Increased mortality can promote evolutionary adaptation of forest trees to climate change

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A B S T R A C T

Forecasts of rapid climate change raise the question how quickly species can evolutionarily adapt to future climates. The adaptability of forest trees to environmental changes is generally promoted by high levels of genetic diversity and gene flow, but it can also be slowed down by long generation times and low mortality of established trees. Here, we investigate the adaptation of Scots pine (Pinus sylvestris) and Silver birch (Betula pendula) to climate change induced prolongation of the thermal growing season. We use quantitative genetic individual-based simulations to disentangle the relative roles of mortality, dispersal ability and maturation age for the speed of adaptation. The simulations predict that after 100 years of climate change, the genotypic growth period length of both species will lag more than 50% behind the climatically determined optimum. This lag is reduced by increased mortality of established trees, whereas earlier maturation and higher dispersal ability had comparatively minor effects. The evolutionary lag behind environmental change shown in our simulations stresses the importance of accounting for evolutionary processes in forecasts of the future dynamics and productivity of forests. Sensitivity of the adaptation speed to mortality suggests that species experiencing high mortality rates as well as populations subject to regular disturbances such as storms or fires might be the quickest to adapt to a warming climate.

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1. Introduction

Climate change is predicted to increase average air surface temperatures by several degrees in this century (from +1.8 to +4 °C; Meehl et al., 2007). In northern areas, relative changes in temperature are expected to be larger than parallel changes in other environmental variables such as precipitation or wind conditions (ACIA, 2005). Species exposed to changes in the environmental conditions may first show plastic phenotypic responses (e.g. Rehfeldt et al., 2002) but, in the long term, rapid climate change raises the question how quickly species can evolutionarily adapt to future climates in their habitats (e.g. Thuiller et al., 2008). Nevertheless, the models currently used to forecast future plant diversity and dynamics ignore genetic differentiation within species ranges (for a discussion, see e.g. Davis and Shaw, 2001; Harte et al., 2004). Moreover, they omit likely delays in and constraints to evolutionary adaptation that may limit the future productivity of plants (Harte et al., 2004).

Forest trees have generally been found to harbour a high level of genetic diversity at both neutral and quantitative trait loci (e.g. Hamrick, 2004). They also often have good dispersal ability and high rates of gene flow which promote the establishment of better adapted genotypes in local populations (Austerlitz et al., 2000; Davis and Shaw, 2001; Savolainen et al., 2007; Aitken et al., 2008). While high levels of genetic diversity and gene flow should generally help trees to adapt to climatic changes, their adaptation can still be slow due to long generation times (Savolainen et al., 2004, 2007; Petit and Hampe, 2006; Aitken et al., 2008). Moreover, the timing of selection can further slow down adaptation of trees. The tree traits showing strongest climatic adaptation are those that regulate the timing of growth, e.g. bud set timing, cessation of growth, frost hardiness (Rehfeldt, 1989; review by Howe et al., 2000, 2003; Savolainen et al., 2007). In many species, selection on these traits is most severe at the seedling stage: seedlings that stop growing too early are likely to get outcompeted whereas seedlings that do not cease growth before frosts get killed. On the other hand, established trees are fairly tolerant to frost damage (Eiche, 1966; Persson, 1994, reviewed by Savolainen et al., 2007). Hence, the low mortality of maladapted established trees can slow down the production and establishment of better adapted seedlings (Savolainen et al., 2004; Kramer et al., 2008). The relative roles

of maturation age, dispersal ability and mortality in the evolutionary adaptability of trees to warming climates are still largely unknown. A particularly intriguing question in this respect is whether tree species differing in these life history traits also differ in their evolutionary potential.

For many tree species, the timing of growth cessation is a critical trait governing the length of the growth period (Howe et al., 2003). Here, we compare the evolutionary potential of two co-occurring boreal tree species (Scots pine, *Pinus sylvestris*, and Silver birch, *Betula pendula*) that differ in dispersal ability and maturation age, and that show clinal variation in their timing of growth cessation (e.g. Mikola, 1982; Savolainen et al., 2004; Viherä-Aarnio et al., 2005). We concentrate our investigation on a single trait—the length of a plant's growth period (later referred to as genotypic/phenotypic growth period length), and use information on the genetics of growth cessation to model the genetic architecture of this trait. By running a quantitative genetic individual-based simulation model along a large-scale climatic cline we examine (1) how fast pine and birch can adapt their genotypic growth period length to climatically induced prolongation of the thermal growing season and (2) how the speed of adaptation depends on dispersal, maturation age and mortality.

