altered for any species, because removing variation in this trait amounted to removing most variation in fitness. Dotted arrows on Fig. 1 show the relationships that were bypassed in PHENOFIT to create the altered plasticity models.

Analysis of simulations

Fitness distribution maps of models were compared on a pixel-by-pixel basis in either the geographical or the climatic space (see Fig. S2 for a worked example). To describe the cli-

Table 1 Nested model design showing which sources of phenological variation are included in the models (X) or not (–). Comparing models 0 and 1 provides the fitness contribution of interannual variation in phenology due to plasticity; comparing models 1 and 2 provides the further fitness contribution of spatial variation in phenology due to plasticity; and comparing models 2 and 3 provides the additional contribution of the trend variation in phenology under warmer climates

Source of variation	Interannual	Spatial	Trend
Model 0: Reference model with empirically fitted reaction norms Dates of spring and fall events vary with locality and across years.	X	X	X
Models 1: Removing the effect of year-to-year fluctuations Dates of spring (1a), fall (1b), or spring & fall events (1c) are forced to their local period average.	–	X	X
Models 2: Removing the effect of spatial variation Dates of spring (2a), fall (2b), or spring & fall events (2c) are forced to their rangewide period average.	–	–	X
Models 3: Removing the effect of trend variation Dates of spring (3a), fall (3b), or spring & fall events (3c) are forced to their rangewide 1981–2000 average.	–	–	–

matic space, we used the first two axes of a principal component analysis conducted on the concatenated climatic data sets (historical and scenarios) of Europe, using eight bioclimatic variables (as in Gritti *et al.*, 2013): mean temperature of the coldest month (°C), mean temperature of the warmest month (°C), number of chilling days, a drought index (Sykes *et al.*, 1996), growing day degrees above 5 °C (°C. day), total amount of precipitation (mm), amount of precipitation during the growing season (mm) and the coefficient of variation of precipitations among seasons. The first axis is mostly driven by temperature variables and the second axis by precipitation variables; they together explain 81% of the total variance.

To compute modelled range area and niche breadth, we considered pixels of the geographical (or climatic) space with mean fitness exceeding 0.1 over the considered period as potentially harbouring the species (or virtual species with altered levels of plasticity). Using this threshold resulted in realistic representations of the species' observed distributions (Section SII.2).

Under climatic scenarios, we distinguished five types of pixels: newly colonized, increase in fitness, decrease in fitness, gone extinct or species absent under current and future conditions. To establish whether plasticity differently affected fitness in these five categories of pixels, we generated generalized least squares models explaining fitness differences among models as a function of pixel type, and assuming spatial autocorrelation followed a Gaussian kernel. Due to computational constraints, these models were established on a subsample of the 10' grid, resampled at a 0.5° resolution, containing 3740 points. Significance of pairwise *t*-tests was assessed using the multcomp R library. All analyses were performed in R 3.0.2 (<http://www.r-project.org/>).

Results

Is phenological plasticity adaptive under historical climatic conditions?

Comparing models 2c and 0 under historical conditions (1981–2000) gives access to the total contribution of phenological plasticity in all traits to fitness under current conditions. Plasticity increases the niche breadth of sessile oak (4.2%) and beech (10.8%) and the range size of beech (6.7%), while it decreases that of oak (−1.5%; Table 2). Note that because geographical locations are not evenly spread in the climatic space (Fig. S3), an increase in climatic niche breadth does not always translate into an increase in range size. In contrast, phenological plasticity strongly decreases the niche breadth (−22.3%) and range size (−15.9%) of Scots pines (Table 2).

Plasticity in phenological events is mostly neutral throughout the niche and distribution of all three species (Fig. 2). For beech and oak, phenological plasticity is strongly adaptive towards the warm (low latitude or altitude) margins, but maladaptive towards their cold

margins (high latitude or altitude). By contrast, in Scots pine, phenological plasticity is rarely adaptive and is maladaptive towards both the warm and – to a lesser extent – cold margins of its niche and distribution in Western Europe (Fig. 2).

The effects of plasticity of spring (Fig. S4) or fall event dates only (Fig. S5) on niche breadth and range size are qualitatively the same (Table 2).

Is phenological plasticity adaptive under future climatic conditions?

