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4 Why does phenology drive species distribution?

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16

Abstract

Despite the numerous studies which have been conducted the last decade on species ranges and their relationship to environment, our understanding of how environmental conditions shape species' distributions is still far from being 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. I discuss here why phenology is a key adaptive traits 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.

Key words

Species distribution, niche, fitness-based models

Introduction

More than ever an accurate understanding of how environmental conditions shape species' distributions 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 is still a challenging question (Parmesan et al. 1999, Johnstone & Chapin 2003).

Species distribution, and more precisely species habitat, has been linked to the concept of species niche for the first time in 1917 by Grinnell (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 been also called the "address" of the species and the second one its "profession" (Odum 1959). Thirty years later, Hutchinson 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 this is only sixty years later that the concept of species niche was linked to the concept of species traits by Rosenzweig (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 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 have been called initially "envelop models", the envelop 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 species observed distribution and use several statistical models from simple linear models to neuronal networks and random forest classification methods (Thuiller 2003, Thuiller et al. 2003, Thuiller et al. 2005). Species distribution models that try to describe the niche following Rosenzweig’s definition are more recent and rarer. Such models are based on the concept of fitness and will be called hereafter “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 first definition of the niche, i.e. that according to the environment, is as important as the second one i.e. that according to the traits; and their analogy points out the crucial role of 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 aspect of plant and poikilotherm species strategies 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 the survival of the individuals (Post 2003, Sparks et al. 2003). Several recent findings converge in identifying phenology as one and maybe 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 favorable climatic conditions and avoid unfavorable climatic conditions. Yet, it is only recently that species distribution models based on this idea have been developed. These models have proven that

phenology was a keystone trait in the niche of perennial plant and insect species (Chaine & Beaubien 2001, Régnière & Nealis 2002, Régnière & Logan 2003, Morin et al. 2007). Second, several studies suggest that phenology play 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 the most affected by climatic conditions and this is probably the reason why it is the first trait which has been documented as highly affected by climate change (Parmesan & Yohe 2003, Root et al. 2003, Walther et al. 2005, Menzel et al. 2006). Concomitantly to phenological changes, many studies have documented shifts in species distributions due to climate change with mostly northward and upward shifts (Parmesan & Yohe 2003, Root et al. 2003, Walther et al. 2005).

In this paper I intend to explain why phenology is one of the most important traits defining a species niche 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 type of organisms such as birds (Visser et al. 2010) or fishes (Mooij et al. 2008) has been discussed elsewhere in the literature. In the following, the term phenology stands for the occurrence of phenological events such as flowering or leaf unfolding.

Why is phenology an adaptive trait?

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 a species range (Garcia-Ramos & Kirkpatrick 1997, Kirkpatrick & Barton 1997, Case & Taper 2000, Garcia-Ramos & Rodriguez 2002, Holt 2003). However, 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 pointed out the adaptive nature of phenology indirectly. 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, Chuine et al. 2001, Rehfeldt et al. 2002, 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). 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 these indirect evidences, 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, Kozlowski 1992). The timing of flowering affects the success of fruit maturation and the 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). Phenological traits also usually show high level of heritability and of genetic variability within and among populations in plants and insects (Etterson & Shaw 2001, Etterson 2004a, b, Franks et al. 2007, van Asch et al. 2007, Volis 2007).

All these evidences make phenological traits particularly adaptive which explains that they can evolve relatively rapidly (for review see Levin 2006). Climate Change is already inducing the genetic evolution of some adaptive traits in many species, although several studies indicate that the

rate of evolution is unable to match predicted rate of warming (for review see Jump & Penuelas 2005). Documented cases concern dispersion traits in insect species (Hill et al. 1999, Thomas et al. 2001), but most of them concern 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 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 last twenty years and this change was the result both of 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.

The genetic evolution of phenological traits is however often constrained by genetic correlations among them (Ehrlén & Münzbergova 2009) and 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 occurring at a time minimizing both frost and drought damages on the reproductive organs, and the length of the maturation period. Since fruit maturation timing is dependent on flowering timing itself related to onset of growth timing in most species (Chuine, unpublished results), seed size thus constrains the entire annual cycle of plants.

How is phenology involved in reproductive success, survival and growth?

As we will 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 tradeoffs. For example, in the boreal and temperate zone, there is a tradeoff 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 tradeoff 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, Chuine et al. 2001, Badeck et al. 2004).

Studies which 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). This 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 the 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* (Anacardiaceae) 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 snowpack 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. High fitness cost of asynchronisation between reproductive timing of insect species and plant beginning of growth have been reported in many species (Regnière & Logan 2003, Mjaaseth et al. 2005, Parmesan 2006). Such asynchronisation has been shown to affect severely bird populations feeding on caterpillars (Visser et al. 2004, Both & Visser 2005, Visser & Both 2005).

