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*Review*

# Why does phenology drive species distribution?

Isabelle Chuine\*

*Equipe BIOFLUX, Centre d'Ecologie Fonctionnelle et Evolutive–CNRS, 1919 route de Mende,  
34293 Montpellier cedex 05, France*

Despite the numerous studies which have been conducted during the past decade on species ranges and their relationship to the environment, our understanding of how environmental conditions shape species distribution is still far from complete. Yet, some process-based species distribution models have been able to simulate plants and insects distribution at a global scale. These models strongly rely on the completion of the annual cycle of the species and therefore on their accomplished phenology. In particular, they have shown that the northern limit of species' ranges appears to be caused mainly by the inability to undergo full fruit maturation, while the southern limit appears to be caused by the inability to flower or unfold leaves owing to a lack of chilling temperatures that are necessary to break bud dormancy. I discuss here why phenology is a key adaptive trait in shaping species distribution using mostly examples from plant species, which have been the most documented. After discussing how phenology is involved in fitness and why it is an adaptive trait susceptible to evolve quickly in changing climate conditions, I describe how phenology is related to fitness in species distribution process-based models and discuss the fate of species under climate change scenarios using model projections and experimental or field studies from the literature.

**Keywords:** fitness; species distribution; adaptation; niche

## 1. INTRODUCTION

More than ever an accurate understanding of how environmental conditions shape species distribution at the continental scale is necessary to predict future range shifts of species and their consequences on biodiversity. Which environmental factors determine the range boundaries of species and by which mechanisms are still challenging questions (Parmesan *et al.* 1999; Johnstone & Chapin 2003).

Species distribution, and more precisely species habitat, was linked to the concept of species niche for the first time by Grinnell (1917) who defined the species niche as all the sites where organisms of a species can live (where conditions are suitable for life). Ten years later, Elton (1927) proposed another definition of the niche based on the functions performed by the species in the community of which it is a member. The first definition has also been called the 'address' of the species and the second one its 'profession' (Odum 1959). Thirty years later, Hutchinson (1957) proposed a new formulation of Grinnell's definition of the niche as a region in a multi-dimensional space of environmental factors ( $n$ -dimensional hypervolume) that affect the welfare of a species. Hutchinson also proposed the concepts of fundamental niche and realized niche, the fundamental niche being the hypervolume of

environmental variables within which individuals can survive and reproduce indefinitely, and the realized niche being the expression of the fundamental niche affected by species interactions. A species distribution is therefore often assimilated to the species realized niche. But it was only 60 years after Elton that the concept of species niche was linked to the concept of species traits by Rosenzweig (1987), who defined a species niche as the ensemble of traits that allow a species to survive in a particular environment. One needs to note that both definitions of the niche help in understanding species distributions but mainly at the global and regional scales, since at local scales species distribution is also highly dependent on stochastic events.

Historically, species distribution models have tried to describe the niche following Grinnell's or Hutchinson's definition. These models were initially called 'envelope models', the envelope referring to the hypervolume of Hutchinson. They have been renamed 'niche-based models' and more recently 'habitat models' (Guisan & Zimmermann 2000; Guisan & Thuiller 2005), which is from my point of view more adequate. Such models try to identify the environmental variables (e.g. climatic, pedologic, orographic, biotic) that describe a species distribution. They are calibrated on the observed species distribution and use several statistical models from simple linear models to neuronal networks and random forest classification methods (Thuiller 2003; Thuiller *et al.* 2003, 2005). Species distribution models that try to describe the niche following Rosenzweig's definition are more

\*isabelle.chuine@cefe.cnrs.fr

One contribution of 11 to a Theme Issue 'The role of phenology in ecology and evolution'.

recent and rarer. Such models are based on the concept of fitness and hereafter will be called 'fitness-based models'. They try to identify those traits which determine the fitness of individuals of species in particular environmental conditions, i.e. their annual survival and reproductive success (Régnière & You 1991; Régnière 1996; Chuine & Beaubien 2001; Régnière & Nealis 2002; Régnière & Logan 2003; Morin *et al.* 2007).

The two definitions of the niche that have been proposed are complementary and point out the crucial role of those traits affected by the environment in species distribution. Many traits of plant species are affected by the environment and since the trait-based definition of the niche, many studies have been devoted to identifying the limited set of traits that is responsible for a species distribution.