Future European climatic space and climatic niches of all three species are projected to expand (Figs 2 and S3), under both scenarios (+18.5–41.9% by 2081–2100 for the climatic niches). Indeed, new combinations of climatic variables are projected to appear, some of which are favourable to these species (especially with moister climates). However, these favourable conditions are projected to appear in scarce locations (Fig. S3); hence, the potential distribution of all three species is projected to shrink by 2.8–17.3% under scenario A1Fi. Under the less extreme scenario B2, the geographical range of Scots pines is projected to shrink by 3.5%, while those of beech and oak is projected to expand by 3.4–6.8% (Fig. S6).

Under scenario A1Fi, plasticity strongly increases niche breadth (by 35.3% and 17.8%) and range size (by 55.1% and 39.7%) in beech and oak, respectively (Table 2). Positive effects of plasticity are widespread through the niches and ranges of beech and oak, especially towards the southern part of their future range – which may include newly colonized regions (Table 2 and Figs 2–3, bottom rows). In Scots pine, the negative effect of plasticity on fitness observed under historical climates increases under scenario A1Fi and results in a 32.8% loss of niche breadth and a 45.0% loss of geographical range (Table 2 and Figs. 2–3, bottom rows). Milder but consistent effects are observed for all three species under scenario B2 (Table S3, Figs S7 and S8).

How do interannual, spatial and trend variation in phenology impact fitness?

The nested design of the models allows us to disentangle how interannual (model 1 – model 0), spatial (model 2 – model 1) and trend variation in traits (model 3 – model 2) affect fitness. Interannual variation in phenology due to plasticity in spring and fall events considered jointly has a surprisingly low, yet positive, effect on niche breadth and range size (0.5–16.8%; Table 2). However, in beech and oak, interannual variation in fall event dates negatively affects fitness (Table 2). In Scots pine (and to a lesser extent in oak),

Table 2 Changes in climatic niche size and geographical range size due to various components of phenotypic plasticity (see Table 1), under historical climatic conditions and scenario A1Fi. In the geographical space, 10' pixels are weighted by their geographical area. Figures shown are relative to the 'plastic' run (model 0)

Trait	Contribution of expressed part of plasticity (relative to model 0)		<i>Fagus sylvatica</i> (%)		<i>Quercus petraea</i> (%)		<i>Pinus sylvestris</i> (%)	
			2081–2100		2081–2100 A1Fi		2081–2100	
			1981–2000	A1Fi	1981–2000	2081–2100 A1Fi	1981–2000	A1Fi
Niche change								
Spring events (models a)	Interannual	0–1a	1.8	1.8	3.5	3.1	3.0	7.9
	Spatial	1a–2a	1.9	8.3	–1.8	–7.2	–25.3	–39.3
	Trend	2a–3a	–	5.3	–	7.8	–	–1.4
	Total	0–3a or 0–2a	3.7	15.4	1.7	3.6	–22.3	–32.8
Fall events (models b)	Interannual	0–1b	–0.6	–1.6	–0.4	–1.4	–	–
	Spatial	1b–2b	4.8	18.2	4.5	6.7	–	–
	Trend	2b–3b	–	15.3	–	10.6	–	–
Both (models c)	Total	0–3b or 0–2b	4.2	31.9	4.1	15.9	–	–
	Interannual	0–1c	1.1	0.5	2.6	1.5	–	–
	Spatial	1c–2c	9.7	22.3	1.7	3.6	–	–
Both (models c)	Trend	2c–3c	–	12.5	–	12.7	–	–
	Total	0–3c or 0–2c	10.8	35.3	4.2	17.8	–	–
	Range change							
Spring events (models a)	Interannual	0–1a	2.0	3.3	7.9	5.5	3.4	16.8
	Spatial	1a–2a	2.3	14.9	–10.1	1.3	–19.3	–59.7
	Trend	2a–3a	–	9.0	–	13.3	–	–2.0
	Total	0–3a or 0–2a	4.3	27.2	–2.2	20.1	–15.9	–45.0
Fall events (models b)	Interannual	0–1b	0.0	–2.2	–0.5	–0.8	–	–
	Spatial	1b–2b	1.8	20.5	–1.5	15.1	–	–
	Trend	2b–3b	–	17.0	–	14.8	–	–
Both (models c)	Total	0–3b or 0–2b	1.7	45.3	–2.0	29.1	–	–
	Interannual	0–1c	2.0	0.6	7.4	4.3	–	–
	Spatial	1c–2c	4.7	27.4	–8.9	17.4	–	–
Both (models c)	Trend	2c–3c	–	27.2	–	18.0	–	–
	Total	0–3c or 0–2c	6.7	55.1	–1.5	39.7	–	–