There have been also many documented evidences 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 due to global warming has been positively correlated to longer carbon uptake period, and to increased net annual CO₂ flux and net primary productivity (Goulden et al. 1996, Churkina et al. 2005, Piao et al. 2007). Contrarily, leaf senescence tends to be later due to global warming but is

concomitant with less favorable 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 CO₂ fluxes data and Dynamic Global Vegetation models that the reduction in carbon uptake in fall 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, roots distribution and leaves lifespan determine the ability to use soil resources and uptake carbon. Mobile (water, nitrogen, silicon, magnesium, calcium) and immobile (phosphorus, potassium, ammonium) soil resources acquisition is thought to increase with longer growing season and vice versa (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 resources 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).

How is phenology involved in species distribution? The proof by fitness-based species distribution models

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 favorable 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 on 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 have particularly been studied and process-based phenological models for leaf unfolding, flowering, fruit maturation and more recently leaf senescence (Delpierre et al.) have been developed during the last thirty 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, mountain pine beetle (Régnière 1987, Logan et al. 1991, Régnière & You 1991, Régnière 1996, Régnière & Nealis 2002, Régnière & Logan 2003, Logan et al. 2007; and for review see Régnière & Logan 2003). In both cases, the hypotheses formulated in the process-based phenological models come out 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) (Fig. 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 to drought for which data do not exist so far, are derived from observations of the different traits involved in the model rather than from present distributions of the species. 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 coloring, reproductive success is reduced if frost occurs during flowering, etc. The reproductive success integrates the probability to complete fruit maturation by the end of the season and the proportion of fruits (comprised 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 to complete fruit maturation primarily depends on the temperature conditions that prevail after flowering but is also affected by the proportion of leaves (comprised between 0 and 1) that participate to 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 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 be caused mainly by the inability to undergo full fruit maturation and not by killing frost, while the southern limit appears to be caused by the inability to flower or leaf out due to a lack of chilling temperatures that are necessary to break bud dormancy (Fig. 2).

How will climate change affect species phenology and distribution?

There have been a large number of studies which have reported phenological changes during the last 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 species distributions have also been reported in numerous species ((Hughes 2000, Walther et al. 2001., Walther et al. 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, etc; but delay of autumn events such as leaf senescence, diapause entrance, etc. Reported changes in species distribution are mainly northward 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 is 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 has 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 the reported changes in species distributions. These latter studies usually report potential growth limitation by low temperature and drought (Rehfeldt et al. 1999, Seynave et al. 2008); reproduction limitation (Pigott & Huntley 1981, Tape et al. 2006). Most studies have rather investigated the relationship between fitness and adaptive traits, in particular phenology. Some of these studies concluded for example that although late-flowering alpine and subarctic plants may enhance their reproductive performance in warming scenarios due to an 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 species niche and thereby distribution. These models have been used with climate scenarios of the 21st century to study the evolution of species distribution and identify the key abiotic variables and biological processes which will be responsible for the upcoming 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 (Fig. 3) (Morin et al 2008). Although predicted distribution shifts appear very species-specific, the loss of habitats southward seem to be mostly due to increased drought mortality and decreased reproductive success in most species, while northward colonization seem primarily promoted by increased probability of fruit ripening and flower frost survival. However, projections show that different species will not face the same risks due 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 traits plasticity to climate of the species, but also the nonlinear responses of the processes involved to temperature (Morin et al. 2008, Morin & Thuiller 2009).

How can we improve fitness-based species distribution models?

Although, fitness-based models are able in their present state to predict relatively accurately species distributions for 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. (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 21st century for many North American tree species, and that some species may even experience abnormal budburst due 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. Thus, 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 in measuring dormancy break dates in temperate tree species in order to provide robust calibration of phenological process-based models.

Secondly, 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 models have been developed so far that could be integrated to 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, Clark et al. 2001) and Gibbs-based models (Saltré et al. 2009).

Thirdly, fitness-based tree distribution models, contrary to Dynamic Global Vegetation Models, do not integrate so far growth processes such as photosynthesis, respiration, carbon allocation etc. At the level of the species, 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 modeling 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, noticeably interspecific competition to provide an accurate representation of species distributions at a regional scale.

Last but not least, none of the species distribution models existing so far does integrate genetic evolution of the traits they simulate in response to climate change. Yet, we have seen previously that ongoing genetic evolution was under way 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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References