Phenology is a key feature of plant and poikilotherm species niche because it determines the ability to capture variable resources and it defines the season and duration of growth and reproduction (Schwartz 2003). In other animals, phenology is still essential to the reproductive success and survival of the individuals (Post 2003; Sparks *et al.* 2003). Several recent findings converge in identifying phenology as one and perhaps the most important trait-shaping species distribution. First, it is quite straightforward to understand that it is crucial for a species living in temperate or boreal environments to time its seasonal activities: when to begin developing in the spring, when to reproduce, when to enter dormancy or when to migrate, in order to exploit favourable climatic conditions and avoid unfavourable climatic conditions. Yet, it is only recently that species distribution models based on this idea have been developed. These models have proven that phenology is a keystone trait in the niche of perennial plant and insect species (Chuine & Beaubien 2001; Régnière & Nealis 2002; Régnière & Logan 2003; Morin *et al.* 2007). Second, several studies suggest that phenology plays an important role in fitness (Rathcke & Lacey 1985; Reekie & Bazzaz 1987; Kozłowski 1992), and should therefore play an important role in species distribution. Third, phenology is one of the traits most affected by climatic conditions and this is probably the reason why it is the first trait which has been documented as being highly affected by climate change (Parmesan & Yohe 2003; Root *et al.* 2003; Walther *et al.* 2005; Menzel *et al.* 2006).

In this paper I intend to explain why phenology is one of the most important traits defining a species niche and therefore shaping its distribution. The vast majority of studies dealing with phenology have primarily concerned plant species and secondarily insect species. Almost all of them were conducted on temperate, boreal, alpine and Mediterranean species. I will thus limit my demonstration to these types of organisms and these regions. The importance of phenology in other types of organism such as birds (Visser *et al.* 2010) or fishes (Mooij *et al.* 2008) has been discussed elsewhere in the literature. In the following review, the term phenology stands for the occurrence of phenological events such as flowering or leaf unfolding.

## 2. WHY IS PHENOLOGY AN ADAPTIVE TRAIT?

Despite the increasing number of investigations on species distributions and niches, little is known about what types of traits contribute to local adaptation across broad geographic gradients, i.e. to the niche according to Rosenzweig's definition. Several studies have indirectly pointed out the adaptive nature of phenology. First, many experimental and field studies have found clinal patterns in the phenology of plant species and these patterns are usually correlated to some environmental variables such as temperature, precipitation, latitude or altitude (Santamaria *et al.* 2003; Caicedo *et al.* 2004). For example, earlier reproduction is often found in northern populations and interpreted as an adaptation to cooler and shorter growing seasons and vice versa (e.g. *Xanthium strumarium*, Griffith & Watson 2005; *Potamogeton pectinatus*, Santamaria *et al.* 2003). Clinal pattern in leaf unfolding or bud set has also been widely documented in forest trees (Rehfeldt 1989; Rehfeldt *et al.* 1999, 2002; Chuine *et al.* 2001; Savolainen *et al.* 2004). Second, phylogenetic studies have shown that flowering time is a particularly conserved trait within temperate and tropical phylads (for review see Levin 2006), and explained the phylogenetic nature of extinction risk among plants experiencing rapid climate change (Willis *et al.* 2008). Davis *et al.* (2010) also identified similar phylogenetic patterns in long-term phenological response traits across geographically disjunct communities. Third, macroecological studies have shown that species niche position was correlated to time of flowering and that species growing in similar eco-regions had developed similar phenologies (Thuiller *et al.* 2004).

Along with this indirect evidence, other studies have shown experimentally that plant phenology, and more particularly reproductive phenology was an important determinant of fitness (Rathcke & Lacey 1985; Reekie & Bazzaz 1987; Kozłowski 1992). The timing of flowering affects the success of fruit maturation and progeny quality (Pigott & Huntley 1981; Galloway 2002; Lacey *et al.* 2003) but also the success of pollination as well as the level of seed and fruit herbivory (for review see Levin 2006).

Finally, phenological traits also usually show a very high level of heritability and high level of genetic variability within and among populations in plants and insects (Etterson & Shaw 2001; Etterson 2004a,b; Franks *et al.* 2007; Volis 2007; van Asch *et al.* 2007). This shows that phenological traits have a strong potential to evolve rapidly pending strong enough selection gradients.

All this evidence shows directly and indirectly that phenological traits are a key component of fitness and are able to evolve relatively rapidly (for review see Levin 2006). Indeed, climate change is already inducing the genetic evolution of some adaptive traits in many species, such as dispersion traits in insect species (Hill *et al.* 1999; Thomas *et al.* 2001), and phenological traits in insects, mammals and plants (for review in animals see Bradshaw & Holzapfel 2008). The mosquito *Wyeomyia smithii* has, for example, shifted toward shorter, more southern daylengths as growing seasons have become longer. This shift was