interannual variation of phenological dates shows curious effects around the margins, with a negative effect within the occupied range at the margin, a neutral effect at the margin and a positive effect outside the margin (Fig. 4).

Further removing spatial variation in phenology has a much larger effect on fitness, range width and niche breadth, explaining a large part of the total effect of removing phenotypic plasticity, with, in consequence, similar patterns of variation in the sign and extent of these effects among species, time periods and positions in the climatic and geographical space, as described for the total effect of plasticity above (Table 2, Fig. 2). This is because climatic variations across the geographical range of the three species are much stronger than those encountered across years in any given location.

The observed reaction norms of phenological events further affect fitness under warmer climates. For beech and oak, phenological plasticity tends to advance spring events and to delay fall events under warmer climates. This trend variation positively affects fitness at

the core and trailing edge of the projected distributions of both species (Fig. 3). For Scots pines, spring events are projected to be delayed in most of its current range under warmer climate; hence, the trend variation in spring events due to phenological plasticity negatively affects fitness towards the trailing edge and most of the distribution of this species (Fig. 3).

Discussion

Determining the contribution of phenotypic plasticity to fitness, niche breadth and range size is not an easy task, especially for long-lived species. In temperate trees, leaf unfolding and flowering phenology are constrained by two opposite selective pressures: early leaf unfolding increases carbon assimilation and early flowering increases the probability to achieve fruit maturation before adverse meteorological conditions arise, but they both also increase the probability of spring frost damage on leaves and flowers or developing fruits. Temperature also drives the rates of biochemical

