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² The home page of the website should contain the generic European flag and the FP7 logo which are available in electronic format at the Europa website (logo of the European flag: http://europa.eu/abc/symbols/emblem/index_en.htm; logo of the 7th FP: http://ec.europa.eu/research/fp7/index_en.cfm?pg=logos). The area of activity of the project should also be mentioned.

Final publishable summary report

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PROJECT TRECC



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EXECUTIVE SUMMARY

Climate change will modify species' distribution ranges (e.g. Thuiller *et al.* 2005; Intergovernmental Panel on Climate Change 2007; Hickler *et al.* 2012). Whether species, and especially temperate trees, will be able to track favourable climates, is currently unknown (Jump & Penuelas 2005). This depends on each species' ability to disperse towards favourable habitats (Kremer *et al.* 2012; Meier *et al.* 2012). Aside from migration, tree species may respond to changing climates by genetic and/or by plastic changes in key traits (such as winter chilling requirements; Chuine 2010). The pace of trait evolution depends on population size, on the strength of selective pressures, on the genetic variance available for these traits, and on genetic trade-offs and multivariate selective pressures acting jointly on them (e.g. Pease *et al.* 1989; Kirkpatrick & Barton 1997; Hoffmann *et al.* 2003; Kirkpatrick 2009; Polechová *et al.* 2009; Walsh & Blows 2009).

This two-year project aimed at (1) determining how genetic correlations between traits and joint selective pressures affected a species' distribution ranges in the context of changing environments; (2) assessing whether genetic evolution could dampen the pessimistic forecasts of future forest trees' ranges in Europe, as provided by a process-based species distribution model.

For this second part, the fellow intended to consider pedunculate oak (*Quercus robur*) as a biological model, and to assess its present and future distribution using an already existing process-based tree distribution model (PHENOFIT, Chuine & Beaubien 2001; Morin & Chuine 2005), whose realism would be improved through its combination with a model of trait evolution (as developed in (1)). To this aim, it was first necessary to (a) allow the process-based model to account for local adaptation; (b) determine the strength of selective pressures; (c) check whether it produced accurate projections of current species distribution ranges (before proceeding to forecasts).

Objective 1 was validated; so were objectives (2-a-c). Objectives (2-a) and (2-c) raised general issues, which were tackled prior to completing the initial Objective 2:

- objective (2-a) raised the question of the extent to which phenotypic plasticity contributes to enlarging the geographic range (or ecological niche) of a species (new objective (2-g)).
- objective (2-c) raised the question of the existence of reliable atlas data for species presence/absence. Indeed, different reference atlases exist in the literature. Model accuracy depends on the map used as a reference. More importantly, for correlative species distribution models, the choice of a reference map modifies the factors recognised as driving a species' distribution, and strongly impacts its forecast. (new objective (2-f))
- objective (2-c) raised the issue of building consensual forecasts or species distributions, taking into account what we know of the strengths and weaknesses of each model (new objective (2-e)).

The fellow considered these issues were important, and tackled them before completed objective 2. As a result, objective 2 is not achieved, but more general and necessary prerequisite questions have been answered instead.

The overall schedule of the project was expanded by 16 weeks, given that the fellow's contract was interrupted for that duration during year 1, for a maternity leave.

CONTEXT & OBJECTIVES

CONTEXT

Ongoing global change, and particularly climatic changes, will strongly affect the demography and geographic range of numerous species. Different types of models have so far investigated how species distributional ranges could evolve when faced to climate change. These can be classified into three broad categories:

1. **theoretical evolutionary models assume that a species' persistence in a given environment depends on the matching between a quantitative trait (e.g. flowering date, size at maturity, ...) and a hypothetical optimal phenotype.** They describe how a species responds to a changing environment (in a spatially heterogeneous or homogeneous environment), according to the speed of the environmental shift, the species' dispersal abilities, and on the magnitudes of selective pressures and of genetic variance. These models offer general results, such as an expression for the maximum speed of change a species can endure without going extinct (e.g. Pease *et al.* 1989). However, these models usually make numerous simplifying assumptions, so that they can be handled analytically. Therefore, their vision of environmental heterogeneity and of species' responses to spatial heterogeneity is greatly oversimplified.

2. **correlative species distribution models describe species distributional ranges as a function of environmental variables, and rely upon the observed relationships between occurrence and bioclimatic variables** (yearly or monthly normals of temperatures and precipitation, soil quality, etc; Thuiller *et al.* 2008). These models are based on purely statistical relationships, which are not related to the species biology and cannot be disentangled from historical contingencies. A strong limitation to these models is therefore that the statistical relationships between climate and geographic distribution will not necessarily be valid under future climates.

3. **process-based species distribution models describe species distributional ranges as a function of environmental variables, based on known relationships between these variables and processes that are important to the species' survival or reproduction** (e.g. growth, respiration, offspring production). These models require calibration on observations or experimental results for each species (e.g. phenological observations together with climatic observations, calibration of a realistic dispersal model, etc). They can then be used to predict species responses to climatic change. Because they describe causal relationships between species growth, survival, or reproductive success, and climate, they are liable to be more conservative than are niche-based models (Morin & Thuiller 2009).

Climatic projections indicate that species or population extinctions will be more frequent in the future (Thomas *et al.* 2004; Morin *et al.* 2008). Even though these modifications are easily observed where climate warming is faster, i.e. in boreal and high-altitude regions, tropical species are also affected by climate change (Warren *et al.* 2001; Walther *et al.* 2002; Parmesan 2006).

Species' extinctions due to climate change may, however, be hampered, or at least delayed, through the modification of their ecological characters (i.e., through adaptation; e.g. Hughes 2000) and/or of their distributional range (i.e., latitudinal displacement; Davis & Shaw 2001; Warren *et al.* 2001; Johnstone & Chapin 2003; Thomas *et al.* 2004; Jump & Penuelas 2005; Parmesan 2006; Walther *et al.* 2007).

Modification of ecological characters often implies changes in phenology, with spring events happening earlier than they used to (e.g. Hughes 2000; Inouye *et al.* 2000; Walther *et al.* 2002; Parmesan & Yohe 2003; Chuine *et al.* 2004; Menzel *et al.* 2006; Cleland *et al.* 2007). Traits may be modified either through phenotypic plasticity (Charmantier *et al.* 2008) or genetic adaptation (Bradshaw & Holzapfel 2001; Davis & Shaw 2001; Jump & Penuelas 2005; Bradshaw & Holzapfel 2006).

While genetic changes are well-considered in theoretical models of species' distribution evolution, changes in dispersal abilities or phenotypic plasticity are usually not considered. These are taken into account by process-based models (and to a lesser extent, by correlative models), which however generally do not consider genetic evolution. Only very recently have process-based models begun to take genetic evolution into account, in a very simplistic way (Kearney *et al.* 2009; Kramer *et al.* 2010).

OBJECTIVES.

The project for this fellowship was to assess how species' distributional ranges would evolve under different scenarios for future climate change, combining the predictive value of an ecological, process-based model (Chuine & Beaubien 2001) with realistic assumptions stemming from a theoretical evolutionary model (Kirkpatrick & Barton 1997), and to apply this model to the case of pedunculate oak (*Quercus robur*) in Europe.

OBJECTIVE 1: BUILD A THEORETICAL MODEL FOR SPECIES' RANGE EVOLUTION UNDER CHANGING ENVIRONMENT.

Initially, the fellow proposed to take genetic drift into account in the model of Kirkpatrick & Barton (1997; i.e. to account for small population sizes towards the edges). However, this question had already been addressed by Alleaume-Benharira *et al.* (2006). Instead, the fellow chose to investigate the extent to which multivariate selective pressures may slow down the evolutionary response of populations facing environmental change. Indeed, this question has long been posed in the literature (Pease & Bull 1988; Etterson & Shaw 2001; Blows & Hoffmann 2005; Agrawal & Stinchcombe 2009; Walsh & Blows 2009), but never addressed directly.

Adaptation to changing environments can be hampered by a number of factors, such as dispersal limitation, interspecific competition, lack of suitable habitats, or reduced densities of peripheral populations (Gaston 2003). An important determinant of species range limits may be the potential for adaptation of quantitative traits to changing environments. Theoretical studies addressing this question have, however, never considered jointly two facts: species adaptation to a given environment depends on numerous traits, and environments are spatially heterogeneous. The fellow built on an earlier model (Kirkpatrick & Barton 1997) to address the following questions:

- how do multivariate constraints, local adaptation, and migration abilities affect a species' persistence when the environment changes?
- how much do they slow adaptation to changing environmental conditions?

OBJECTIVE 2: COMBINE THIS MODEL FOR TRAIT EVOLUTION TO A MODEL GENERATING REALISTIC FITNESS FUNCTIONS, IN ORDER TO PREDICT THE EVOLUTION OF A SPECIES' RANGE.

The ultimate aim of this project was to combine a model of trait evolution (as described above) with a model providing realistic fitness estimates, and to use pedunculate oak (*Quercus robur*) as a model species for conducting forecasts of future ranges.

However, in the model described above, there is a balance between local adaptation and migration (which allows the species to shift its range, but at the same time disrupts locally adapted gene combinations). Moreover, this kind of theoretical model typically assumes a Gaussian-shaped adaptive landscape. However in nature, selection may be neither stabilising nor Gaussian. Finally, before to combine the models, it was necessary to validate the process-based model, through a comparison of the fitness it modelled for *Quercus robur* and the actual distribution of this species.

Objective 2 was thus divided into the following steps:

- (2-a) parameterize PHENOFIT to take local adaptation of *Quercus robur* into account
- (2-b) determine the strength of selective pressures (i.e. the shape of the adaptive landscape)
- (2-c) check that PHENOFIT produced a realistic view of the fitness of *Quercus robur* over Europe, through comparing the fitness output by PHENOFIT over Europe with reference distribution maps of the species;
- (2-d) couple a model of trait genetic evolution with the PHENOFIT model, so as to allow the production of forecasts of future species' distribution ranges that take genetic evolution into account.

Objective (2-a) was attained (indeed, locally adapted parameterizations for the model PHENOFIT were obtained for sessile and pedunculate oaks, *Quercus petraea* & *Quercus robur*; and for common beech, *Fagus sylvatica*). It raised the more fundamental issue of understanding how local adaptation and trait plasticity (i.e. trait variation across years or across locations, for a given genotype) contributed to delineate a species' geographic range. This question was tackled by a Masters student co-supervised by the fellow during Spring 2012.