- Alatalo, J. M. & O. Tøtland 1997 Response to simulated climatic change in an alpine and subarctic pollen risk strategist, *Silene acaulis*. *Glob. Change Biol.* **3**, 74-79.
- Badeck, F. W., A. Bondeau, K. Bottcher, D. Doktor, W. Lucht, J. Schaber, & S. Sitch 2004 Responses of spring phenology to climate change. *New Phytol.* **162**, 295-309.
- Baldocchi, D. D. & K. B. Wilson 2001 Modeling CO₂ and water vapor exchange of a temperate broadleaved forest across hourly to decadal time scales. *Ecol. Mod.* **142**, 155-184.
- Barr, A. G., T. A. Black, E. H. Hogg, T. J. Griffis, A. Theede, N. Kljun, K. Morgenstern, & Z. Nasic 2007 Climatic controls on the carbon and water balances of a boreal aspen forest, 1994-2003. *Glob. Change Biol.* **13**, 561-576.
- Berteaux, D., D. Réale, A. G. McAdam, & S. Boutin 2004 Keeping pace with fast climate change: can arctic life count on evolution? *Integrative and Comparative Biology* **44**, 140-151.
- Both, C. & M. E. Visser 2005 The effect of climate change on the correlation between avian life-history traits. *Glob. Change Biol.* **11**, 1606-1613.
- Bradshaw, W. E. & C. M. Holzapfel 2001 Genetic shift in photoperiodic response correlated with global warming. *PNAS* **98**, 14509-14511.
- Bradshaw, W. E. & C. M. Holzapfel 2008 Genetic response to rapid climate change: it's seasonal timing that matters. *Molecular Ecology* **17**, 157-166.
- Caicedo, A. L., J. R. Stinchcombe, K. M. Olsen, J. Schmit, & M. D. Purugganan 2004 Epistatic interaction between *Arabidopsis* FRI and FLC flowering time genes generates a latitudinal cline in a life history trait. *PNAS* **101**, 5670-5675.
- Case, T. J. & M. L. Taper 2000 Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *Am. Nat.* **155**, 583-605.
- Chidumayo, E. N. 2006 Fitness implications of late bud break and time of burning in *Lannea edulis* (Sond.) Engl. (Anacardiaceae). *Flora* **201**, 588-594.
- Chuine, I., S. N. Aitken, & C. C. Ying 2001 Temperature thresholds of shoot elongation in provenances of *Pinus contorta*. *Can. J. For. Res.* **31**, 1444-1455.
- Chuine, I. & E. Beaubien 2001 Phenology is a major determinant of temperate tree range. *Ecol. Lett.* **4**, 500-510.
- Chuine, I. & P. Cour 1999 Climatic determinants of budburst seasonality in four temperate-zone tree species. *The New Phytologist* **143**, 339-349.
- Chuine, I., P. Cour, & D. D. Rousseau 1999 Selecting models to predict the timing of flowering of temperate trees: implication for tree phenology modelling. *Plant, Cell & Env.* **22**, 1-13.
- Chuine, I., K. Kramer, & H. Hänninen 2003 Plant Development Models. In *Phenology: An Integrative Environmental Science* (ed. M. D. Schwarz), pp. 217-235. The Netherlands: Kluwer.
- Churkina, G. D., B. H. Schimel, X. M. Braswell, & G. J. Xiao 2005 Spatial analysis of growing season length control over net ecosystem exchange. *Glob. Change Biol.* **11**, 1777-1787.
- Clark, J. S. 1996 Testing disturbance theory with long-term data: alternative life-history solutions to the distribution of events. *Am. Nat.* **148**, 976-996.
- Clark, J. S. 1998 Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *Am. Nat.* **152**, 204-224.
- Clark, J. S., C. Fastie, G. Hurtt, S. T. Jackson, C. Johnson, G. A. King, M. Lewis, J. Lynch, S. Pacala, C. Prentice, E. W. Schupp, T. Webb, & P. Wyckoff 1998 Reid's paradox of rapid plant migration - Dispersal theory and interpretation of paleoecological records. *Bioscience* **48**, 13-24.
- Clark, J. S., M. Lewis, & L. Horvath 2001 Invasion by extremes: Population spread with variation in dispersal and reproduction. *Am. Nat.* **157**, 537-554.