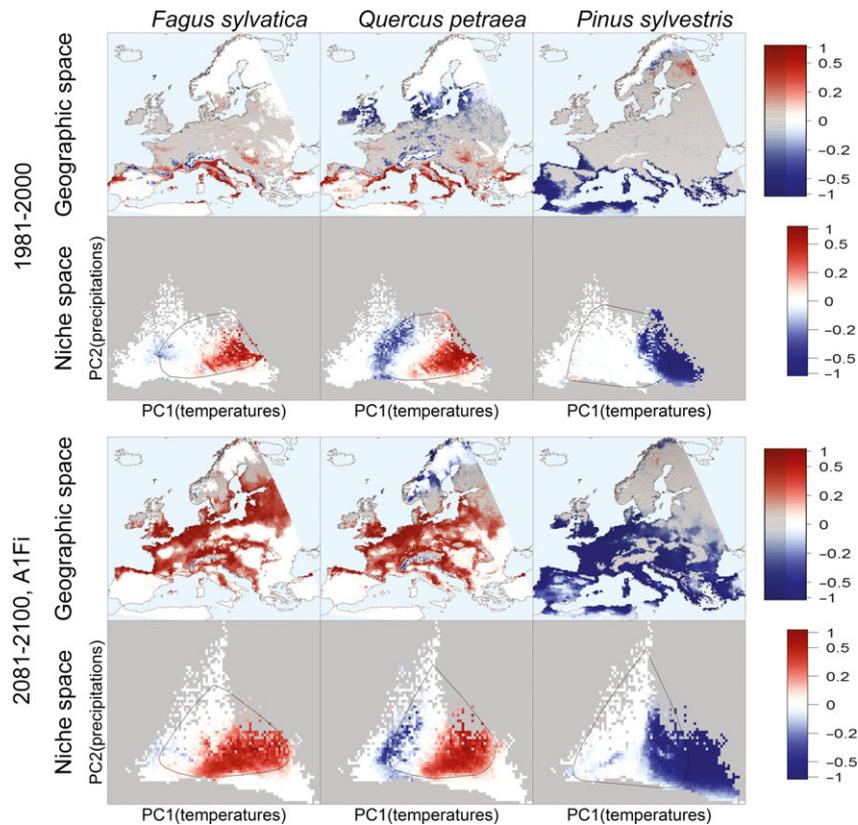


Fig. 2 Total contribution of plasticity to fitness, in the geographical (top and third row) and climatic spaces (second and bottom row), under historical conditions (1981–2000, model 0 – model 2c; top two rows) and under scenario A1Fi (2081–2100; model 0 – model 3c; bottom two rows). Blue zones indicate locations where phenological plasticity is costly and red zones, where it is advantageous. Black dots in the geographical space and black lines in the climatic space represent the regions where modelled fitness in model 0 exceeds 0.1. Geographical space: Lambert azimuthal equal area projection.

processes, setting constraints on the timing of organ development. Hence, a plant's phenology results both from physiological constraints and from adaptive strategies. Thus, it may not be adaptive everywhere and/or each year. Using a process-based tree species distribution model, we show that plasticity of phenological traits increases niche breadth and range size of oak and beech, especially in future climatic conditions. This result is in line with the common expectations that plasticity, when adaptive, increases niche breadth (Richards *et al.*, 2006; Willis *et al.*, 2008) and helps species adapt to climate change (Gienapp *et al.*, 2013; Franks *et al.*, 2014). It is also in line with previous studies showing that high plasticity in various fitness-related traits facilitates range expansions during invasions (Davidson *et al.*, 2011). However, we also show that phenological plasticity decreases niche breadth and range size of Scots pine, illustrating the limits of plasticity due to physiological constraints. The common expectation that plasticity increases niche breadth and helps species adapt to climate change therefore thus holds true for some species only.

Different species, different reaction norms and different effects of plasticity

As compared to the two deciduous species, phenological plasticity in Scots pines shows very different effects. This is because the phenology of Scots pines shows a distinct reaction norm of bud development to temperature.

Bud dormancy break requires higher amounts of chilling in Scots pine than in oak and beech (Hänninen & Pelkonen, 1989; Heide, 1993; Vitasse *et al.*, 2010). This generates different spatial trends of leaf unfolding and flowering across the species range (Fig. S10, second row). Beech and oak show a more or less linear trend from earlier dates at the warmer margins to later dates at the colder margins because, while chilling requirements are always met, cell growth rate is higher under warmer climates. In contrast, Scots pine shows a unimodal trend with earlier dates at the core of the distribution where chilling requirements are met and cell growth rate is high, and later dates towards the warmer margins – where insufficient chilling delays dormancy break – and towards the colder margins –