Objective (2-b) was also attained. While assessing the validity of the newly parameterized model PHENOFIT (objective 2-c), two issues were discovered:

- First, several plant distribution atlases exist in the literature, and they do not agree on the distribution of these common species. The measure of accuracy of any model strongly depends on which map is used as a reference. This is a general issue, concerning not only the process-based model PHENOFIT, but also the widely used correlative environmental niche models such as MAXENT (Phillips et al. 2006) or the various models implemented in the platform BIOMOD (Thuiller et al. 2009). More importantly, since these correlative models (contrary to PHENOFIT) rely on observed distribution ranges to determine which factors limit a species' niche, their forecasts also vary according to the reference map used.

- Second, evaluating the accuracy of the PHENOFIT model required comparison with other models. Correlative and process-based models are known to provide very different forecasts (Buckley 2008; Kearney *et al.* 2009; Morin & Thuiller 2009; Kramer *et al.* 2010; Keenan *et al.* 2011b). The same holds for algorithms underlying correlative niche models (Pearson *et al.* 2006; Thuiller *et al.* 2009; Buisson *et al.* 2010; Grenouillet *et al.* 2011). However, so far the only proposed ways to build consensual models are to let them vote (Araújo & New 2007), sometimes after weighing them according to some confidence measure (Marmion *et al.* 2009), the validity of which relies on which reference distribution map is to be trusted (see point just above). Together with colleagues, the fellow proposed a method to build consensus estimates of species distributions, taking advantage of the strengths of each model, and jointly identifying their weaknesses using projections of current distributions. This method enables one to build robust estimates of future distribution ranges, together with maps of uncertainty.

These two issues were tackled, leaving objective (2-d) yet unfinished. However, this objective will be validated in the next months, given that the fellow obtained further financing to extend this project.

In addition, the fellow was associated to side projects with the research team where she conducted her PhD work, leading to one publication and two submitted papers.

RESULTS

1. A THEORETICAL MODEL FOR SPECIES' RANGE EVOLUTION UNDER CHANGING ENVIRONMENT.

Collaborations: Ophélie Ronce (ISEM Montpellier, France), François Massol (IRSTEA Aix en Provence)

Context: Species can respond to environmental change through a combination of dispersal and (genetically driven or not) phenotypic changes. While both the existence of multivariate constraints to adaptation and the spatial heterogeneity of environments are long recognised, no theoretical model addressed their interplay in shaping a species' response to environmental change.

Model: The model developed here considers the joint evolution of the demography and adaptation of multiple traits of a species distributed along an environmental gradient (space axis x) shifting in time t at speed v (mimicking a latitudinal shift of environmental conditions). At each point in space, the local population's selective value is determined by the matching of the average multitrait phenotype $\bar{\mathbf{z}}$ to an optimum phenotype. We assume that each trait is under stabilizing selection, *i.e.* there is an optimal value for each trait (this optimum varies across space and time).

Population density evolves in space and time through two mechanisms: (i) local population growth rate, due to local selective value, which itself depends on local traits means, and (ii) dispersal of the individuals, which is assumed diffusive, with standard deviation of parent-offspring distance σ . Trait means evolve through three forces: (i) diffusive dispersal of individuals exhibiting some trait values, (ii) asymmetric dispersal of individuals, with more individuals migrating from high-density to low-density regions, and (iii) trait evolution, depending on the selective pressures and on the available genetic variation \mathbf{G} .

Results: Under the assumption that selection is weak, it is possible to analytically solve this model. As in univariate models, the population density is bell-shaped along the spatial axis, and **the peak of population density follows the environmental shift, with a lag L_n (Figure 1, lower panels)**. Trait means develop linear clines, whose slopes are most often much smaller than those of the optima: **local adaptation is imperfect (Figure 1, top panels)**. However, in the presence of correlational selection, some **clines may be in a direction opposite to univariate predictions**: one trait can exhibit higher values where lower values would be selected for, in the absence of other traits.

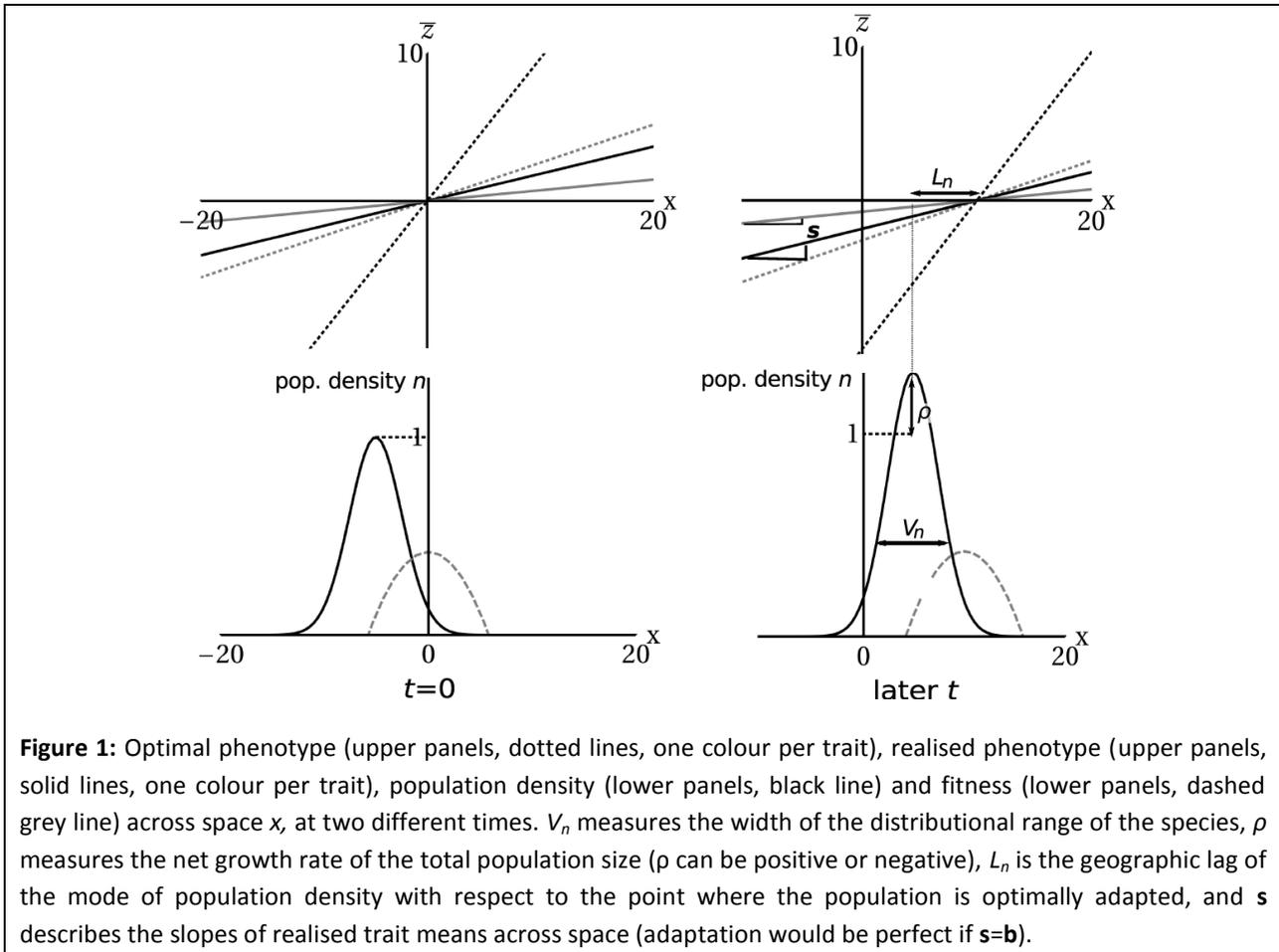
The species' extinction is certain when the environment shifts at a speed faster than

$$v_c = \sigma \sqrt{2r_0 - A\sqrt{B} + \frac{A}{B}}, \text{ where } A \text{ is the adaptive potential of the species } (A = \mathbf{b}^T \mathbf{W}^{-1} \mathbf{G} \mathbf{W}^{-1} \mathbf{b}) \text{ and } B$$

the spatial fitness contrast (*i.e.* the decrease in fitness through a spatial displacement of one unit when at the optimum; $B = \mathbf{b}^T \mathbf{W}^{-1} \mathbf{b}$).

The higher the adaptive potential and the lower the spatial fitness contrast, the faster environmental shifts can be sustained, the wider the species' range and the greatest local adaptation are. These conditions are favoured when nonlinear (stabilising) selection is weak in the phenotypic direction of the change in optimum, and genetic variation is high in the phenotypic direction of the selection gradient (Figure 2).

The effects of dispersal are mixed: while long-distance dispersal lowers local adaptation, because of gene swamping, it increases the size of the distributional range, and increases the geographic lag the population can sustain behind its phenotypic optimum. Hence, **maximal growth rate is obtained for intermediate values of dispersal**.



Implications: These results are important because they pinpoint the role of genetic constraints and of constraints stemming from multivariate selection, on the rate of evolution. This model makes numerous simplifying assumptions, but may be used to assess species persistence on small gradients and over short time scales.

Published paper: P2⁶. Duputié A., Massol F., Chuine I., Kirkpatrick M., Ronce O. 2012. How do genetic correlations affect species range shifts in a changing climate? *Ecology Letters*, 15: 251-259.

⁶ Publications are listed under section « Impacts, training and Dissemination ». The names of the fellow and of the coordinators appear in bold face.

Perspectives: Apart from calibrating this model for pedunculate oak and from combining this model with the process-based model PHENOFIT (objective 2), there are several perspectives to this work:

1. Using this model to predict the fate of actual populations.

Despite the recognized multivariate nature of natural selection, few studies quantify multitrait selective pressures or genetic correlations. We found no study reporting both a spatial selection gradient, stabilizing selective pressures, and genetic variances and covariances for multiple traits. Several studies, however, provide two of these three components, which are crucial to the understanding of multitrait adaptation to environmental changes. In addition, Ruth Shaw and Julie Etterson have such a data set, which is not fully published (2001; Etterson 2004). Using this dataset as an example, we hope to convince ecologists that multitrait constraints can matter and should be considered when evaluating the response of species to environmental changes.

Collaborators: Isabelle Chuine, Julie Etterson⁷, Ophélie Ronce⁸ and Ruth Shaw⁹.