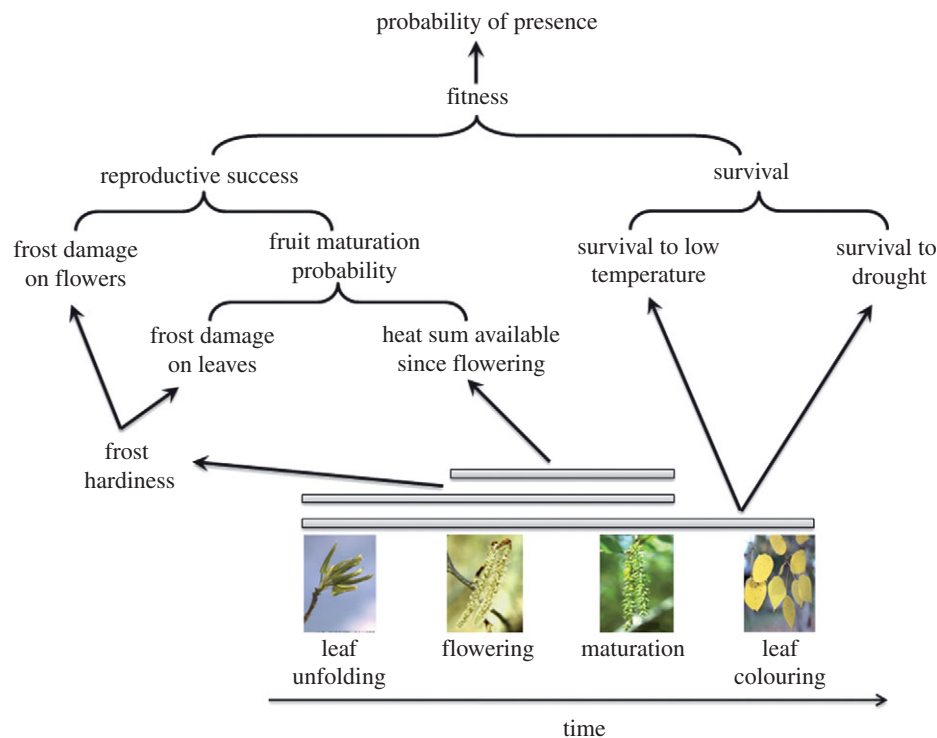


Figure 1. Conceptual scheme of the process-based model PHENOFIT. The annual cycle is simulated using process-based phenological models calibrated on time series of each phenological event for several geographic provenances of the species.

detectable over a time interval as short as 5 years (Bradshaw & Holzapfel 2001). Berteaux *et al.* (2004) showed that the parturition date in a population of North American red squirrels has advanced during the past 20 years and this change was the result of both plasticity (62%) and genetic evolution (13%). Franks *et al.* (2007) showed that the evolutionary response of the annual plant *Brassica rapa* to a recent climate fluctuation resulting in a multiyear drought led to the evolution of earlier onset of flowering. However, several studies indicate that the rate of evolution is unable to match predicted rate of warming (for review see Jump & Penuelas 2005).

Now a question arises: if phenological traits are adaptive and able to evolve rapidly, why do they not evolve to adapt to the environment surrounding the distributional ranges of species and expand those ranges? I see two major hypotheses that could explain this contradiction. First of all, like other adaptive traits involved in species niche, the evolution of phenological traits will depend on the balance between selection and migration. Theoretical work has demonstrated that evolutionary constraints on one or several adaptive traits such as asymmetric gene flow between margins and centre of the range, could limit the evolution of these traits and therefore of species range (Garcia-Ramos & Kirkpatrick 1997; Kirkpatrick & Barton 1997; Case & Taper 2000; Garcia-Ramos & Rodriguez 2002; but see Polechova *et al.* 2009). Second, the genetic evolution of phenological traits is constrained by genetic correlations among them (Ehrlén & Münzbergova 2009) but also with other adaptive traits such as drought or frost tolerance (for review see Levin 2006), or life-history traits such as seed size. Several studies converge in identifying seed size as a key trait shaping species niche. Seed size has

been shown to be highly correlated to species range and to species northern range limits (Morin & Chuine 2006), with small-seeded species having larger ranges because of higher latitude limits. Although it has been shown in many species that seed size and mass was negatively correlated to seed number within a species (Fenner & Thompson 2005), seed size cannot vary too much within a species because if a critical mass is not reached, a seed's ability to germinate decreases drastically (Leadem 1985; Pitel & Wang 1989). As a key trait defining a species strategy (Fenner & Thompson 2005), the evolution of seed size is thus very much constrained and often associated to speciation events (Moles *et al.* 2005a,b). This most important life-history trait is thus likely to constrain the evolution of other key adaptive traits shaping species niche such as phenology. The time necessary to mature seeds indeed depends on seed size and on the environmental conditions, such as temperature, prevailing after flowering time (Moles & Westoby 2003). Flowering time should evolve in order to maximize seed maturation success, and thus occur at a time minimizing both frost and drought damage on the reproductive organs, and the length of the maturation period. Since fruit maturation timing is dependent on flowering timing, that is itself related to onset of growth timing in most species (I. Chuine 2010, unpublished results), seed size thus constrains the entire annual cycle of plants.

### 3. HOW IS PHENOLOGY INVOLVED IN REPRODUCTIVE SUCCESS, SURVIVAL AND GROWTH?

As we shall see later on, a plant species phenology results from natural selection to optimize the period of activity and reproduction under given



environmental conditions of temperature, light and water availability. This optimization has to cope with several trade-offs. For example, in the boreal and temperate zone, there is a trade-off between maximizing annual carbon assimilation with early leaf unfolding and late leaf senescence and reducing the risk of damage caused by frost on vegetative organs. Similarly, there is a trade-off between maximizing fruit set with early flowering and reducing the risk of damage by frost on reproductive organs. Plant species have adapted their phenology to their local environment using primarily temperature and photoperiod to detect such optimal conditions (Sarvas 1972, 1974; Hänninen 1990, 1991; Hänninen *et al.* 1993; Heide 1993a,b; Kramer 1994b, 1995; Chuine & Cour 1999; Chuine *et al.* 1999, 2001; Badeck *et al.* 2004).