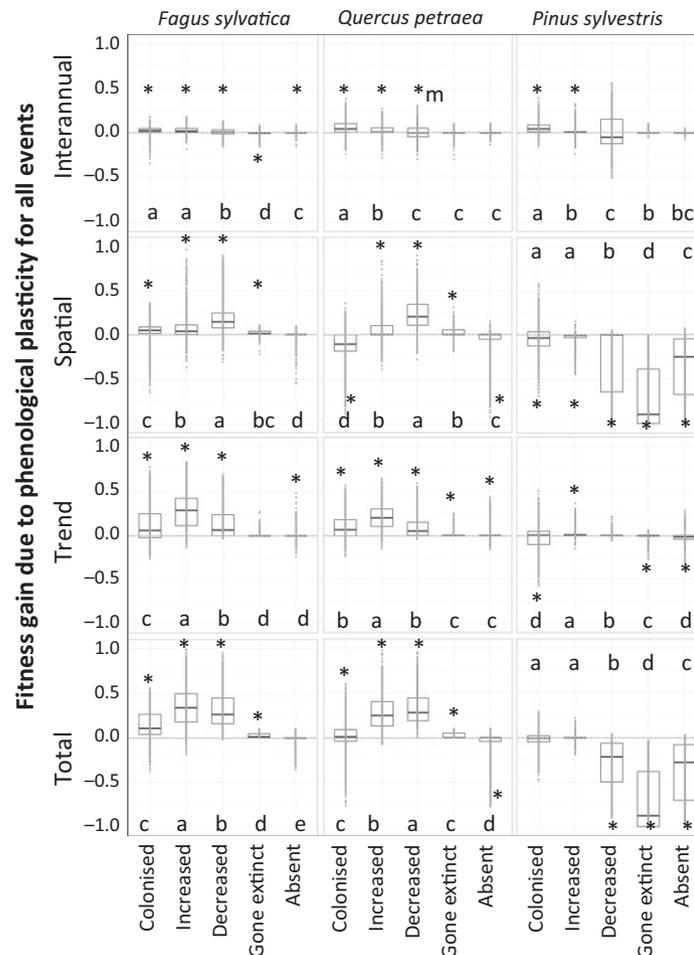


Fig. 3 Box plot showing fitness gains (positive values) or losses (negative values) due to plasticity for the three species (columns), as a function of classes of fitness difference between 2081–2100 (scenario A1Fi) and 1981–2000 (colonized, increased, decreased, gone extinct and absent). Top row: fitness contribution of interannual variation in trait means (model 0 – model 1c). Second row: fitness contribution of geographical variation in trait means (model 1c – model 2c). Third row: fitness contribution of trend variation in trait means (model 2c – model 3c). Fourth row: total contribution of phenological plasticity to fitness (model 0 – model 3c). Stars indicate significant difference from zero at the 5% level, with star location showing the sign of the difference.

where colder temperatures slow down cell growth. The geographical variation in Scots pines' phenology thus also reflects a physiological constraint set by the chilling required to break bud dormancy. Artificially removing the geographical expression of plasticity in Scots pine thus artificially allows the production of fruits in regions where leaf unfolding would naturally occur late in the season, or not at all because of insufficient chilling. Thus, the reaction norm of leaf unfolding date to temperature defines a strong limit to the expansion of Scots pines at the south-western edge of its range.

Among the three species studied here, European beech is the least sensitive to artificial removal of plasticity. Phenology in plants is driven primarily by temperatures and secondarily by photoperiod (Chuine *et al.*, 2013). European beech is known to show a lower

variability in leaf unfolding date than other species, supposedly because this trait is under stronger photoperiodic control in this species compared to others (Vitasse & Basler, 2012). In our simulations, spring event dates indeed showed less variation for this species than for the other two; this may explain why phenological plasticity was found to weakly affect beech fitness.

Why and where is phenological plasticity adaptive?

To understand the different effects of phenological plasticity, one needs to understand the impact of phenology on fitness at the scale of the species' range. Too early leaf unfolding and flowering increase the risk of frost damage, while too late leaf unfolding and flowering compromise the possibility to set fruits.