2. Test this model's assumptions using empirical data.

A major assumption of the above model is that the structure of genetic correlations remains unchanged through space and time; and selective pressures are also assumed constant. Using 18 time series of trait data on pedigreed bird populations, we aim at determining to what extent these assumptions differ from reality, and assess how observed changes in the **G** matrix or in the **W** matrix alter predictions about the speed of phenotypic change. This work will be part of a large ANR¹⁰-funded project conducted by Anne Charmantier¹¹ and Céline Teplitsky¹².

Collaborators: Anne Charmantier, Céline Teplitsky and the PEPS-BIOADAPT consortium.

3. Allowing dispersal to evolve.

The model described above assumes that dispersal occurs in a diffusive way, i.e. with no preferential direction, but the diffusion rate is assumed constant. Dispersal abilities are not equivalent across a species' distributional range. These changes may be plastic (e.g. Clobert et al. 2009) or genetic (Hanski & Saccheri 2006). Several recent studies have shown increased dispersal at the poleward margin of the distributional range of various species (mainly insects; Thomas *et al.* 2001; Simmons & Thomas 2004; Hill *et al.* 2011). A short-term perspective is therefore to allow dispersal to evolve in the model described above.

Collaborator: François Massol¹³. **Publication in prep:** IP2. Massol F. & Duputié A. Evolution of dispersal in a continuous environment. *In prep.*

⁷ <http://www.d.umn.edu/~jetterso/>

⁸ http://www.metapop.univ-montp2.fr/?page_id=91

⁹ <http://www.cbs.umn.edu/eeb/faculty/ShawRuth/>

¹⁰ Agence Nationale de la Recherche (French National Research Agency ; <http://www.agence-nationale-recherche.fr/en/project-based-funding-to-advance-french-research/>)

¹¹ <http://annecharmantier.free.fr/>

¹² <http://www2.mnhn.fr/cersp/spip.php?rubrique96>

¹³ <http://www.irstea.fr/massol>

2. COMBINE THIS MODEL FOR TRAIT EVOLUTION TO A MODEL GENERATING REALISTIC FITNESS FUNCTIONS, IN ORDER TO PREDICT THE EVOLUTION OF A SPECIES' RANGE.

Initially, this project aimed at improving the realism of a process-based model, through incorporating genetic trait evolution, or equivalently, to improve the projections of theoretical models, through feeding them with realistic fitness functions. Indeed, theoretical quantitative genetic models assume Gaussian-shaped, spatially uniform, stabilising selection. Given the difficulty to obtain data on selective pressures acting on trees, we planned to use a process-based model to generate these fitness functions. The model we chose to use is named PHENOFIT, and was developed by the return host coordinator (Chuine 2000; Chuine & Beaubien 2001; Morin & Chuine 2005).

The model PHENOFIT: This model, is based on the assumption that the survival of trees is linked to their ability to avoid frost and drought damage, and that their reproductive success is tightly linked to their ability to adapt the timing of leafing, flowering, and leaf senescence events to the local conditions (so as to avoid leaf damage due to frost, and to maximize the length of the growing season). Given local climatic conditions, the model can output an average tree's survival probability, and its probability to yield mature fruits, i.e. its fitness. **Figure 2** gives some detail on how PHENOFIT works.

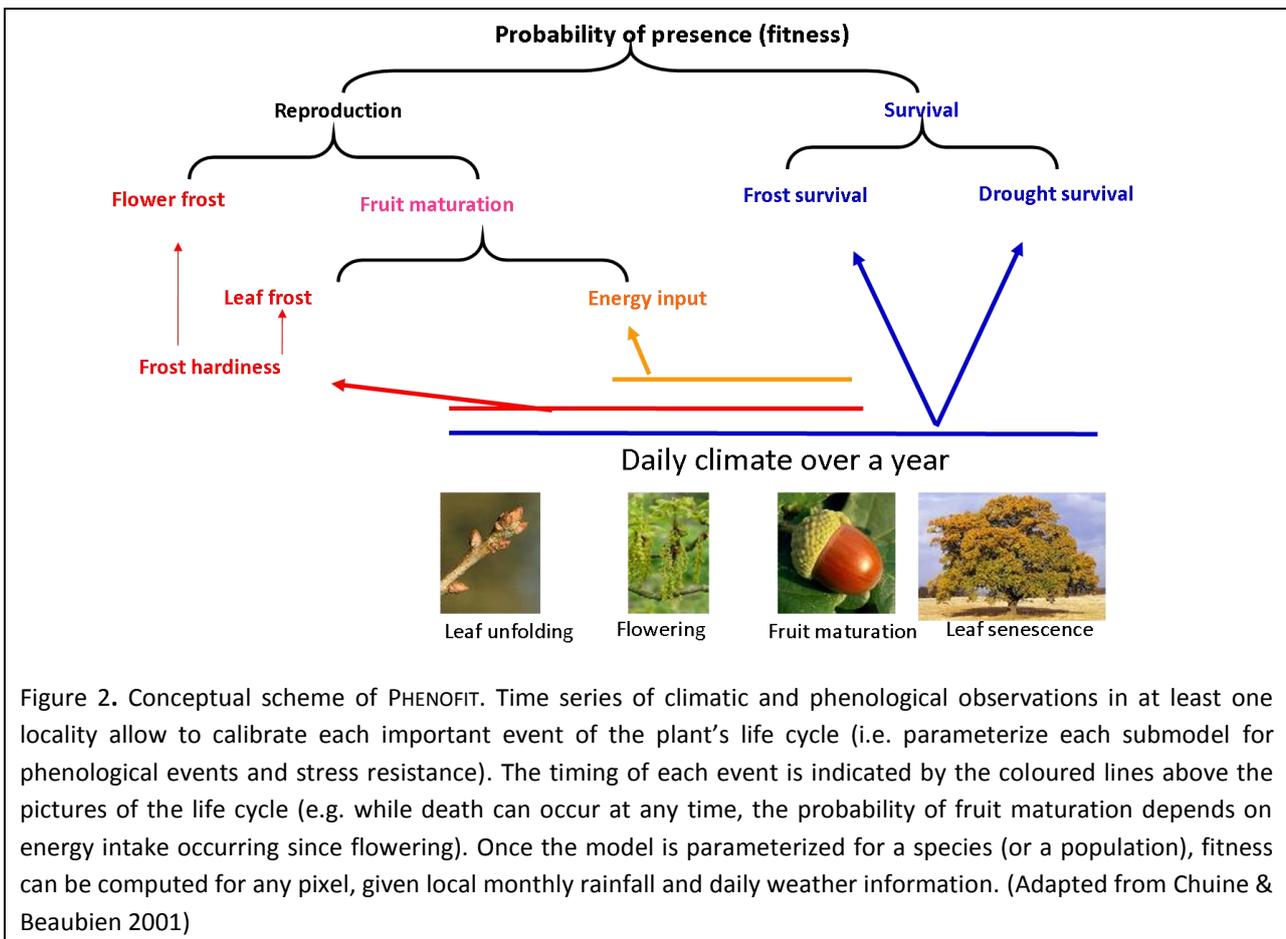


Figure 2. Conceptual scheme of PHENOFIT. Time series of climatic and phenological observations in at least one locality allow to calibrate each important event of the plant's life cycle (i.e. parameterize each submodel for phenological events and stress resistance). The timing of each event is indicated by the coloured lines above the pictures of the life cycle (e.g. while death can occur at any time, the probability of fruit maturation depends on energy intake occurring since flowering). Once the model is parameterized for a species (or a population), fitness can be computed for any pixel, given local monthly rainfall and daily weather information. (Adapted from Chuine & Beaubien 2001)

Objectives: The traits that will be allowed to evolve are linked to leafing date. Temperate trees require a certain amount of frost during winter (for bud dormancy, a.k.a. vernalisation, to take place), followed by a certain amount of heat (allowing cell division and growth). Both these phases are modelled in PHENOFIT, and we chose to allow the duration of both phases to evolve, because these determine the onset beginning of the vegetation season, and thus strongly determine the tree's reproductive success.

To combine PHENOFIT with a model of trait evolution (i.e. winter chill and spring warming requirements), we chose to first allow for local adaptation to take place. This requires parameterisation of all sub-models with species-specific and location-specific parameters. Parameterization requires time series of observations of phenological events (i.e. leafing dates) together with local daily weather. Pedunculate oak (*Quercus robur*) was one of the only species for which such data was available for several locations when the project started, and thus was chosen as a model species.

2A. PARAMETERIZE PHENOFIT FOR POPULATIONS OF *QUERCUS ROBUR*.

Methods: To do this, we used phenological time series obtained from a French database¹⁴ and a European database¹⁵. Daily weather information (minimal and maximum temperatures) was obtained from MétéoFrance¹⁶ and from the National Climatic Data Center¹⁷. Only those phenological observation series spanning more than three years at a given location, all posterior to 1970, were conserved. Of these, only those phenological stations for which a weather station was available in a radius of 20 km within 200 m altitude were conserved, leaving several thousand usable observations.

The parameters for the phenological models (i.e. those predicting the dates of leafing, flowering, fruit maturation and leaf senescence) were calibrated using the software PMP¹⁸ (Chuine *et al.* 2013). The parameter optimisation method uses simulated annealing (Metropolis algorithm), so as to minimise the sum of squares of the differences between simulated and observed dates. This optimisation was performed for regions of increasing size, using the procedure described in Chuine *et al.* (2000a; 2000b) to determine which populations had significantly different responses to climate in determining leafing, flowering, fruit maturation and leaf senescence dates. Parameters for drought stress resistance and frost resistance were obtained from the literature.

Results: Using this approach, we were able to identify seven populations that exhibited different responses to temperatures to complete their life cycles: one from the Balkan region, one from the Central Europe (Germany, Czech Republic) region, one from Eastern Europe (Baltic countries and Russia), one from North-Western France, one from North-Eastern France, one from the Pyrenees and one from the UK (the fitness of each population, as computed by PHENOFIT, is given on the middle and bottom rows of **Figure 3**). Considering the maximum fitness obtained by each population, one obtains the fitness map on the right of the top row of **Figure 3**. This map is closer to observed occurrences (top left of **Figure 3**) than what can be obtained from a “global” simulation, using a unique set of parameters (top row, third column of **Figure 3**), whatever the accuracy measure considered (data not shown).