Studies that have aimed at demonstrating the link between phenology and reproductive success are not numerous and have all concerned flowering phenology (Chidumayo 2006; Gimenez-Benavides *et al.* 2006; Volis 2007; Inouye 2008; Ehrlén & Münzbergova 2009). It is quite intuitive to imagine that flowering phenology will affect the reproductive success of a plant, particularly in temperate, alpine, boreal and Mediterranean regions. However, demonstrating this link experimentally is not always an easy task. If all these studies showed that flowering phenology is important in determining reproductive success, they do not converge on the relationship between the two. This relationship indeed depends on the climatic conditions that prevail in the region investigated and the life-history traits of the species. The high-mountain Mediterranean species *Silene ciliata*, for example, has a higher reproductive success when flowering earlier because it can take advantage of the snow melt for growing (Gimenez-Benavides *et al.* 2006). The perennial woody savanna species *Lannea edulis* also has a higher reproductive success when flowering earlier because of a higher germination rate of seeds produced earlier in the season (Chidumayo 2006). The authors explain this result by a selective pressure to flower earlier to escape dry season fires. On the contrary, the perennial herbaceous mountain species *Delphinium barbeyi*, *Erigeron speciosus* and *Helianthella quinquenervis* show a lower reproductive success when flowering earlier (Inouye 2008). This is explained by the fact that reproductive success of these species is correlated to snowpack. Greater snowpacks induce a later snowmelt and thereby a later beginning of growth and later flowering so that buds and flowers experience less frost damage.

The phenology of many insect species is also key for their reproductive success and survival. van Asch *et al.* (2007) have shown, for example, a severe fitness cost for the winter moth *Operophtera brumata* of a few days delay between egg-hatching and *Quercus robur* leaf unfolding (see also Singer & Parmesan 2010). A high fitness cost of asynchronisation between reproductive timing of insect species and beginning of plant growth has been reported in many species (Regnière & Logan 2003; Mjaaseth *et al.* 2005; Parmesan 2006). Such asynchronisation has been shown to severely affect bird populations feeding on caterpillars (Visser *et al.* 2004; Both & Visser 2005; Visser & Both 2005).

There is also much documented evidence that phenology is an important determinant of plant growth and survival. Leaf unfolding and leaf senescence timing have been shown to have a major control on spatial and temporal variation in biologically mediated sources and sinks of carbon in the Mediterranean, temperate and boreal latitudes at stand scale (e.g. White *et al.* 1999; Baldocchi & Wilson 2001; Barr *et al.* 2007), and at global scale (Keeling *et al.* 1996). Earlier leaf unfolding owing to global warming has been positively correlated to longer carbon uptake period, and to increased net annual CO<sub>2</sub> flux and net primary productivity (Goulden *et al.* 1996; Churkina *et al.* 2005; Piao *et al.* 2007). Contrarily, leaf senescence tends to be later owing to global warming but is concomitant with less favourable conditions for photosynthesis than bud burst timing (Morecroft *et al.* 2003; Piao *et al.* 2007). Thus, warmer temperatures in spring increase carbon uptake because they enhance growth more than soil decomposition, but warmer temperatures in autumn reduce carbon uptake because they enhance growth less than soil decomposition. Piao *et al.* (2007) showed using net CO<sub>2</sub> flux data and dynamic global vegetation models that the reduction in carbon uptake in autumn was more important than the increase in carbon uptake in spring, and as a consequence that temperate ecosystems were losing carbon with global warming.

In plant species, phenology, root distribution and leaf lifespan determine the ability to use soil resources and take up carbon. Mobile (water, nitrogen, silicon, magnesium, calcium) and immobile (phosphorus, potassium, ammonium) soil resource acquisition is thought to increase with longer growing season (Nord & Lynch 2009). Transpiration is indeed the major driver for the acquisition of mobile resources and is related to leaf lifespan, while root lifespan is the major driver of immobile resource acquisition. Phenology of leaves and roots is also very important to match the availability of resources which show a seasonal variability and acquisition capacity. Phenology also affects resource utilization, particularly for reproduction. For example, increased temperature tends to shorten the reproductive phase of annual plants by decreasing seed-filling duration, which is responsible for decreased yield (Egli 2004).