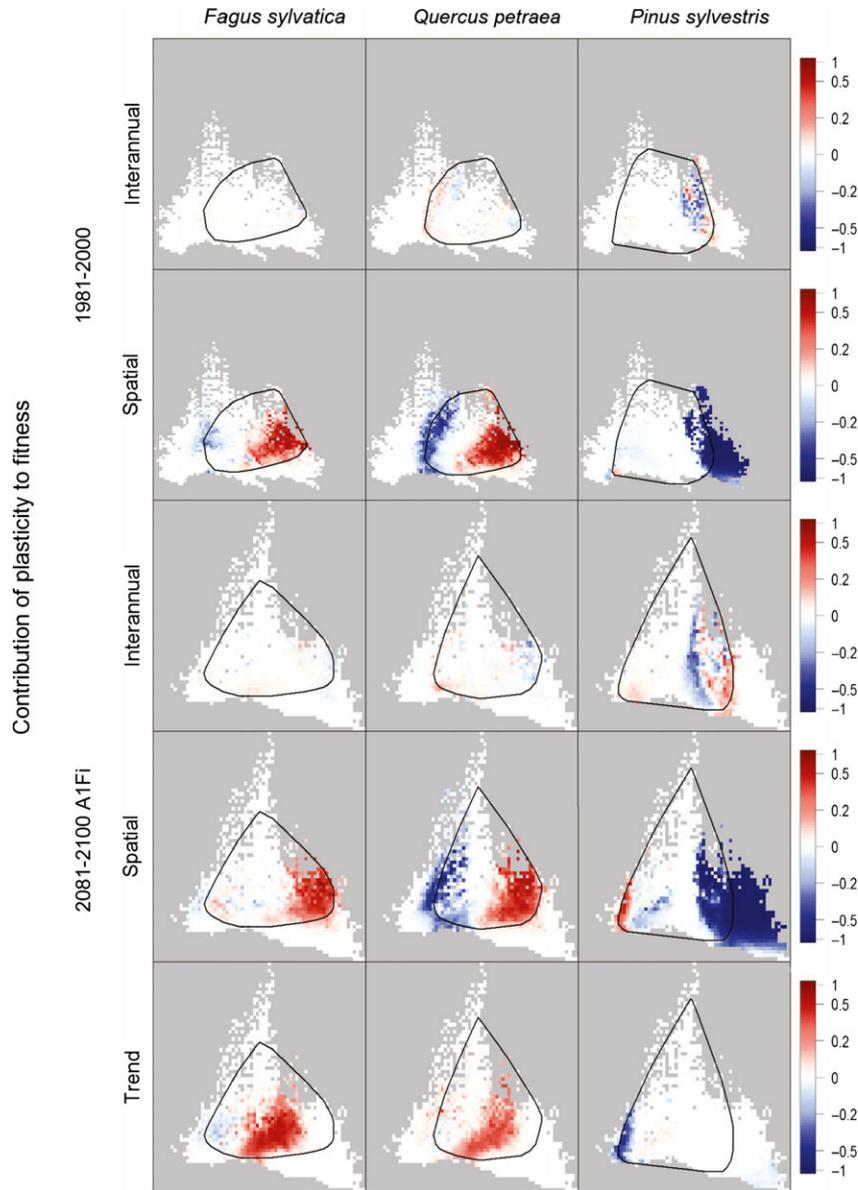


Fig. 4 Fitness gains (or losses) in the climatic space, attributable to the expression of phenological plasticity for all traits (set jointly) among years, across the range and among years under climate warming. The fitness contribution of interannual variation in trait mean is computed as model 0 – model 1c; that of geographical variation in trait mean as model 1c – model 2c; that of trend variation as model 2c – model 3c. Red regions show where plasticity is adaptive; blue regions show where the expression of the trait's reaction norm is maladaptive. The black line indicates the envelope of climatic space where modelled fitness is above 0.1. Note scales differ among rows.

Within the range of all three species, leaf unfolding occurs in a range of 26 (beech), 46 (oak) and 71 (pine) days (Fig. S10) without substantially affecting the ability to set seed (Fig. S11). Thus, within this range, interannual variation in leaf unfolding and flowering dates is almost neutral. Nevertheless, outside this range, fitness decreases rapidly (Fig. S11). Thus, fitness is almost null towards the edges of the species' distributions, where leaf unfolding occurs very late on aver-

age. As a result, interannual variation in phenology can only increase fitness there (see red pixels towards niche margins on the top row of Fig. 4). On the contrary, towards the inner margin of the distribution (and niche), fitness is high on average but not maximal. Hence, interannual variation in phenological dates tends to decrease fitness (blue pixels towards the inner margins of the niche on Fig. 4). Note that at the scale of the whole distribution, the positive fitness

effect of interannual variation in spring events dates dominates over the negative effect of variation in leaf senescence dates (Table 2, and Figs S3 and S4). Indeed, the photosynthesis rate is higher during spring and summer than during fall, and therefore, leaf senescence dates contribute less to fruit maturation than do leaf unfolding dates.

The effect of spatial variation in phenological dates due to plasticity is very contrasted between Scots pine and the two deciduous species because they show different reaction norms to temperature. The spatial variation in phenology due to plasticity negatively affects fitness of the three species towards their colder margins because low temperatures slow down the cell growth which critically delays leaf unfolding and flowering and jeopardize fruit maturation. But its effects at the warmer margins are contrasted: while it positively affects fitness of beech and oak because higher temperatures accelerate the cell growth and result in earlier development, it negatively affects fitness of Scots pine because of the physiological constraint of unmet chilling requirements.