It has to be noted that PHENOFIT does not rely on observed distributions. Thus, observed distributions merely constitute a tool for validating the model. In this case, clearly, **several populations of oaks exist and use different clues to determine their dates of leafing, flowering, fruit maturation or senescence.**

Paper in prep.: IP4. Duputié A., Gritti E.S., Chuine I. Local adaptation of the phenological response to climate in pedunculate oak. *In prep.*

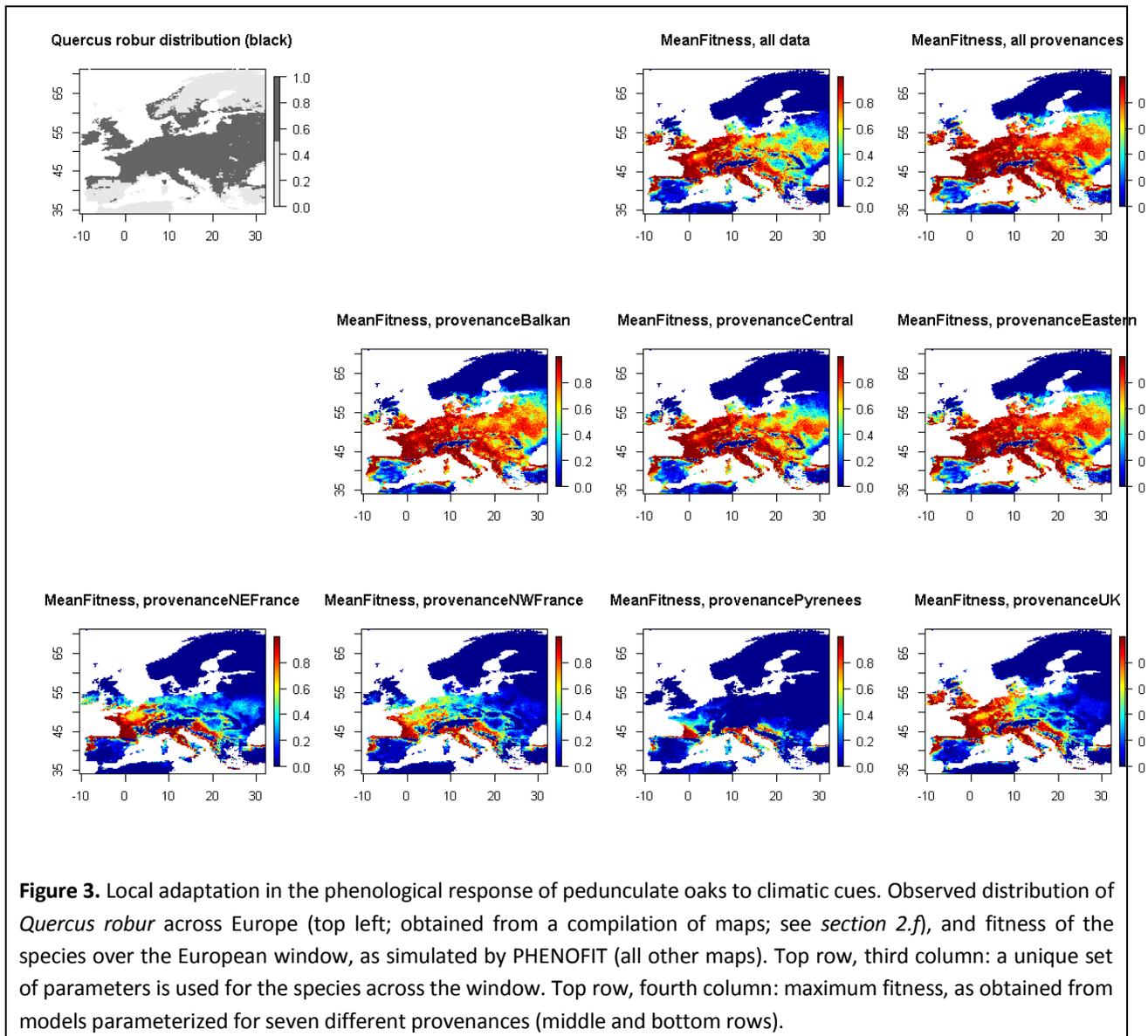
¹⁴ <http://www.gdr2968.cnrs.fr/>

¹⁵ <http://www.pep725.eu/>

¹⁶ <http://publitheque.meteo.fr/okapi/accueil/okapiWebPubli/index.jsp>

¹⁷ <http://www.ncdc.noaa.gov/cgi-bin/res40.pl?page=climvisgsod.html>

¹⁸ <http://www.cefe.cnrs.fr/en/biodiversity-and-ecosystem-processes-under-global-change/pmp>



Implications:

1. **This has implications concerning the response of different populations to climate change:** these populations do not respond to climate warming in the same way (not shown). Therefore, migration will be an even more strong limitation to range shifts than previously assumed. While local adaptation is acknowledged as an important factor for limiting range shifts, only recently has it begun to be taken into account in environmental (correlative) niche distribution models (Banta *et al.* in press).
2. When the project started, we were unaware of the European phenological database. **The same multi-site parameterization was carried for sessile oak (*Quercus petraea*) and common beech (*Fagus sylvatica*, data not shown).** This parameterization is to be used in a paper aiming at projecting the future range of common beech across Europe by the end of next century, under various scenarios. This paper considers a realistic dispersal scenario for beech.

Paper in prep.: IP1. Saltré F., Gaucherel C., Gritti E.S., Duputié A., Rutschmann A., Chuine, I. Impact of dispersal abilities of *Fagus sylvatica* on its future European distribution. *In prep.*

3. Unfortunately, **the parameters of the phenological models vary irregularly across Europe, thus preventing from considering a simple (e.g. linear) clinal response for chill or heat requirements;** and compromising the straightforward combination of the trait evolution model and of the process-based model (*section 2-d*), when considering local adaptation. However, genetic evolution of the reaction norms of leafing date to climate can be modelled without taking local adaptation into account.

Before combining the theoretical trait evolution model with the process-based distribution model, we also needed to determine the strengths of selective pressures across space.

2B DETERMINE THE STRENGTH OF SELECTIVE PRESSURES ACTING ON THE PHENOLOGY OF *QUERCUS ROBUR*

Context & aim: The aim here was to determine whether the considered traits (i.e. those determining flowering date) were, as hypothesized by all theoretical models of trait evolution, under simple, symmetric, Gaussian-shaped stabilising selection. Indeed, all models of trait evolution are based on this hypothesis, which greatly simplifies calculations, and is sometimes close to truth in nature (e.g. Lande & Arnold 1983; Blows et al. 2004; Brooks et al. 2005). However, selection is not always stabilising (Brodie III 1992; Kingsolver et al. 2001; Kingsolver & Diamond 2011), and Gaussian shape, implying symmetrical selective pressures, is always an approximation. Most traits are under conflicting selective pressures. For example, producing offspring earlier (so as to outcompete other plants) can select earlier-flowering plants; yet late-flowering plants are favoured in the event of late frosts, and stabilising selective pressures also stem from the necessity to find a mate (and therefore, to flower at roughly the same time as the neighbouring plants), and from the need to flower when pollinators (if any) are present (e.g. Devaux & Lande 2009; Galloway & Burgess 2012).

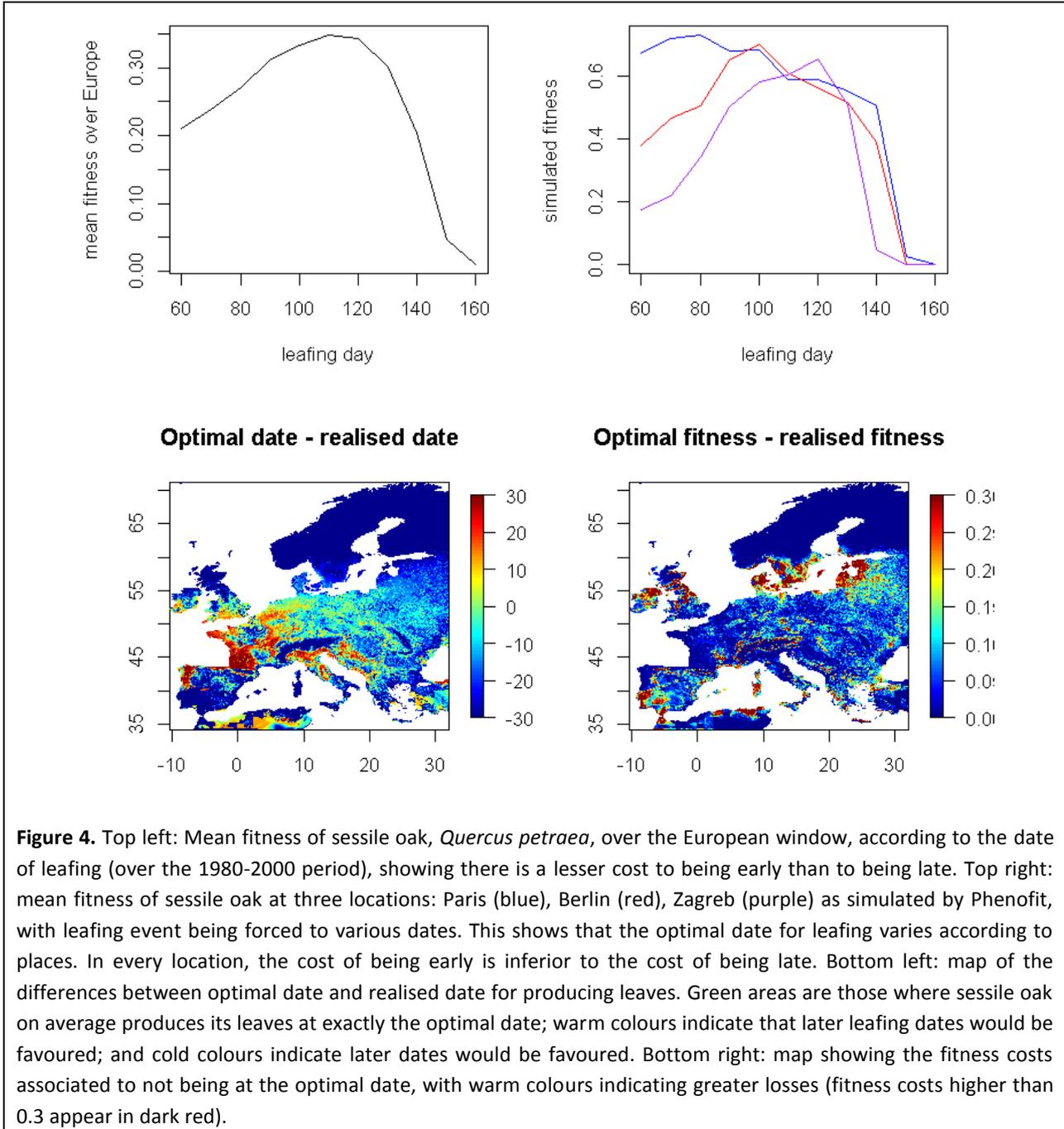
Because it provides a proxy for the fitness of an average adult tree under given climatic conditions, the model PHENOFIT can be used to assess the shapes of selective pressures, i.e. whether selection for leafing and flowering time is stabilising, and whether it is symmetric.