#### 4. HOW IS PHENOLOGY INVOLVED IN SPECIES DISTRIBUTION?

Northern range limits are often associated with decreased growing season length and mean temperature (Morin & Chuine 2006). Therefore, in the northern range limits, growth and reproduction must be completed in a shorter time period and, in addition, in less favourable conditions than in lower latitudes. Therefore, plants have to adapt the timing of their annual life cycle to the varying conditions they encounter throughout their range. This can be achieved by two means; firstly by a plastic response of their phenology to some environmental cues such as temperature or photoperiod; secondly by genetic differentiation of the populations for this response.

We have seen earlier that genetic differentiation among populations of a plant species for its phenological traits was usually common, especially between northern range limit populations and more southern populations. However, phenological traits vary across a species range mainly because of a high level of plasticity in response to temperature and photoperiod.

The case of temperate tree species has particularly been studied and process-based phenological models for leaf unfolding, flowering, fruit maturation and more recently leaf senescence (Delpierre *et al.* 2009) have been developed during the past 30 years (for review see Chuine *et al.* 2003). Such models have also been developed for some insect species responsible for important damage in forest stands, such as gipsy moth, spruce budworm and mountain pine beetle (Régnière 1987, 1996; Logan *et al.* 1991, 2007; Régnière & You 1991; Régnière & Nealis 2002; Régnière & Logan 2003; for review see Régnière & Logan 2003). In both cases, the hypotheses formulated in the process-based phenological models derive from the results of experimental studies in controlled conditions, which aimed at identifying the environmental cues of the phenological events (for review see Chuine *et al.* 2003; Régnière & Logan 2003). These models have been used to develop fitness-based models. Fitness-based models aim at estimating the survival and reproductive success either of an average individual of a given population (for tree species) or a set of individuals of a population (for insect species) according to the environmental conditions which are primarily temperature, photoperiod and precipitation. Such models have been developed primarily to study the impact of phenology on fitness, but they rapidly revealed their ability to predict species distribution (Chuine & Beaubien 2001; Régnière & Logan 2003; Morin & Chuine 2005; Morin *et al.* 2008). In the following, I will describe the model PHENOFIT developed for temperate tree species and explain how phenology affects survival and reproductive success (Chuine & Beaubien 2001).

PHENOFIT outputs a probability of presence over several years for an individual of a particular species, estimated by the product of a probability to survive until the next reproductive season and the probability to produce viable seeds by the end of the annual cycle (reproductive success; figure 1). PHENOFIT is based on different process-based models: phenological models (Chuine 2000; Chuine *et al.* 2003), a frost-injury model (Leinonen 1996), a survival model and a reproductive success model. All parameters of these models, except that for survival in drought, for which very few data exist so far, are derived from observations of the different traits involved in the model rather than from present distributions of the species. These observations are primarily dates of leaf unfolding, of flowering, of fruit maturation and of leaf senescence. These can be obtained from natural population surveys. A second set of important information is the resistance of buds and leaf tissue to frost, which requires measurements in the laboratory using, for example, the method of electrolyte leakage following artificial frost. The third important information is the resistance of the species to drought,

which is very difficult to assess and is currently under investigation in several research programmes. Such observations are unfortunately currently too rare to allow a rapid development and parameterization of such a model. Finally, although it is less crucial than for habitat models, which are fitted on species present distribution, information on the presence and absence of the species is important to validate the models. Yet, such information remains of poor quality, and efforts to compile species inventories at a fine spatial resolution, including land use history, would be necessary to yield good quality information. Given the extent of the task, this may require resort to citizen science programmes.

The frost injury, survival and reproductive success models are based on the match between the simulated development and climate seasonality, e.g. survival is reduced if severe drought occurs between leafing and leaf colouring, reproductive success is reduced if frost occurs during flowering, etc. The reproductive success integrates the probability of completing fruit maturation by the end of the season and the proportion of fruits (between 0 and 1) that will reach this state, i.e. that will not be damaged by frost at either stage (from flower bud to mature fruit). The probability of completing fruit maturation primarily depends on the temperature conditions that prevail after flowering but is also affected by the proportion of leaves (between 0 and 1) that participate in carbon uptake, i.e. that have not been damaged by frost during their lifespan. PHENOFIT only uses climatic (daily temperatures and precipitation) and soil (water holding capacity) data as input variables.

This model has been used to identify the climatic factors as well as the biological processes involved in determining tree species' ranges (Morin *et al.* 2007). The model showed that climatic constraints limit species' distributions primarily through their impact on phenological processes, and secondarily through their impact on drought and frost mortality. Contrary to what has been thought until recently, the northern limit of species' ranges appears to result mainly from the inability to undergo full fruit maturation and not from killing frost, while the southern limit appears to result from the inability to flower or unfold leaves because of a lack of chilling temperatures that are necessary to break bud dormancy (figure 2).

Fitness-based models are very much complementary to habitat models. Although they are limited when explaining species distributions, especially in the sense of Rosenzweig, and suffer some methodological problems, habitat models are currently the only ones able rapidly to provide simulations of thousands of species distributions to assess the impact of global change on biodiversity for the following decades. Fitness-based models are, on the contrary, very time consuming to build up, but provide a more comprehensive understanding of species distribution, allowing precise identification of which processes or traits are responsible for species range limits in interaction with environmental factors. The limit of such models is clearly the quantity of information required to build and calibrate them, which makes their development much slower.