2. Methods

To investigate the adaptation of forests to increased thermal growing season length, we simulated the evolutionary dynamics of birch and pine along a climatic cline of 800 km from southern to northern Finland. The considered cline is representative of a range of climatic conditions experienced by both species. To simplify the model, the cline does not comprise range edges. Our simulation model is based on a model by Savolainen et al. (2004) but describes the dynamics of genetic variation along the entire cline and uses a state-of-the art mechanistic model (Kuparinen et al., 2007) to quantify long-distance seed and pollen dispersal. To efficiently simulate evolutionary dynamics along this large-scale gradient, we restricted individual-based simulations to 10 focal populations of 100 established individuals and 1000 seedlings placed at equal intervals along the gradient. Genetic clines between these focal populations were described through regression models (see below). Under current climate, the length of the thermal growing season (i.e. the period within which the daily average temperature is higher than 5 °C) in the southern- and northernmost populations is 170 and 120 days, respectively, whereas warming over the next 100 years is expected to lengthen the respective periods to 220 and 170 days (Savolainen et al., 2004). Along the cline, thermal growing season was assumed to decrease linearly from south to north.

Many studies have found that the effects of individual loci on the timing of growth are small (Jermstad et al., 2001; Hurme et al., 2000). Thus, we assumed the growth period length to be additively coded by 10 unlinked diploid loci with two alleles each (coded with 0 and 1). The dynamics of the focal populations were driven by mortality and recruitment. For established trees we considered annual mortalities of 2, 3 or 4% that roughly cover the range of previously suggested mortality rates (Savolainen et al., 2004; Kramer et al., 2008). Recruitment was modelled so that a dying established tree was replaced by 1 of 10 randomly chosen seedlings. Among these 10 seedlings, the seedling with the longest phenotypic growth period was assumed to win the competition among seedlings because it utilizes the growing season most efficiently (i.e. it has grown larger than its competitors). This seedling thus became established and replaced the dead adult. Seedlings that had not yet become established were assumed to experience 20% annual mortality. Every year, both dead seedlings and those that had replaced dead adults and thus been removed

from the seedling pool were replaced by new seedlings to maintain the size of the seedling pool.

All established trees above the maturation age [20 years for pine (Sarvas, 1964), 13 years for birch (Viherä-Aarnio and Esko Oksa, pers. comm.)] were assumed to have equal reproductive output. Genotypes of new seedlings entering the seedling pool of each focal population were created by first sampling the mother and the father of the seedling and then randomly choosing the alleles of the seedling at each locus from the alleles of the mother and the father at the same locus. To obtain realistic rates of pollen- and seed-mediated gene flow along the cline, the location of the mother was drawn from a distribution of seed dispersal distances and then the distance between father and mother was drawn from a distribution of pollen dispersal distances (seed and pollen movement were described with mechanistic models of wind dispersal, see below). If the mother and/or the father were located within ±100 m from the centre of the seedling's home population, their genotype was drawn at random from the reproductive adults in the home population. In the case of long-distance seed or pollen dispersal (>100 m), maternal and paternal genotypes were simulated by drawing each allele from a binomial distribution, so that the expected genotype matched the mean genotype at the respective locations along the cline. These mean genotypes were derived by (1) fitting a regression model to the genotypic values of all adults in the 10 focal populations in order to describe how mean genotypic growth period length varies with distance along the cline, and (2) using this regression model to predict the mean genotypic growth period length at the location of the mother/father along the cline. Finally, the growth period length of a seedling was drawn from a normal distribution with mean given by the genotypic growth period length and a variance of 0.1 times the genotypic growth period length (see above). This resulted in individual heritabilities similar to those observed in common garden experiments with Scots pine (Notivol et al., 2007 found h^2 to be on average 0.5). The detailed genetics of growth cessation has not been studied in Silver birch but in *Populus tremula*, another angiosperm tree with a similar cline, this trait also has moderate heritability ($h^2 \approx 0.3$; Luquez et al., 2008). To be able to enter the seedling pool of a population, the phenotypic growth period of a new seedling had to be less than or equal to the prevailing thermal growing season length, otherwise the seedling was assumed to be killed immediately by frost.

To derive simplified but representative descriptions of pollen and seed dispersal kernels in birch and pine, dispersal was simulated with a Lagrangian stochastic 3D wind dispersal model, assuming neutral atmospheric conditions (Monin Obukhov length−10,000) and a friction velocity of 0.4 m/s (for details of the model and its parameterization, see Kuparinen et al., 2007). Falling velocity was set to 0.04 m/s for pine pollen (Jackson and Lyford, 1999), 0.6 m/s for pine seeds (Tackenberg, 2001), 0.012 m/s for birch pollen (Sofiev et al., 2006) and 0.3 m/s for birch seeds (Tackenberg, 2001) and release height was assumed to be 10 m. Dispersal kernels were derived by simulating 5000 dispersal trajectories that were then transformed into marginal distances by assigning each dispersal trajectory a random direction and projecting its location onto an arbitrarily oriented line (thereby assuming isotropic dispersal). The resulting distributions of pollen and seed dispersal distances for birch and pine are shown in Fig. 1.