Method: We bypassed the models regulating leafing and flowering time in *Quercus robur*, and forced these events to occur at various fixed dates. The rest of the life cycle was then left to be regulated by climatic constraints. For each location across the European window, we thus obtained fitness estimates for virtual populations which would have produced their leaves and flowers for a range of dates. Leafing and flowering events were considered jointly, because leaves and flowers are produced in a common bud in oaks; hence their production is not independent in nature.

Results: We found that **leafing and flowering dates are under stabilising selection**. In other words, there is an optimal date for leaf and flower production: early trees risk leaf and flower damage from late frosts, while late trees lack time to achieve fruit maturation before leaves fall. This optimal date **varies according to the location** (more precisely, according to climatic conditions). Overall, the fitness peak is **asymmetric**: the cost associated to being late is superior to the cost associated to being early (**Figure 4**).

Corollary project: Determining the shape of the optimum was most easily done through bypassing the trees' response to climatic cues to determine their phenology. This is equivalent to cancelling their plastic response to climate. Using the same kind of approach, we addressed several questions: (i) does this plastic response increase the potential distribution area and/or enlarge the climatic niche of three widespread European tree species? (ii) where is plasticity adaptive? (iii) at what spatial scale is it adaptive, and how did it evolve? (iv) will it be adaptive under future climatic scenarios, and where? (*section 2g*)

Paper in prep.: IP5. Duputié A., Ronce O. & Chuine I. Investigating the shape of the adaptive landscape for phenological traits in trees. *In prep.*



2C CHECK THAT PHENOFIT PRODUCES A REALISTIC VIEW OF THE FITNESS OF *QUERCUS ROBUR* OVER EUROPE

We found that PHENOFIT reproduced this species' geographic range relatively well, according to the widely used Atlas Flora Europaea (Jalas & Suominen 1972-2010; AFE; Figure 5, top panels). However, some zones are not well modelled (e.g. Ireland or the eastern part of the range). Different modelling techniques (correlative models or hybrid models) also perform well in depicting species' current distributions, but their errors seem to be clustered in different zones. **This raised a new objective (2e), which aimed at providing consensual maps of distribution, based on the outputs of different models (process-based, correlative or hybrid distribution models), but most importantly, to provide associated maps of uncertainty.**

Furthermore, we subsequently discovered different atlases providing distribution data:

- the EuroVegMap atlas¹⁹, compiled in the 1970's to 2000's, providing potential vegetation maps;
- the EUFORGEN atlas²⁰, based on expert knowledge and bibliography;
- the Joint Research Centre Forest database²¹, compiled in the 2000's from satellite data, and constantly updated;
- the GBIF database²², based on georeferenced herbarium specimens.

The latter two databases do not aim at being exhaustive; the JRC database is based on continuous forest data and the GBIF database on some georeferenced specimens. However, both these databases provide certain occurrence points.

We realised that **the distributions of *Quercus robur* varied consequently according to the atlas used (Figure 5, all panels but the top left one).**

This has little consequence for our purpose (this merely changes the measure of the accuracy of the simulated distribution), but **is extremely relevant to the use of correlative distribution models (see new objective 2f). The fellow chose to deal with this problem before handling task 2d.**

¹⁹http://www.floraweb.de/vegetation/dnld_eurovegmap.html

²⁰http://www.euforgen.org/distribution_maps.html

²¹<http://forest.jrc.ec.europa.eu/distribution>

²²<http://data.gbif.org/species/>

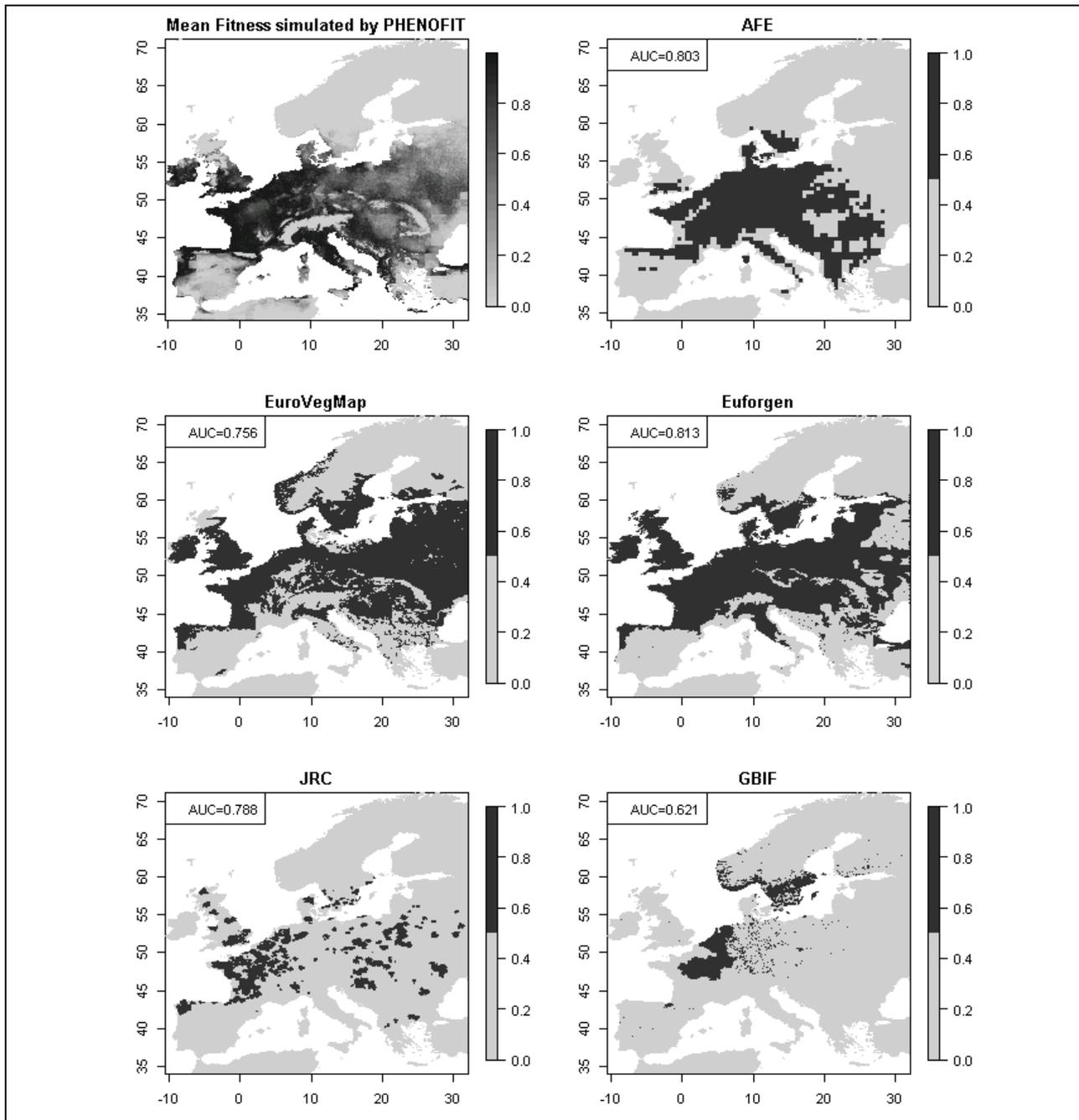


Figure 5. Top left: Mean fitness for pedunculate oak (*Quercus robur*) as simulated by PHENOFIT (darker shades indicate higher mean fitness, hence more favourable environments). All other panels: distribution of pedunculate oaks across Europe (black pixels), according to three atlases (AFE, EuroVegMap and Euforgen, see text for details) and two databases covering forest areas (JRC database) or georeferenced herbarium samples (GBIF database). The latter two databases do not intend to be comprehensive, but they indicate locations where pedunculate oak is certainly present. Values in the top left corner of each map indicate the match between simulated fitness (top left map) and each reference distribution map, as indicated by the area under the receiving operator curve (AUC-ROC; Swets 1988, where values above 0.7 indicate a good match to the data).

Note that the distributions provided by each reference map do not match (see e.g. in the UK or towards the eastern or northern margins of the range).

2D COUPLE A MODEL OF TRAIT GENETIC EVOLUTION WITH THE PROCESS-BASED PHENOFIT MODEL

As mentioned in 2c, this objective is not yet attained, because the fellow considered issues developed in 2e-f-g to be of greater importance. However, this step will be carried within the next months.

2E PROVIDE CONSENSUS MAPS ASSOCIATED WITH AN ESTIMATION OF UNCERTAINTY (NEW OBJECTIVE ARISING FROM 2C).

Collaborations: E Gritti (CEFE Montpellier, France), F Massol (IRSTEA Aix en Provence)

Context: Forecasting shifts in biome and species distribution is crucially needed in the current context of global change. So far, most projections of vegetation distribution rely on correlative species distribution models (SDMs). Yet, process-based or hybrid models based on explicit physiological description may be more robust to extrapolation under future climatic conditions (also see *section 2f*). **Forecasts of future distribution vary according to the correlative model used** (e.g. Pearson *et al.* 2006), and between correlative and process-based SDMs (Buckley 2008; Kramer *et al.* 2010; Keenan *et al.* 2011a; Cheaib *et al.* 2012; but see Kearney *et al.* 2010). This may puzzle stakeholders and policy makers, and even jeopardise the credibility of species distribution projections. Ensemble or consensus approaches, using information provided by different SDMs, have been advocated to tackle this problem (Araújo & New 2007): models can vote for the species' presence or absence. Votes can be weighted by the models' accuracy (e.g. Marmion *et al.* 2009).

Providing consensus maps is, however, not sufficient to guide stakeholders. All models may agree with each other, while their uncertainty is very large. Mapping this uncertainty is therefore as important as mapping the consensus in itself. Yet, few studies have provided uncertainty maps of SDM projections. When combining several models, the partitioning of variance among and within models can yield insight into spatial discrepancies (Hartley *et al.* 2006). This approach only reflects uncertainty associated with different model projections, not the uncertainty associated with the relevance of the climatic descriptors or the processes considered. Should an important environmental descriptor have been omitted in the individual SDMs, its variation would be absent from any multimodel, and even the best model among those studied would be unable to project the species' range (Dormann *et al.* in press).