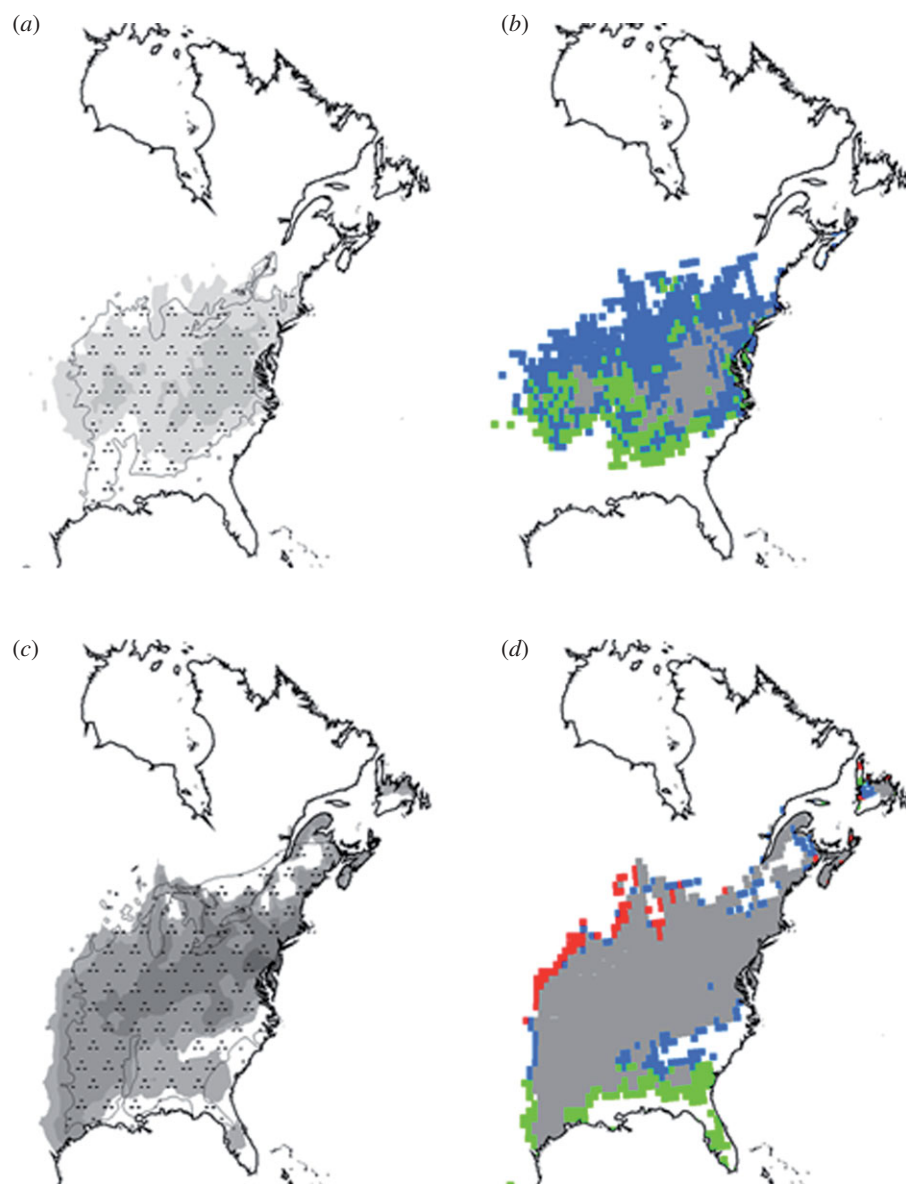


Figure 2. Simulated present distributions of (a) *Carya ovata* and (c) *Fraxinus americana* using the process-based model PHE-NOFIT and climatic data CRU TS 2.0 (New *et al.* 2000). Presently observed distributions are dashed and simulated probabilities of presence according to the model are in grey. Limiting processes at the distribution margins of (b) *Carya ovata* and (d) *Fraxinus americana*: red (survival), green (flowering), blue (fruit maturation). Adapted from Morin *et al.* (2007).

## 5. HOW WILL CLIMATE CHANGE AFFECT SPECIES PHENOLOGY AND DISTRIBUTION?

There have been a large number of studies which have reported phenological changes during the past 60 years in various types of organisms (see for review Parmesan & Yohe 2003; Root *et al.* 2003; Walther *et al.* 2005; Menzel *et al.* 2006). Phenological shifts have been the first reported biological footprint of the impact of climate change. Along with these changes, shifts in distribution have also been reported in numerous species (Hughes 2000; Walther *et al.* 2001, 2002; Parmesan & Yohe 2003; Root *et al.* 2003; Walther 2003; Lenoir *et al.* 2008). Reported changes in phenology are mainly advancement of spring events such as leaf unfolding, flowering, emergence of adult forms of some insects, but delay of autumn events such as leaf senescence, diapause entrance. Reported changes in species distribution are mainly poleward and upward shifts and southern range local extinctions. According to the

environmental determinisms of spring phenological events, advancements observed are explained by warmer springs that speed up cell growth once dormancy has been broken (Menzel *et al.* 2006). The late-autumn phases in plants are, however, less well understood as the environmental determinism of leaf senescence has not been elucidated so far (but see Delpierre *et al.* 2009).