- Delpierre, N., E. Dufrêne, K. Soudani, E. Ulrich, S. Cecchini, J. Boé, & C. François 2009 Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in France. *Agr Forest Meteorol* **149**, 938-948.
- Egli, D. B. 2004 Seed-fill duration and yield of grain crops. *Advances in agronomy* **83**, 243-279.
- Ehrlen, J. & Z. Münzbergova 2009 Timing of Flowering: Opposed Selection on Different Fitness Components and Trait Covariation. *Am. Nat.* **173**, 819–830.
- Elton, C. S. 1927 *Animal Ecology*. London: Sidgwick & Jackson.
- Etterson, J. R. 2004a Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. I. Clinal patterns of selection along an environmental gradient in the great plains. *Evolution* **58**, 1446-1458.
- Etterson, J. R. 2004b Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. II. Genetic architecture of three populations reciprocally planted along an environmental gradient in the great plains. *Evolution* **58**, 1459-1471.
- Etterson, J. R. & R. G. Shaw 2001 Constraint to adaptive evolution in response to global warming. *Science* **294**, 151-154.
- Fenner, M. & K. Thompson 2005 *The Ecology of Seeds*. Cambridge: Cambridge University Press.
- Franks, S. J., S. Sim, & A. E. Weis 2007 Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *PNAS* **104**, 1278–1282.
- Galloway, L. F. 2002 The effect of maternal phenology on offspring characters in the herbaceous plant *Campanula Americana* *J. Ecol.* **90**, 851-858.
- Garcia-Ramos, G. & M. Kirkpatrick 1997 Genetic models of adaptation and gene flow in peripheral populations. *Evolution* **5**, 21-28.
- Garcia-Ramos, G. & D. Rodriguez 2002 Evolutionary speed of species invasions. *Evolution* **56**, 661-668.
- Gaston, K. J. 2003 *The Structure and Dynamics of Geographic Ranges*. New York: Oxford University Press.
- Gimenez-Benavides, L., A. Escudero, & J. M. Iriondo 2006 Reproductive limits of a late-flowering high-mountain Mediterranean plant along an elevational climate gradient. *New Phytol.* **173**, 367-382.
- Goulden, M. L., J. W. Munger, S. M. Fan, B. C. Daube, & S. C. Wofsy 1996 Exchange of carbon dioxide by a deciduous forest: Response to interannual climate variability. *Science* **271**, 1576-1578.
- Griffith, T. M. & M. A. Watson 2005 Stress avoidance in a common annual: reproductive timing is important for local adaptation and geographic distribution. *J. Evol. Biol.* **18**, 1601-1612.
- Grinnell, J. 1917 Field tests of theories concerning distributional control. *Am. Nat.* 115-128.
- Guisan, A. & W. Thuiller 2005 Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* **8**, 993-1009.
- Guisan, A. & N. E. Zimmermann 2000 Predictive habitat distribution models in ecology. *Ecol. Mod.* **135**, 147-186.
- Hänninen, H. 1990 Modelling bud dormancy release in trees from cool and temperate regions. *Acta For. Fenn.* **213**, 1-47.
- Hänninen, H. 1991 Does climatic warming increase the risk of frost damage in northern trees? *Plant, Cell & Env.* **14**, 449-454.
- Hänninen, H., S. Kellomäki, K. Laitinen, B. Pajari, & T. Repo 1993 Effect of increased winter temperature on the onset of height growth of Scots pine: a field test of a phenological model. *Silva Fenn.* **27**, 251-257.
- Heide, O. M. 1993a Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physio. Plant.* **88**, 531-540.
- Heide, O. M. 1993b Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. *Physio. Plant.* **89**, 187-191.
- Heide, O. M. 2003 High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. *Tree Physiol* **23**, 931-936.

- Hill, J. K., C. D. Thomas, & D. S. Blakeley 1999 Evolution of flight morphology in a butterfly that has recently expanded its geographic range. *Oecologia* **121**, 165-170.
- Holt, R. D. 2003 On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research* **5**, 159-178.
- Hughes, L. 2000 Biological consequences of global warming: is the signal already apparent. *Trends Ecol. Evol.* **15**, 56-61.
- Inouye, D. W. 2008 Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* **89**, 353-362.
- Johnstone, J. F. & F. S. Chapin 2003 Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Glob. Change Biol.* **9**, 1401-1409.
- Jump, A. S. & J. Penuelas 2005 Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol. Lett.* **8**, 1010-1020.
- Keeling, C. D., J. F. S. Chin, & T. P. Whorf 1996 Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature* **382**, 146-149.
- Kirkpatrick, M. & N. H. Barton 1997 Evolution of a species' range. *Am. Nat.* **150**, 1-23.
- Kozlowski, J. 1992 Optimal allocation of resources to growth and reproduction : implications for age and size at maturity. *TREE* **7**, 15-18.
- Kramer, K. 1994a A modelling analysis of the effects of climatic warming on the probability of spring frost damage to tree species in The Netherlands and Germany. *Plant, Cell & Env.* **17**, 367-377.
- Kramer, K. 1994b Selecting a model to predict the onset of growth of *Fagus sylvatica*. *J. Appl. Ecol.* **31**, 172-181.
- Kramer, K. 1995 Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. *Plant, Cell & Env.* **18**, 93-104.
- Kuparinen, A. 2006 Mechanistic models for wind dispersal. *Trends Plant Sci* **g**, 296-301.
- Lacey, E. P., D. A. Roach, D. Herr, S. Kincaid, & R. Perrot 2003 Multigenerational effects of flowering and fruiting phenology in *Plantago lanceolata*. *Ecology* **84**, 2462-2475.
- Leadem, C. L. 1985 Seed dormancy in three *Pinus* species of the Inland Mountain West. Pages 117-124 in *Conifer tree seed in the Inland Mountain West Symposium*, Missoula, MT.
- Leinonen, I. 1996 A simulation model for the annual frost hardiness and freeze damage of Scots Pine. *Ann. Bot.* **78**, 687-693.
- Lenoir, J., J. C. Gégout, P. A. Marquet, P. d. Ruffray, & H. Brisse 2008 A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century. *Science* **320**, 1768-1771.
- Levin, D. A. 2006 Flowering phenology in relation to adaptive radiation. *Systematic Botany* **31**, 239-246.
- Logan, J. A., R. A. Casagrande, & A. M. Liebhold 1991 Modeling Environment for Simulation of Gypsy-Moth (Lepidoptera, Lymantriidae) Larval Phenology. *Environmental Entomology* **20**, 1516-1525.
- Logan, J. A., J. Regniere, D. R. Gray, & A. S. Munson 2007 Risk assessment in the face of a changing environment: Gypsy moth and climate change in Utah. *Ecol. Appl.* **17**, 101-117.
- Lomolino, M. V., B. R. Riddle, & J. H. Brown 2005 *Biogeography, 3rd Ed.* Sunderland: Sinauer Associates, Inc.
- Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Aha, K. Alm-Kubler, P. Bissolli, O. Braslavska, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, A. Dahl, C. Defila, A. Donnelly, Y. Filella, K. Jatcza, F. Mage, A. Mestre, O. Nordli, J. Penuelas, P. Pirinen, V. Remisova, H. Scheifinger, M. Striz, A. Susnik, A. J. H. Van Vliet, F. E. Wielgolaski, S. Zach, & A. Züst 2006 European phenological response to climate change matches the warming pattern. *Glob. Change Biol.* **12**, 1969-1976.
- Midgley, G. F., W. Thuiller, & S. I. Higgins 2007 Plant species migration as a key uncertainty in predicting future impacts of climate change on ecosystems: progress and challenges. In *Terrestrial ecosystems in a changing world* (ed. D. G. J. Canadell, D. E. Pataki, & L. F. Pitelka), pp. 129-137. Berlin, Germany: Springer.