The performance of conceptually different SDMs may vary with environmental conditions: each individual SDM may surpass the others in projecting a species' presence under a given set of climatic conditions, for the environmental variables or the processes it takes into account are more relevant in these conditions. **Here we build a simple consensus between SDMs, and assimilate its uncertainty due to the poor parameterisation or omission of important processes to its statistical deviance.** To account for the environmental clustering of SDM errors, uncertainty is modelled as a function of composite, independent environmental descriptors, in a multimodel framework. Both the probabilities of occurrence and the associated uncertainty can then be projected onto forecasted climatic conditions.

Method: This consensus relies on the conditional projections of each SDM, and its uncertainty is assessed through multimodel regression of deviance maps with respect to climatic conditions (**Figure 6**). Because process-based and hybrid models cannot model all important processes, their accuracy is bound to rely upon environmental descriptors, hence uncertainty (modelled as the deviance of the consensus model) is assumed to rely upon environmental descriptors.

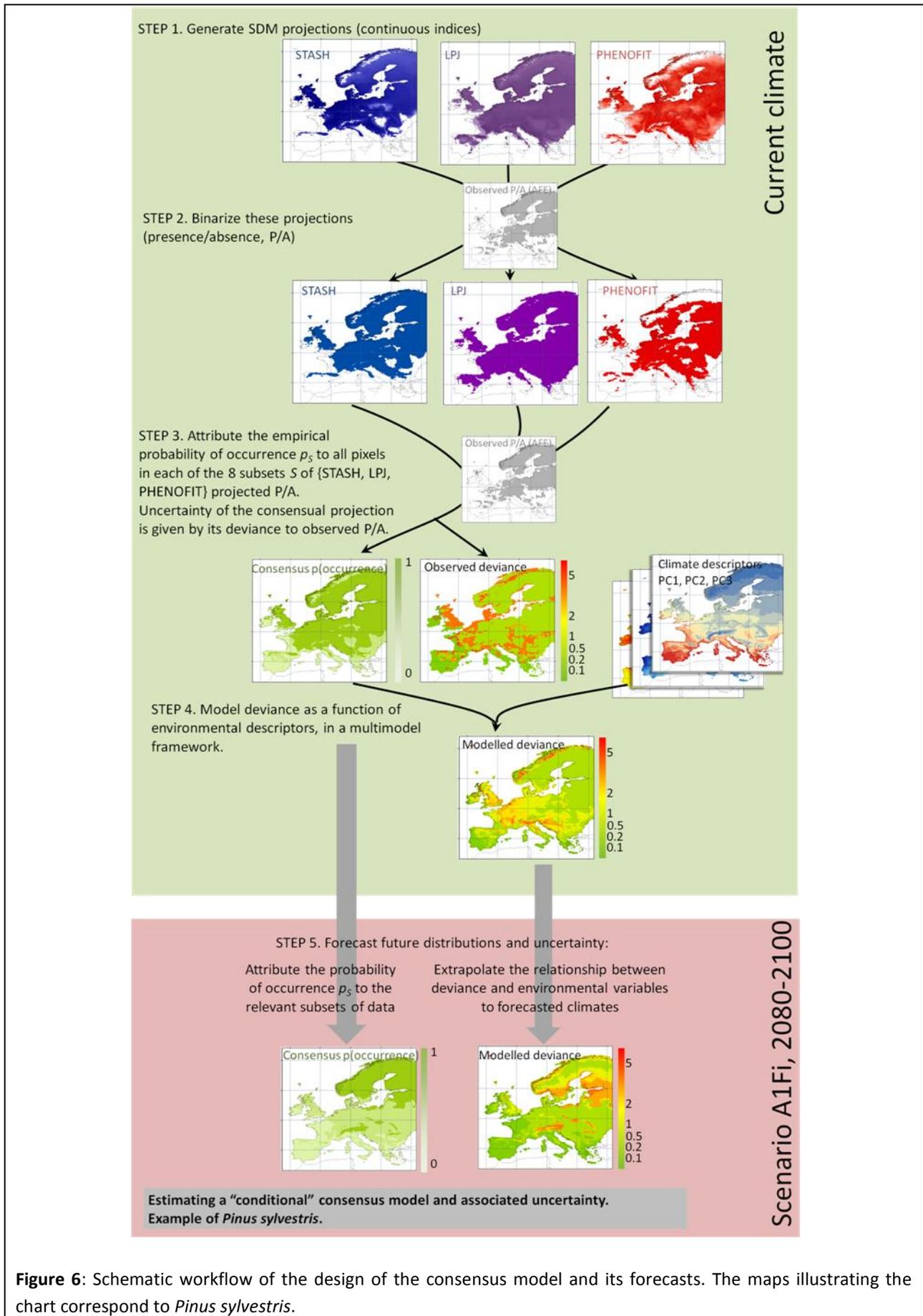


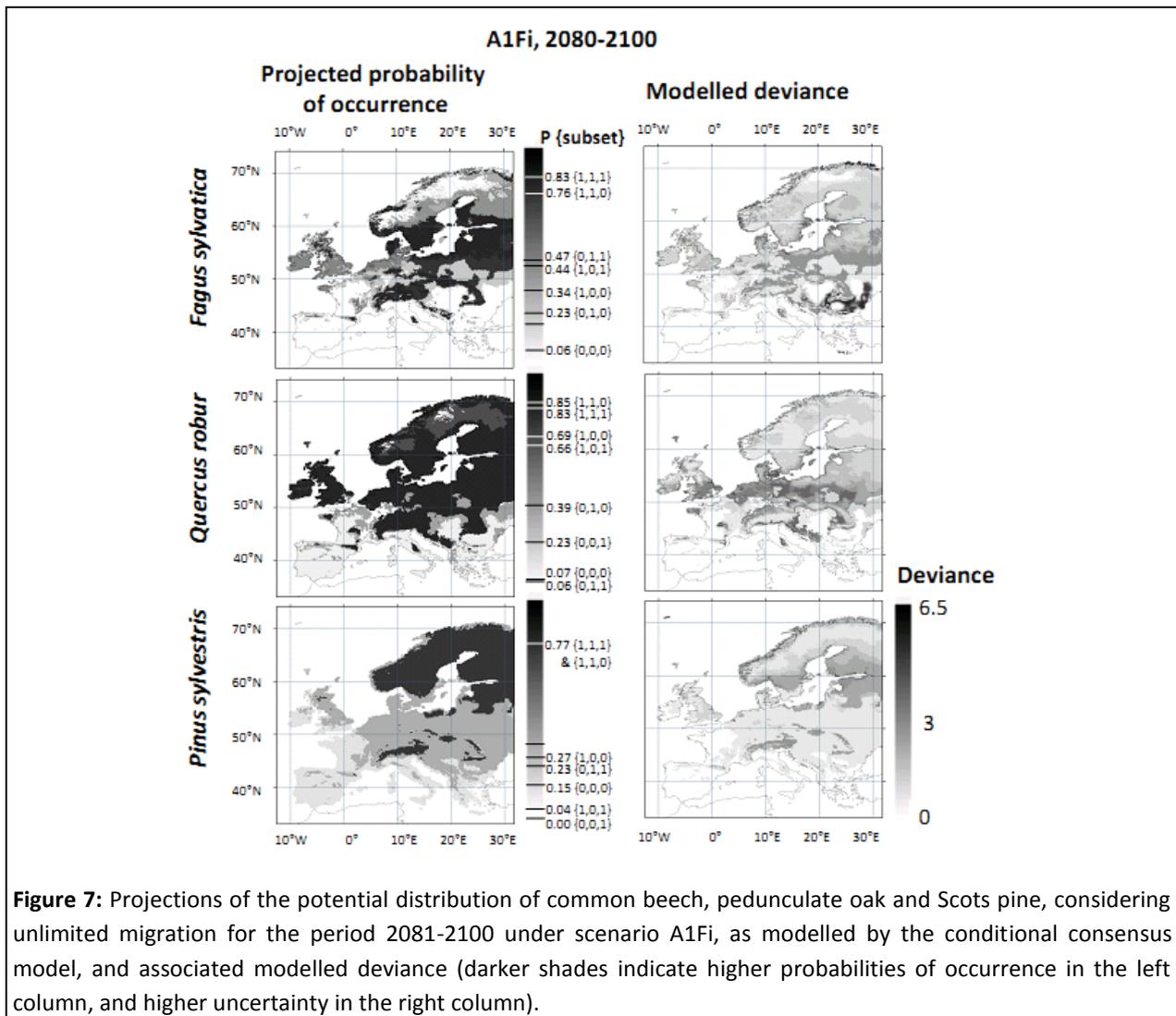
Figure 6: Schematic workflow of the design of the consensus model and its forecasts. The maps illustrating the chart correspond to *Pinus sylvestris*.

Results: The consensual model performs better than previously published consensus methods in predicting current occurrences (especially when using likelihood as a model performance criterion). Environmental predictors perform well at pinpointing the regions of maximal error.

For future climatic scenarios, the consensus model (like the three individual models) projects an expansion of the range of suitable habitats (not necessarily of the occupied area) of the two deciduous species, pedunculate oak (*Quercus robur*) and common beech (*Fagus sylvatica*) and a contraction of the range of Scots pine (*Pinus sylvestris*). However, **uncertainty is very high around the retreating margins of the distributions and at high altitudes (Figure 7).**

Implications: This approach can help modellers identify the limitations of each SDM and stakeholders pinpoint the regions of models agreement and highest certainty.

Publication (submitted): S1. Gritti E.S.*, Duputié A.*, Massol F. & Chuine I. Estimating consensus and uncertainty of inherently different species distribution models. Submitted to *Ecology Letters*. * these authors contributed equally to this work.



2F DIFFERENCES BETWEEN REFERENCE MAPS AND CONSEQUENCES FOR DISTRIBUTION MODELS (NEW OBJECTIVE ARISING FROM 2C).

The existence of several quite different distribution maps, even for well-known, well-detectable, European tree species (section 2c and Figure 5), has apparently been overlooked. Indeed, it has **very important consequences for the widely used correlative distribution models.** These models rely on the assumption that distribution patterns match the variation of environmental variables. Hence, their output will strongly rely on the map used to calibrate it.