Although there have been a tremendous number of studies which have investigated the environmental cues of species distributions (for review see Gaston 2003; Lomolino *et al.* 2005), very few studies have been devoted to identifying the traits or processes responsible for species distributions. These latter studies usually report potential growth limitation by low temperature and drought (Rehfeldt *et al.* 1999; Seynave *et al.* 2008) and reproduction limitation by low temperature (Pigott & Huntley 1981). Instead, most studies have investigated the relationship between fitness and adaptive traits, in particular



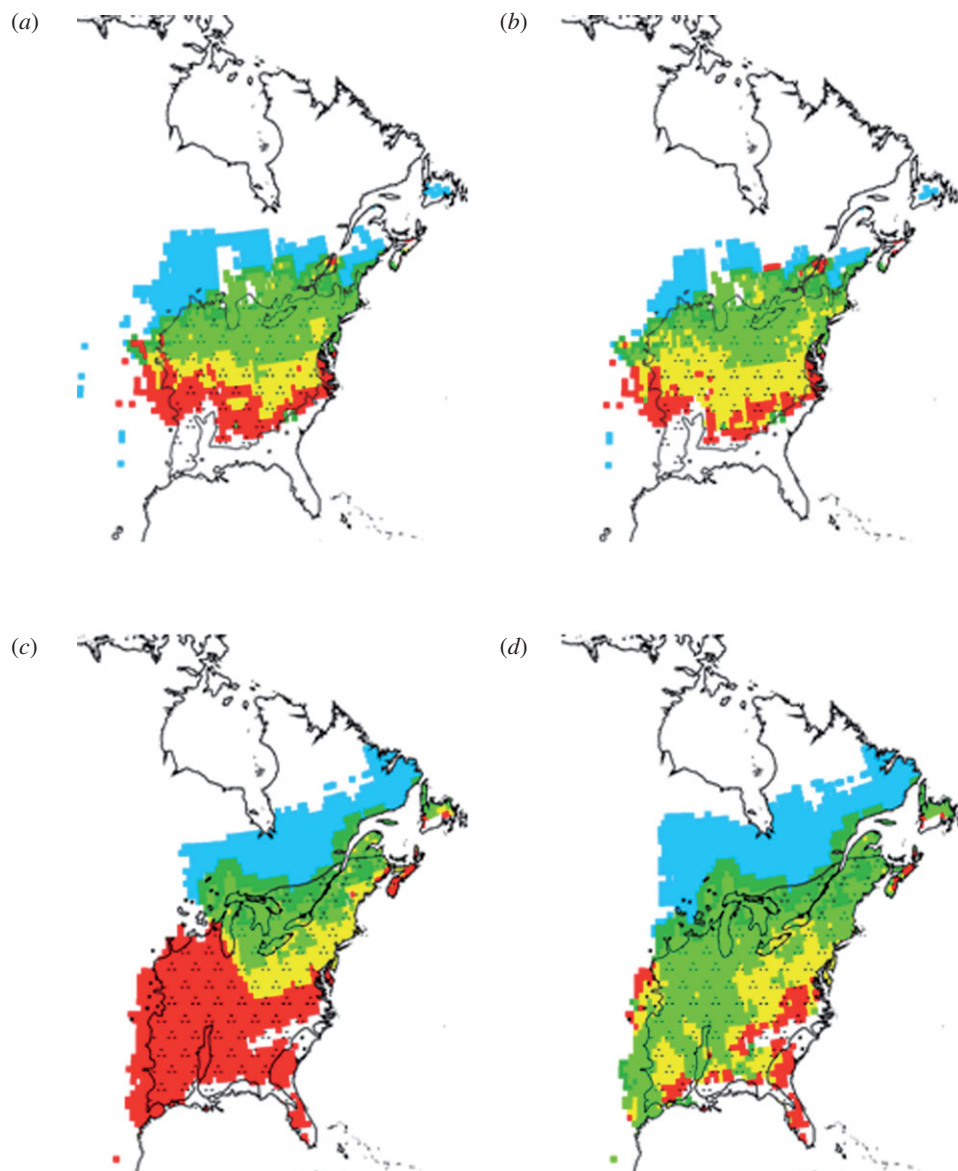


Figure 3. Projected distributions of *Carya ovata* (a,b) and *Fraxinus americana* (c,d) in 2100 following IPCC scenario A2 (a,c) and B2 (b,d) and GCM HadCM3 using PHENOFIT: red (extinction), yellow (decreased fitness), green (increased fitness), dark green (colonized area), blue (unreached suitable area). Adapted from Morin *et al.* (2008).

phenology. Some of these studies concluded, for example, that although late-flowering alpine and sub-arctic plants may enhance their reproductive performance in warming scenarios because of earlier flowering triggering a better seed set (number and/or mass) (Molau 1993; Alatalo & Tøtland 1997), climate change will decrease reproductive success of high mountain Mediterranean species because of increased summer drought (Gimenez-Benavides *et al.* 2006).