- Mjaaseth, R. R., S. B. Hagen, N. G. Yoccoz, & R. A. Ims 2005 Phenology and abundance in relation to climatic variation in a sub-arctic insect herbivore–mountain birch system. *Oecologia* DOI 10.1007/s00442-005-0089-1,
- Molau, U. 1993 Relationships between flowering phenology and life history strategies in tundra plants. *Arctic and Alpine Research* **25**, 391–402.
- Moles, A. & M. Westoby 2003 Latitude, seed predation and seed mass. *J. of Biogeogr.* **30**, 105-128.
- Moles, A. T., D. D. Ackerly, C. O. Webb, J. C. Tweddle, J. B. Dickie, A. J. Pitman, & M. Westoby 2005a Factors that shape seed mass evolution. *PNAS* **102**, 10540-10544.
- Moles, A. T., D. D. Ackerly, C. O. Webb, J. C. Tweddle, J. B. Dickie, & M. Westoby 2005b A brief history of seed size. *Science* **307**, 576-580.
- Mooij, W. M., L. N. D. S. Domis, & S. Hülsmann 2008 The impact of climate warming on water temperature, timing of hatching and young-of-the-year growth of fish in shallow lakes in the Netherlands. *Journal of Sea Research* **60**, 32–43.
- Morecroft, M. D., V. J. Stokes, & J. I. L. Morison 2003 Seasonal changes in the photosynthetic capacity of canopy oak (*Quercus robur*) leaves: the impact of slow development on annual carbon uptake. *International Journal of Biometeorology* **47**, 221-226.
- Morin, X., C. Augspurger, & I. Chuine 2007 Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? *Ecology* **88**, 2280-2291.
- Morin, X. & I. Chuine 2005 Sensitivity analysis of the tree distribution model PHENOFIT to climatic input characteristics: implications for climate impact assessment. *Glob. Change Biol.* **11**, 1493-1503.
- Morin, X. & I. Chuine 2006 Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecol. Lett.* **9**, 185-195.
- Morin, X. & M. Lechowicz 2008 Contemporary perspectives on the niche that can improve models of species range shifts under climate change. *Biology Letters* DOI 10.1098/rsbl.2008.0181.
- Morin, X., M. J. Lechowicz, C. Augspurger, J. O. Keef, D. Viner, & I. Chuine 2009 Leaf phenology in 22 North American tree species during the 21st century. *Glob. Change Biol.* **15**, 961–975.
- Morin, X. & W. Thuiller 2009 Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* **90**, 1301–1313.
- Morin, X., D. Viner, & I. Chuine 2008 Tree species range shifts at a continental scale: new predictive insights from a process-based model. *J. Ecol.* **96**, 784-794.
- Nathan, R. & R. Casagrandi 2004 A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen-Connell and beyond. *J. Ecol.* **92**, 733-746.
- Nathan, R., U. F. Safriel, & I. Noy-Meir 2001 Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. *Ecology* **82**, 374-388.
- New, M., M. Hulme, & P. Jones 2000 Representing twentieth century space-time climate variability. Part II: development of a 1901-1996 monthly grids of terrestrial surface climate. *J. Clim.* **13**, 2217-2238.
- Nord, E. A. & J. P. Lynch 2009 Plant phenology: a critical controller of soil resource acquisition. *J. Exp. Bot.* **60**, 1927-1037.
- Odum, E. P. 1959 *Foundations of Ecology*. Philadelphia, PA.: Saunders.
- Parmesan, C. 2006 Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* **37**, 637–639.
- Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. A. Thomas, & M. Warrens 1999 Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579-583.
- Parmesan, C. & G. Yohe 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37-42.
- Piao, S. L., P. Ciais, P. Friedlingstein, P. Peylin, M. Reichstein, S. Luyssaert, H. Margolis, J. Y. Fang, L. Barr L, A. P. Chen, A. Grelle, D. Hollinger, T. Laurila, A. Lindroth, A. D. Richardson, & T. Vesala