This implies that, depending on the reference map used, different variables will be considered as limiting the species' occurrence. A straightforward consequence is that **the projections of future distribution will depend heavily on the reference map used (Figure 8).** This calls for **more reliable data concerning distributions even of well-known, easily detectable, European trees.** This also warns against using **correlative models when making forecasts.**

Even for process-based models, the existence of different maps (which, for example, indicate that pedunculate oak is present or absent across almost all of the British Isles; **Figure 5**), compromises their evaluation (see the AUC scores on **Figure 5**, ranging from mediocre to good).

We propose to use the union of all presences, as indicated by the largest possible number of sources, as a source for presence/absence data. Citizen science would be a great tool in filling the gaps in such basic knowledge as species distribution ranges.

We considered that this problem was really important, given the very wide use of correlative niche models to project future species' distributions (Thuiller *et al.* 2005; Zimmermann *et al.* 2009; e.g. Araújo *et al.* 2011; Capinha & Anastácio 2011; Garcia *et al.* 2011; Synes & Osborne 2011; Thuiller *et al.* 2011; Feeley *et al.* 2012; Petitpierre *et al.* 2012), and **chose to treat it before proceeding to step 2d.**

Publication in prep: IP6. Duputié A., Rutschmann A., Chuine I. Where the wild things are: a call for distribution data. *In prep.*

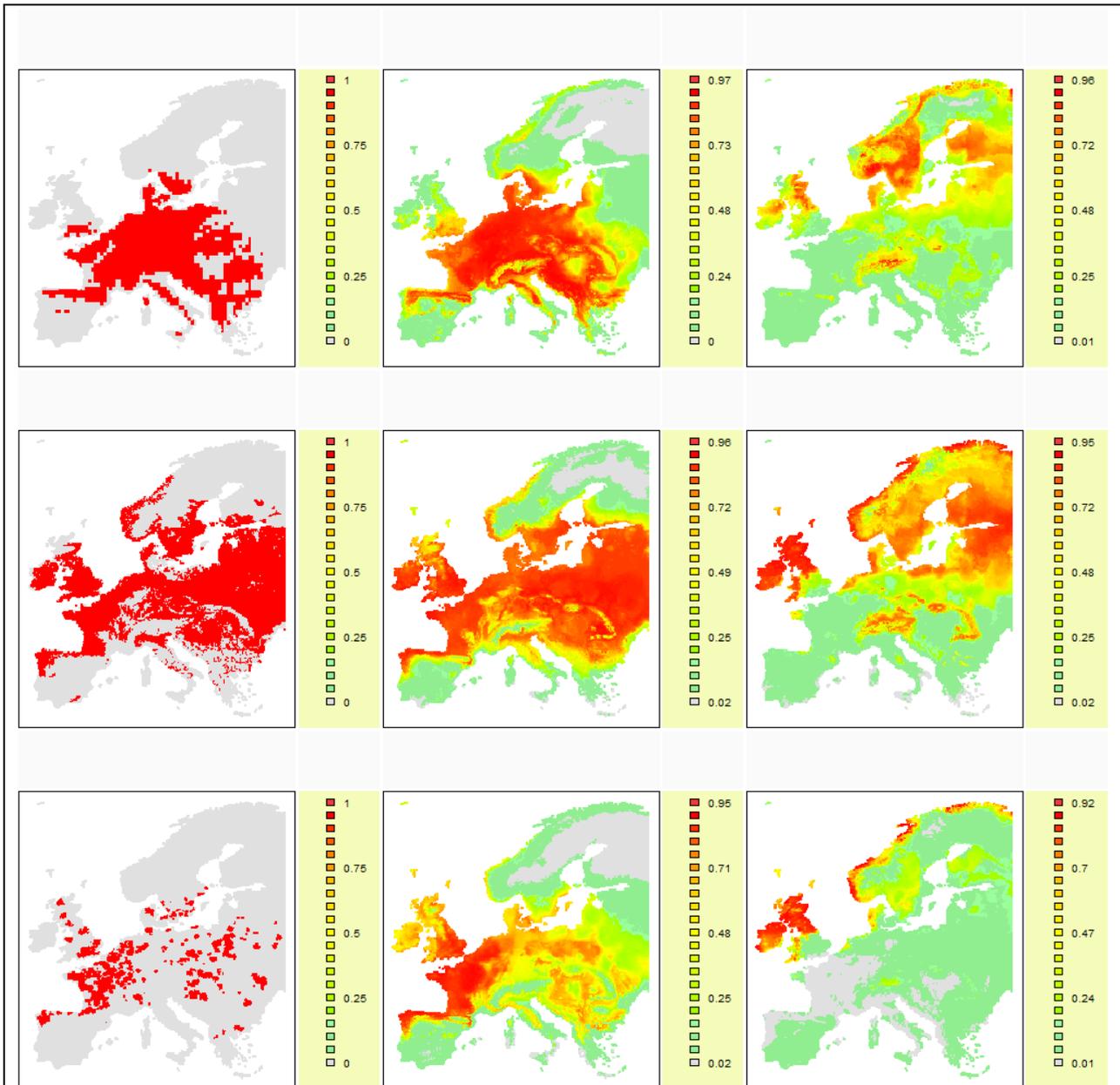


Figure 8: **Left column:** distribution of *Quercus robur*, as found in some databases (section 2c; top to bottom: AFE, EuroVegMap and JCR). **Middle column:** projections of its current probability of occurrence (1980-2000), as modelled by the ensemble consensus platform BIOMOD (Thuiller *et al.* 2009), using all eight correlative algorithms proposed in the platform and based on the maps on the left column. **Right column:** projections of its future distribution (2081-2100 under the HadCM3 A1Fi scenario), based on the maps on the left column. These forecasts differ, preventing the unrestricted use of correlative models for forecasts.

Correlative models are hence very accurate in reproducing observed patterns (see middle column), which is problematic when there is no agreement on these patterns (left column), and lead to identifying different variables as limiting the species' range, and to different forecasts (right column).

2G ESTIMATING THE ROLE OF PLASTICITY IN SHAPING A SPECIES' GEOGRAPHIC RANGE, AND ITS CLIMATIC NICHE (NEW OBJECTIVE ARISING FROM 2A).

Collaboration: Alexis Rutschmann (Masters II student ; CEFE Montpellier, France).

Context & aim: Understanding the determinants of species distribution is a crucial issue in the context of global change. Phenotypic plasticity is seen as a way to extend species fundamental niche and thereby their geographical distribution (e.g. Charmantier *et al.* 2008; Aubret & Shine 2009). For example, invasive populations sometimes show more phenotypic plasticity than non-invasive populations, suggesting plasticity helps enlarging distributional ranges and/or their niches (Richards *et al.* 2006; Lavergne & Molofsky 2007; Caño *et al.* 2008; although a recent work by Petitpierre *et al.* 2012 shows that niche shifts accompanying invasions might be less common than previously thought). In the present work, we tried to understand **how far plasticity could affect niche breadth and the width of the distributional range**, using three emblematic European tree species as examples.

Methods: The process-based species distribution model PHENOFIT simulates trees distribution at a large scale, using mechanistic models simulating phenological and stress resistance traits, and their contribution to survival and reproductive success. For three species (Scots pine, pedunculate oak and common beech), **we manipulated the degree of plasticity of phenological traits** (through simulating (i) natural plasticity, (ii) suppressing interannual plasticity, (iii) suppressing both interannual and intersite plasticity in their response to climatic conditions). We then compared the breadth of the climatic niches (i.e. of the environmental space deemed suitable by PHENOFIT) and of the distributional ranges (i.e. of the geographic area deemed suitable by PHENOFIT) for the plastic and non-plastic (virtual) species.

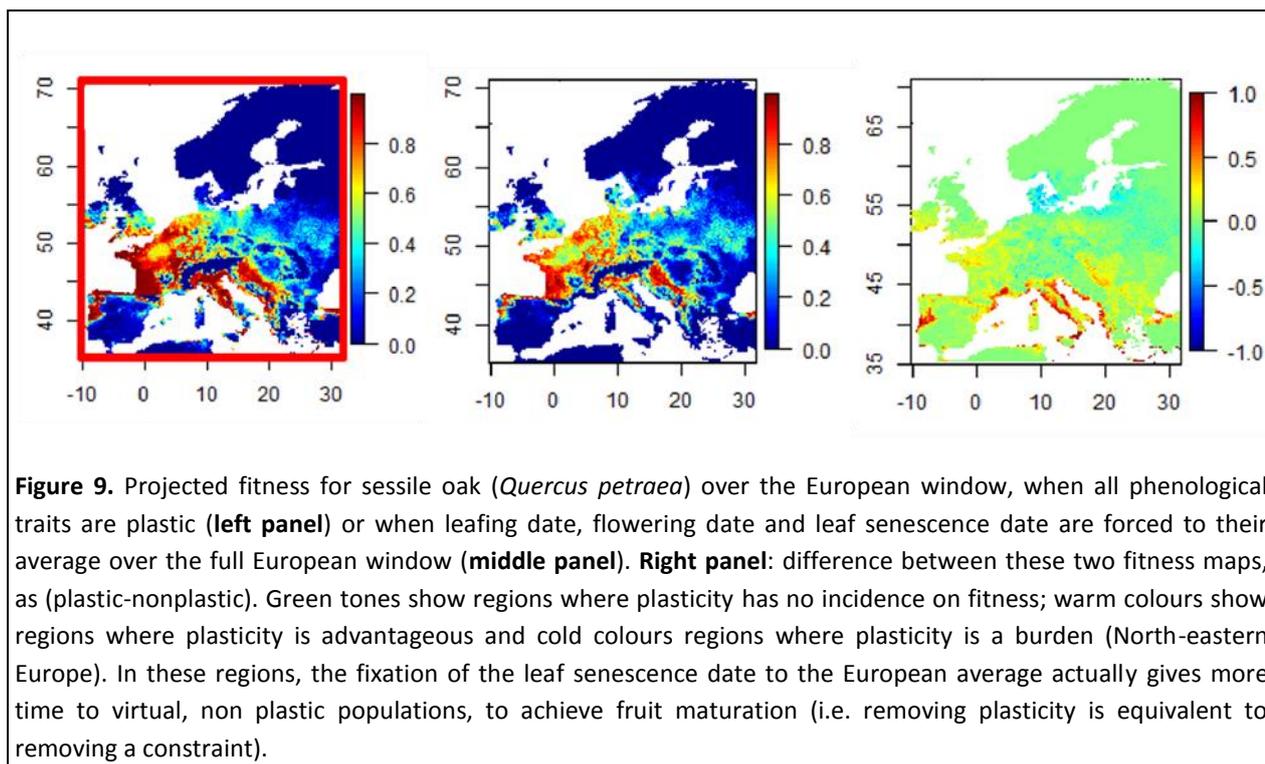
Results: Our results show that **plasticity enlarges both niche breadth and distributional ranges**. Even if that widening is not as important as expected, it increases fitness under **marginal conditions**.