These observations confirm the hypotheses of fitness-based models that phenology and resistance to abiotic stresses such as frost and drought are key processes in determining species niche and thereby distribution. These models have been used with climate scenarios of the twenty-first century to study the evolution of species distribution and identify the key abiotic variables and biological processes which will be responsible for the forthcoming changes (Regnière & Logan 2003; Morin *et al.* 2008). In agreement with reported changes, projections show local

extinctions in the south of species ranges, and colonization of new habitats in the north, though these are limited by dispersal ability for most species (figure 3; Morin *et al.* 2008). Although predicted distribution shifts appear very species-specific, the loss of habitats southward seems to be mostly due to increased drought mortality and decreased reproductive success in most species, while northward colonization seems to be primarily promoted by increased probability of fruit ripening and flower frost survival. However, projections show that different species will not face the same risks owing to climate change, because their responses to climate in terms of phenology and stress resistance differ as well as their dispersal rate. An important result of such projections is also that local extinction may proceed at a slower rate than forecasted so far by niche-based models, which tempers the alarming conclusions of these latter about biodiversity loss (Morin & Thuiller 2009). This important result is explained by the fact that fitness-based models take into account the local adaptation and the trait's



plasticity to climate of the species, but also the non-linear responses of the processes where temperature is involved (Morin *et al.* 2008; Morin & Thuiller 2009).

## 6. HOW CAN WE IMPROVE FITNESS-BASED SPECIES DISTRIBUTION MODELS?

Although, fitness-based models are able, in their present state, to predict relatively accurate species distributions of trees and insects at a global scale, some improvements can be achieved to refine the simulations, especially for tree fitness-based models. Four types of improvement can be pursued. One of them concerns the phenological models specifically and the three others concern the species distribution models. First of all, and most importantly, an important question for temperate and boreal tree species is whether bud-burst will occur earlier or later in a warmer climate (Hänninen 1991; Kramer 1994a; Heide 2003). This depends on the response of the species phenology to chilling temperature and on the temperature that will prevail in autumn and winter. Morin *et al.* (2009) have shown that lack of sufficient chilling temperatures to break bud dormancy should decrease the rate of advancement in leaf unfolding date during the twenty-first century for many North American tree species, and that some species may even experience abnormal budburst owing to insufficient chilling. The study also showed that insufficient chilling exposure and abnormal budburst should appear predominantly in the southern range of the species. These predictions are based on an important assumption of process-based phenological models that chilling temperatures are required to break bud dormancy, which is necessary for subsequent cell growth leading to bud-burst. Yet, parameters of these models are always fitted on leaf unfolding or flowering dates only because no information on the date of dormancy break exists. Therefore, parameter estimates of the dormancy phase cannot be accurately evaluated. Yet, errors in these estimates could substantially change the predictions of leaf unfolding or flowering dates. There is thus an urgent need to measure dormancy break dates in temperate tree species in order to provide robust calibration of phenological process-based models.

Second, all species distribution models have to integrate or improve species dispersal and migration processes to be able to provide accurate projections of future distributions (Midgley *et al.* 2007; Morin & Lechowicz 2008; Thuiller *et al.* 2008). Three types of dispersion model have been developed so far that could be integrated with species distribution models: purely mechanistic dispersion models (Nathan *et al.* 2001; Nathan & Casagrandi 2004; Soons *et al.* 2004; Kuparinen 2006), kernel-based models (Clark 1996, 1998; Clark *et al.* 1998, 2001) and Gibbs-based models (Saltré *et al.* 2009).

Third, fitness-based tree distribution models, contrary to dynamic global vegetation models, at present do not integrate growth processes such as photosynthesis, respiration and carbon allocation. At the species level, such processes do not seem to be essential to provide an accurate representation of the distribution at a global scale. Thus, it seems unnecessary to have an exhaustive representation of the niche

to be able to simulate a species distribution. However, an accurate modelling of growth processes and allocation processes could improve the simulation of some of the survival components of the fitness-based models. Species distribution models should also integrate biotic constraints, notably interspecific competition, to provide an accurate representation of species distributions at a regional scale.

Last but not least, at present none of the existing species distribution models integrates genetic evolution of the traits they simulate in response to climate change. Yet, we have seen previously that ongoing genetic evolution is underway in several species (see also Springer *et al.* 2008), and will affect their fate. In this respect, fitness-based distribution models seem to be the most adequate to integrate a genetic component and efforts should be put into integrating the genetic evolution of phenological traits and stress-resistance traits into such models.

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