Evolvability of phenological reaction norms

Phenological traits are highly heritable (e.g. Anderson *et al.*, 2012) and tightly linked to fitness (Chaine, 2010; Polgar & Primack, 2011; our results). They are thus expected to respond to selection. Indeed, phenological traits have been shown to have evolved over the last decades in various types of organisms (e.g. Bradshaw & Holzapfel, 2001; Nussey *et al.*, 2005; Kovach *et al.*, 2012; Franks *et al.*, 2014). Local adaptation in phenological traits in trees has also been shown by many provenance trials (Savolainen *et al.*, 2007). For example, the temperature threshold below which winter chill affects dormancy release varies among ecotypes of birch (*Betula* spp, Myking & Heide, 1995). We found that, depending on species, the current reaction norm to temperature produces maladaptive phenology in southern and/or northern margins of the range (or warmer and colder margins of the niche), especially under climate change. We would therefore expect selection to favour a different reaction norm in these marginal localities and selection to intensify as climate warms. However, whether tree populations with a long generation time will be able to evolve fast enough to cope with ongoing climate change remains unclear (Savolainen *et al.*, 2004). How much gene flow from populations where the current reaction norm does not compromise fitness, or enhances it, may constrain the differentiation of locally adapted reaction norms at the margins is also an open question. Further genetic adaptation of the reaction norm to warming climate may

instead be facilitated in localities where plasticity of phenology is adaptive and buys time for adaptation to proceed before extinction (Chevin *et al.*, 2010). In that respect, genetic adaptation is more likely to occur in sessile oak and European beech than in Scots pines: for the latter, plasticity is predicted to be maladaptive towards the trailing edge of the range, where conditions will deteriorate under climate warming, making it even less likely that genetic adaptation can rescue the marginal populations from extinction. In contrast, the exact opposite prediction can be made for oak and beech, with phenotypic plasticity being adaptive precisely in locations threatened by climate warming. Accounting for the differentiation of phenological reaction norms across the range could tamper these predictions (Valladares *et al.*, 2014), especially where phenological plasticity appears to be maladaptive. In this regard, acquiring large-scale phenological data for Scots pines is important, to determine whether the results we obtained for this species are due to phenological reaction norms being calibrated on a single population.

We have shown here that phenological plasticity is not always nor everywhere adaptive and will strongly contribute to either increasing or decreasing species range size under future climatic conditions depending on the species. Our results therefore strongly support the idea that species distribution models should explicitly take phenotypic plasticity into account when trying to forecast the distribution of biodiversity under scenarios of climate change (McMahon *et al.*, 2011; Thuiller *et al.*, 2013; Amano *et al.*, 2014; Valladares *et al.*, 2014). We here illustrate a way to quantify the contribution of phenotypic plasticity to range and niche shifts under climate change in tree species, but similar studies can be conducted for a wider range of organisms, plants and animals, thanks to the growing research on process-based species distribution modelling. Such studies should have a major impact on future research on biodiversity modelling, and on the development of natural resources management and biodiversity conservation strategies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Section S1. The model PHENOFIT and its parameterization.

Table S1. Parameters used in PHENOFIT (*Fagus sylvatica* and *Quercus petraea*).

Table S2. Parameters used in PHENOFIT (*Pinus sylvestris*).

Section S2. Model validation.

Section S3. Supplementary figures and table

Figure S1: Observed distribution and modelled fitness of the three species with treatment 0, under historical conditions.

Figure S2. Fitness distribution maps of treatments were compared on a pixel-by-pixel basis in the geographical and niche space.

Figure S3. Density of geographical pixels in the climatic space of Europe under historical and future conditions under both scenarios.

Figure S4. As main text Fig. 2 but showing results for manipulation of spring events only.

Figure S5. As main text Fig. 2 but showing results for manipulation of fall events only.

Figure S6. Projected fitness in the 'plastic' treatment for the three species for 1981–2000, and 2081–2100, under the two greenhouse gas emission scenarios A1Fi and B2.

Figure S7. As main text Fig. 2 but showing results for both scenarios.

Figure S8. As main text Fig. 3, but under scenario B2.

Figure S9. As main text Fig. 4 but showing results in the geographical space only.

Figure S10. Leaf unfolding dates in the 'plastic' treatment for the current period, and factors limiting fitness.

Figure S11. Predicted mean seed set of sessile oak (1950–2000) at a location in northeastern France (5°E, 49°N), for various imposed fixed dates of leaf unfolding and flowering.

Table S3. Changes in climatic niche size and geographical range size due to various components of phenotypic plasticity under historical conditions and climatic scenarios A1Fi and B2.