The plasticity of phenological traits seems to have been **shaped by selective pressures acting at the scale of the species distribution**, and not at the local scale. Interannual climatic variability generates some variation in the expressed traits, however this variation is small, and the fitness cost associated to losing this plasticity at the local scale is generally low (this is because the optimal values for these traits show a wide peak, i.e. fitness is not affected much by a slight deviation from the optimal value).

However, **plasticity is not always adaptive** all over the species distribution, due to developmental constraints. For example, in Scots pine, the plasticity of the leafing date emerges from a constraint: the winter chill requirements, which are not met in south-western Europe. Suppressing plasticity is equivalent to lifting this constraint, and should this plasticity be completely removed, these regions would be considered as suitable for Scots pine.

Implications: Our results bring new insights as to the role of plasticity in species niche breadth, and could help understand the role of plasticity in the adaptation of species to future climatic conditions.

Publication in prep: IP3. Rutschmann A., Duputié A., Chuine I. The role of plasticity in enlarging a species' range. *In prep.*



SIDE PROJECTS: GENETIC STRUCTURE OF CLONALLY PROPAGATED FOOD CROPS.

During years 2010-2012, the fellow was also implicated in several projects initiated in the research team where she conducted her PhD research. Namely, she was involved in two projects aiming at:

- (i) understanding the worldwide genetic structure of sweet and bitter cassava (PI E. Jane Bradbury, Univ. Wisconsin). This work has led to a submitted paper (S2. Bradbury E. J., **Duputié A.**, Delêtre M., Roullier C., Narváez Trujillo, A., Manu-Aduening, J. W., Emshwiller, E. & McKey D. Genetic differentiation of bitter and sweet cassava (*Manihot esculenta* Crantz: Euphorbiaceae): an analysis at global and continental levels. Submitted to *American Journal of Botany*.)
- (ii) identifying the wild progenitors of sweet potato (PI C. Roullier, CEFE Montpellier, France). This work has led to a submitted paper (S3. Roullier C., **Duputié A.**, Wennekes P., Benoit L., Manuel V., Rossel G., Tay D., McKey D. & Lebot V. Disentangling the origins of sweet potato (*Ipomoea batatas* (L.) Lam). Submitted to *PLoS ONE*).

She also finished and published some of her PhD work (publication P1. **Duputié A.**, Salick J. & McKey D. 2011. Evolutionary biogeography of *Manihot*, a rapidly radiating Neotropical genus restricted to dry environments. *Journal of Biogeography*, **38**: 1033-1043).

IMPACT, DISSEMINATION AND TRAINING

IMPACT

This research has broad impacts in the field of ecological modelling and understanding what limits range changes (see previous section).

In particular, this research has helped understanding how the complexity of species can limit their ability to cope with environmental changes. Indeed, all species are confronted to changes in different environmental variables (rainfall, temperature, extreme events, and many more if they also migrate to track their favourite climates), and this leads to selective pressures on multiple characters, which are usually linked by trade-offs. Overall, having to adapt for several traits limits the rate of trait change (and the ability to adapt).

This project has also provided some fundamental insights on the role of phenotypic plasticity in increasing a species' range size. This role appears to be limited for three European trees, and plasticity seems to be adaptive mostly at the margins of the range.

This project provided some warnings concerning the limitations of atlas-based projections of species distributions (i.e. mainly those involving either a large area or a large number of species), and some solutions to provide consensual and robust estimates of species distributions, based on multiple models, which can then be extrapolated more confidently to future climatic scenarios.

TRAINING

The fellow had the opportunity to **gain experience in two fields she was not familiar with; theoretical modelling and ecological niche modelling.**

She gained experience with the formal mathematical software *Mathematica*, which she also used for some simulation purposes (hence she did not, as initially planned, need to learn some low level programming language), with the statistical analysis platform R, and with analytical (hand-made) maths.

She also received training in ecological modelling (ECOCHANGE summer school held in Birmensdorf, Switzerland, Sept. 2010²³) and GIS software (March 2010).

She attended numerous stimulating seminars both at the outgoing and return host institutions.

Networking: The fellow could enlarge her professional network, through participating to several networks: the ANR-funded project EVORANGE²⁴, the FRB²⁵-funded project VARIADAPT²⁶, and two workshops organised by Drs Nick Zimmermann²⁷, Signe Normand²⁸ and Heike Lischke²⁹ (to come).

Student supervision: The fellow also had the opportunity to co-supervise two Masters students (Paul Wennekes, Masters 1, Spring 2011 and Alexis Rutschmann, Masters 2, Spring 2012), both of whose research will lead to publication.

²³ <http://www.ecochange-project.eu/news/summer-school-2010>

²⁴ <http://kimura.univ-montp2.fr/EvoRange/> ; leader Ophélie Ronce; 2009-2013.

²⁵ Fondation pour la Recherche sur la Biodiversité (French Foundation for Research on Biodiversity ; <http://www.fondationbiodiversite.fr/>)

²⁶ Leaders Sylvie Oddou-Muratorio

(http://www.avignon.inra.fr/avignon_eng/les_recherches_1/liste_des_unites/ecologie_des_forets_mediterranee_nnes_urf/les_personnes/oddou_muratorio_sylvie) and Hendrik Davi

(http://www.avignon.inra.fr/avignon_eng/les_recherches_1/liste_des_unites/ecologie_des_forets_mediterranee_nnes_urf/les_personnes/davi_hendrik)

²⁷ <http://www.wsl.ch/staff/niklaus.zimmermann/>

²⁸ <http://www.signenormand.net/>

²⁹ http://www.wsl.ch/info/mitarbeitende/lischke/index_EN

DISSEMINATION.

PAPERS IN PEER-REVIEWED JOURNALS

[P]

- P1. **Duputié A.**, Salick J. & McKey D. 2011. Evolutionary biogeography of *Manihot*, a rapidly radiating Neotropical genus restricted to dry environments. *Journal of Biogeography*, 38: 1033-1043.
- P2. **Duputié A.**, Massol F., Chuine I., Kirkpatrick M., Ronce O. 2012. How do genetic correlations affect species range shifts in a changing climate? *Ecology Letters*, 15: 251-259.

SUBMITTED PAPERS

[S]

- S1. Gritti E.S.*, **Duputié A.***, Massol F. & Chuine I. Estimating consensus and uncertainty of inherently different species distribution models. Submitted to *Ecology Letters*. * these authors contributed equally to this work.
- S2. Bradbury E. J., **Duputié A.**, Delêtre M., Roullier C., Narváez Trujillo, A., Manu-Aduening, J. W., Emshwiller, E. & McKey D. Genetic differentiation of bitter and sweet cassava (*Manihot esculenta* Crantz: Euphorbiaceae): an analysis at global and continental levels. Submitted to *American Journal of Botany*.
- S3. Roullier C., **Duputié A.**, Wennekes P., Benoit L., Manuel V., Rossel G., Tay D., McKey D. & Lebot V. Disentangling the origins of sweet potato (*Ipomoea batatas* (L.) Lam). Submitted to *PLoS ONE*.

PAPERS IN PREP

[IP]

- IP1. Saltré F., Gaucherel C., Gritti E.S., **Duputié A.**, Rutschmann A., Chuine I. Impact of dispersal abilities of *Fagus sylvatica* on its future European distribution. *In prep.*
- IP2. Massol F. & **Duputié A.** Evolution of dispersal in a continuous environment. *In prep.*
- IP3. Rutschmann A., **Duputié A.**, Chuine I. The role of plasticity in enlarging a species' range. *In prep.*
- IP4. **Duputié A.**, Gritti E.S., Chuine I. Local adaptation of the phenological response to climate in pedunculate oak. *In prep.*
- IP5. **Duputié A.**, Ronce O. & Chuine I. Investigating the shape of the adaptive landscape for phenological traits in trees. *In prep.*
- IP6. **Duputié A.**, Rutschmann A., Chuine I. Where the wild things are: a call for distribution data. *In prep.*

COMMUNICATIONS AT INTERNATIONAL CONFERENCES

[C]

- C1. **Duputié A.**, Massol F., Chuine I., Ronce O, Kirkpatrick M. Adaptation in space and time: genetic interactions between traits and species distributional ranges. Ecologie 2010, Montpellier, France, Sept 2010. (Oral)
- C2. **Duputié A.**, Massol F., Chuine I., Kirkpatrick M, Ronce O. How do genetic correlations affect species distribution ranges in a changing environment? ESA 96, Austin, Texas, August 2011. (Oral)
- C3. **Duputié A.**, Massol F., Chuine I., Kirkpatrick M, Ronce O^{speaker}. How does evolution affect extinction and species range dynamics in the context of global change? ESEB XIII, Tuebingen, Germany, August 2011. (Oral)
- C4. **Duputié A.**, Massol F., Chuine I., Kirkpatrick M, Ronce O. « Responding to rapid environmental change» - How fast exactly? A theoretical model in a multivariate environment. EEF 12, Avilá, Spain, Sept 2011. (Oral)
- C5. **Duputié A.**, Gritti E.S., Massol F. & Chuine I. Estimating consensus and uncertainty of inherently different species distribution models. Conférence finale du projet EcoChange; Zürich, Switzerland, March 2012. (Poster)

SEMINARS

[B]

- B1. **Duputié A.**, Massol F., Ronce O., Kirkpatrick M. Species ranges in space and time: some consequences of having to cope with several traits. Austin, TX, 23/03/2010.
- B2. **Duputié A.**, Pujol B., Elias M., McKey D. The evolutionary ecology of clonally propagated crops. EcoLunch, Austin, TX, 01/10/2010.
- B3. **Duputié A.**, Massol F., Ronce O., Kirkpatrick M. Evolution d'une espèce complexe soumise à un gradient environnemental changeant dans le temps. Equipe GENEV, CEFÉ, Montpellier, 21/02/2011.
- B4. **Duputié A.**, Massol F., Chuine I., Kirkpatrick M., Ronce O. Dans quelles conditions l'adaptation permet-elle un déplacement de l'aire de répartition d'une espèce soumise à un changement environnemental? Séminaire EDB, Toulouse, 09/12/2011.
- B5. **Duputié A.** Modélisation de la répartition d'espèces d'arbres européens fondée sur les traits : quelques applications, et incertitudes associées. Séminaire EDB, Toulouse, 07/05/2012.

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