- 2007 Net carbon dioxide losses of northern ecosystems in response to autumn warming. NATURE doi:10.1038/nature06444,
- Pigott, C. D. & J. P. Huntley 1981 Factors controlling the distribution of *Tilia cordata* at the Northern limits of its geographical range. III Nature and cause of seed sterility. The New Phytologist **87**, 817-839.
- Pitel, J. A. & B. S. P. Wang 1989 Physiological and chemical treatments to improve germination of whitebark pine seeds. Pages 130-133 in Whitebark Pine ecosystem Symposium: Ecology and Management of a high-Mountain Resource. USDA Forest Service, Bozeman, MT.
- Post, E. 2003 Timing of reproduction in large mammals. In *Phenology: An Integrative Environmental Science* (ed. M. D. Schwartz), pp. 437-450. London: Kluwer Academic Publisher.
- Rathcke, B. & E. P. Lacey 1985 Phenological patterns of terrestrial plants. Annu. Rev. Ecol. Syst. **16**, 179-214.
- Reeekie, E. G. & F. A. Bazzaz 1987 Reproductive efforts in plants. Am. Nat. **129**, 876-919.
- Régnière, J. 1987 Temperature-dependent development of eggs and larvae of *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) and simulation of its seasonal history. Can. Ent. **119**, 717-728.
- Régnière, J. 1996 A generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. Environmental Entomology **25**, 869-881.
- Régnière, J. & J. A. Logan 2003 Animal life cycle models. In *Phenology: An Integrative Environmental Science* (ed. M. D. Schwartz), pp. 237-254. London: Kluwer Academic Publisher.
- Régnière, J. & V. Nealis 2002 Modelling seasonality of gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), to evaluate probability of its persistence in novel environments. Can. Ent. **134**, 805-824.
- Régnière, J. & M. You 1991 A simulation model of spruce budworm (Lepidoptera: Tortricidae) feeding on balsam fir and white spruce. Ecol. Mod. **54**, 277-297.
- Rehfeldt, G. E. 1989 Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*): a synthesis. Forest. Ecol. Manag. **28**, 203-215.
- Rehfeldt, G. E., N. M. Tchebakova, Y. I. Parfenova, W. R. Wykoff, N. A. Kuzmina, & L. I. Milyutin 2002 Intraspecific responses to climate in *Pinus sylvestris*. Glob. Change Biol. **8**, 912-929.
- Rehfeldt, G. E., C. C. Ying, D. L. Spittlehouse, & D. A. Hamilton 1999 Genetic responses to climate for *Pinus contorta* in British Columbia: niche breadth, climate change and reforestation. Ecol. Monographs **69**, 375-407.
- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, & J. A. Pounds 2003 Fingerprints of global warming on wild animals and plants. Nature **421**, 57-60.
- Rosenzweig, M. L. 1987 Habitat selection as a resource of biological diversity. Evol. Ecol. **1**, 315-330.
- Saltré, F., I. Chuine, S. Brewer, & C. Gaucherel 2009 A phenomenological model without dispersal kernel to model species migration Ecol. Mod. in press.
- Santamaria, L., J. Figuerola, J. J. Pilon, M. Mjelde, A. J. Green, T. De Boer, R. A. King, & R. J. Gornall. 2003 Plant Performance across latitude: the role of plasticity and local adaptation in an aquatic plant. Ecology **84**, 2454-2461.
- Sarvas, R. 1972 Investigations on the annual cycle of development on forest trees active period. Communicationes Instituti Forestalis Fenniae **76**, 110.
- Sarvas, R. 1974 Investigations on the annual cycle of development of forest trees. Autumn dormancy and winter dormancy. Communicationes Instituti Forestalis Fenniae **84**, 1-101.
- Savolainen, O., F. Bokma, R. Garcia-Gil, P. Komulainen, & T. Repo 2004 Genetic variation in cessation of growth and frost hardiness and consequences for adaptation of *Pinus sylvestris* to climatic changes. Forest. Ecol. Manag. **197**, 79-90.
- Schwartz, M. D. 2003 *Phenology : An integrative Environmental Science*. Dordrecht: Kluwer Academic Publishers.
- Seynave, I., J. C. Gegout, J. C. Herve, & J. F. Dhote 2008 Is the spatial distribution of European beech (*Fagus sylvatica* L.) limited by its potential height growth? J. of Biogeogr. **35**, 1851-1862.

- Soons, M. B., G. W. Heil, R. Nathan, & G. G. Katul 2004 Determinants of long-distance seed dispersal by wind in grasslands. *Ecology* **85**, 3056-3068.
- Sparks, T., H. Q. P. Crick, P. O. Dunn, & L. V. Sokolov 2003 Phenology of Selected lifeforms: Birds. In *Phenology: An Integrative Environmental Science* (ed. M. D. Schwartz), pp. 421-436. London: Kluwer Academic Publisher.
- Springer, C. J., R. A. Orozco, J. K. Kelly, & J. K. Ward 2008 Elevated CO₂ influences the expression of floral-initiation genes in *Arabidopsis thaliana*. *New Phytologist* **178**, 63–67.
- Tape, K., M. Sturm, & C. Racine 2006 The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Glob. Change Biol.* **12**, 686–702.
- Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, & L. Conradt 2001 Ecological and evolutionary processes at expanding range margins. *Nature* **411**, 577-581.
- Thuiller, W. 2003 BIOMOD - optimizing predictions of species distributions and projecting potential future shifts under global change. *Glob. Change Biol.* **9**, 1353-1362.
- Thuiller, W., C. Albert, M. B. Araujo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. Midgley, J. Paterson, F. M. Shurr, M. T. Sykes, & N. E. Zimmermann 2008 Predicting global change impacts on plant species distributions: future challenges. *Perspectives in Plant Ecology Evolution and Systematics* **9**, 137–152.
- Thuiller, W., M. B. Araujo, & S. Lavorel 2003 Generalized models vs. classification tree analysis: Predicting spatial distributions of plant species at different scales. *J. Veg. Sci.* **14**, 669-680.
- Thuiller, W., S. Lavorel, G. Midgley, S. Lavergne, & T. Rebelo 2004 Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* taxa. *Ecology* **85**, 1688-1699.
- Thuiller, W., D. M. Richardson, P. Pysek, G. F. Midgley, G. O. Hughes, & M. Rouget 2005 Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Glob. Change Biol.* **11**, 2234-2250.
- van Asch, M., P. H. v. Tienderen, L. J. M. Holleman, & M. E. Visser 2007 Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Glob. Change Biol.* **13**, 1596-1604.
- Visser, M. E. & C. Both 2005 Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. B* **272**, 2561–2569.
- Visser, M. E., C. Both, & M. M. Lambrechts 2004 Global climate change leads to mistimed avian reproduction. In *Birds and Climate Change* (ed. Moller A. P. & W. Fiedler) pp. 89-110, London: Elsevier.
- Visser, M. E., S. Schaper, K. van Oers, S. P. Caro & B. Helm Phenology, seasonal timing and circannual rhythms: towards a unified frame-work. *Philosophical Transactions of the Royal Society*. In press.
- Volis, S. 2007 Correlated patterns of variation in phenology and seed production in populations of two annual grasses along an aridity gradient. *Evol. Ecol.* **21**, 381-393.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, & F. Bairlein 2002 Ecological responses to recent climate change. *Nature* **416**, 389-395.
- Walther, G. R. 2003 Plants in a warmer world. *Perspectives in Plant Ecology Evolution and Systematics* **6**, 169-185.
- Walther, G. R., S. Berger, & M. T. Sykes 2005 An ecological 'footprint' of climate change. *Proceedings of the Royal Society B-Biological Sciences* **272**, 1427-1432.
- Walther, G. R., C. A. Burga, & P. J. Edwards 2001 *Fingerprints of Climate Change - Adapted behaviour and shifting species ranges*. New York and London: Kluwer Academic/Plenum Publishers.
- White, M. A., S. W. Running, & P. E. Thornton 1999 The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *International Journal of Biometeorology* **42**, 139-145.
- Willis, C. G., B. Ruhfel, A. J. M.-R. R. B. Primack, & C. C. Davis 2008 Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *PNAS* **105**, 17029-17033.

Figures

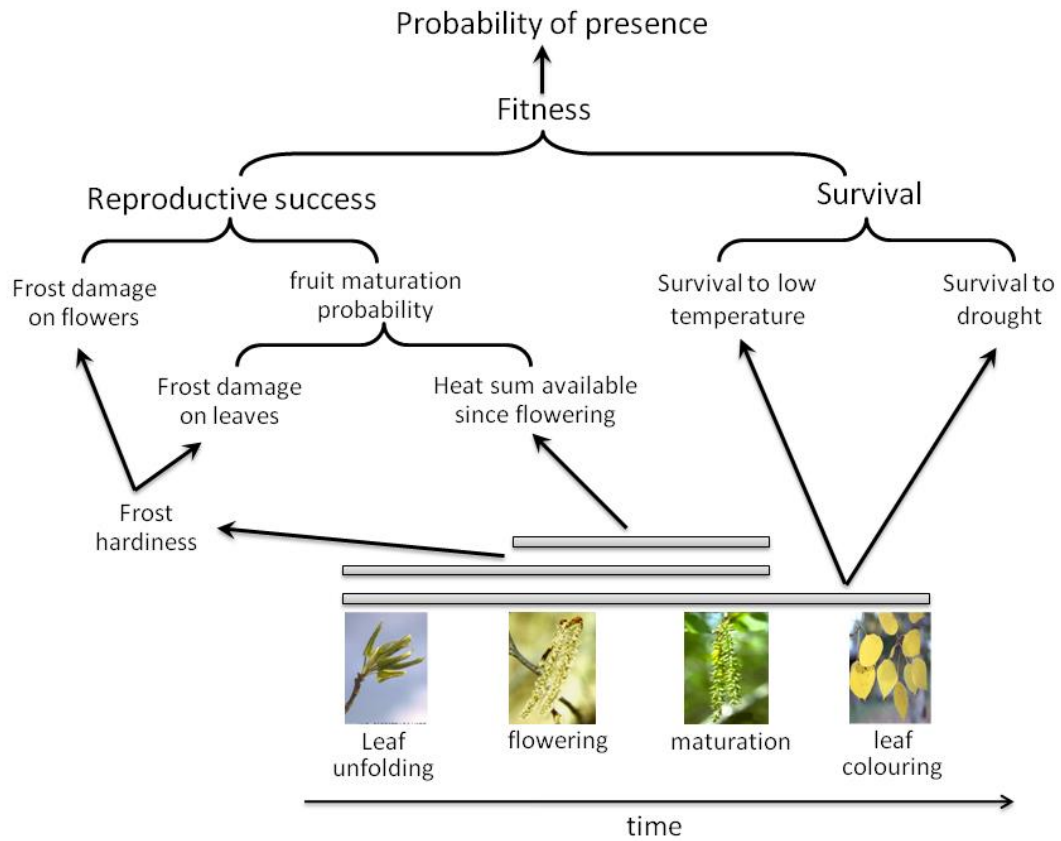


Figure 1 Conceptual scheme of the process-based model PHENOFIT. The annual cycle is simulated using process-based phenological models calibrated on time series of each phenological event for several geographic provenances of the species.

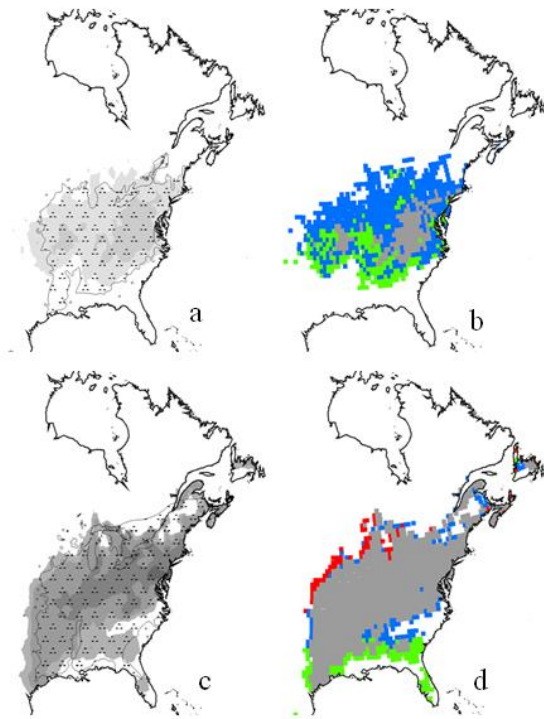


Figure 2 Simulated present distributions of *Carya ovata* (a) and *Fraxinus americana* (c) using the process-based model PHENOFIT and climatic data CRU TS 2.0 (New et al. 2000). Present observed distributions are dashed and simulated probabilities of presence according to the model are in grey. Limiting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

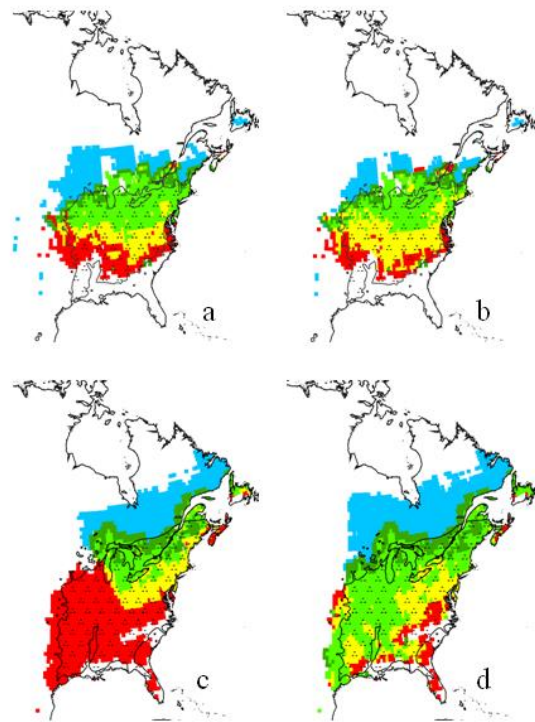


Figure 3 Projected distributions of *Carya ovata* (a), (b) and *Fraxinus americana* (c), (d) in 2100 following IPCC scenario A2 (a), (c) and B2 (b), (d) and GCM HadCM3 using PHENOFIT: red (extinction), yellow (decreased fitness), green (increased fitness), dark green (colonized area), blue (unreached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

Short title:
Phenology and species distribution