Prior to simulating evolutionary adaptation to increasing thermal growing season length, genotype frequencies of the populations were initialized. This was done by first drawing genotypic values of adult trees and seedlings from binomial distributions and then simulating their phenotypic growth period lengths based on the genotypic trait value and the assumed phenotypic variance around it. Then the model was run for 1000 years to allow populations to adapt to their present-day thermal growing season length. Subsequently, simulations continued for
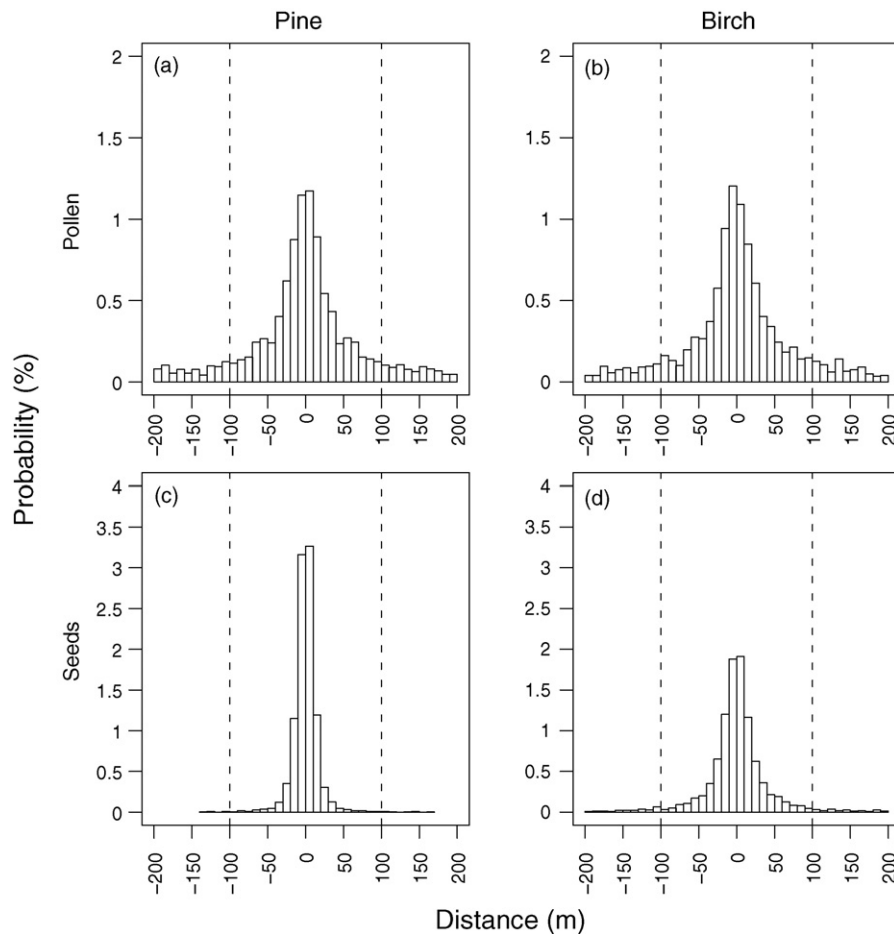
Fig. 1. Histograms of simulated dispersal distances for pollen and seeds of pine (*Pinus sylvestris*) and birch (*Betula pendula*). The proportions of pollen grains/seeds exceeding a 100 m threshold distance were 60.7% for pine pollen, 66.8% for birch pollen, 0.6% for pine seeds, and 10.1% for birch seeds.

another 100 years during which thermal growing season length linearly shifted from present-day conditions to the future scenario (e.g. from 120 to 170 days in the northernmost population). The model was run for a full factorial combination of maturation age (13 and 20 years), dispersal scenario (pine and birch dispersal), and mortality (2, 3 and 4% per year). The lag (in days) between the mean genotypic growth period length of the established trees and the thermal growing season length after 100 years was then analysed statistically using a linear mixed-effect model (LME), with the lag as the response variable, and age at maturation, dispersal scenario, mortality of established trees and their two-way interactions as explanatory variables. Simulation run was included as a random effect to account for the fact that the adaptation of the 10 populations along the cline is not independent due to long-distance gene flow. Simulations and analyses were performed in R 2.7.2.

3. Results

Throughout the cline, populations evolved longer genotypic growth periods but the speed of environmental change was consistently higher than the speed of evolutionary adaptation. This led to a widening gap between the mean genotype and the prevailing climatic optimum (Fig. 2). Consequently, after 100 years of steady increase in the length of the thermal growing season the populations had realized 21–34% (pine) and 24–41% (birch) of the possible increase in their genotypic growth period lengths (Fig. 3).

Mortality of established trees turned out to be the key factor regulating the speed of adaptation (LME: $F_{2,2} = 184.6, p < 0.01$), with higher mortality promoting adaptation and reducing the evolutionary lag (Table 1). Longer pollen and seed dispersal distances (the birch dispersal scenario; Fig. 1) also speeded up adaptation (Table 1; LME: $F_{1,2} = 67.3, p = 0.01$), whereas maturation age and interactions between the explanatory variables had relatively small effects (Table 1) and were insignificant in LME analyses (age at maturation: $F_{1,2} = 0.2, p = 0.74$; age at maturation × dispersal: $F_{1,2} = 1.2, p = 0.39$; dispersal × mortality: $F_{2,2} = 2.0, p = 0.33$; age at maturation × mortality: $F_{2,2} = 1.2, p = 0.46$).

4. Discussion

The presented simulations suggest that the evolutionary adaptation of boreal forests to climate change can substantially lag behind the rate at which climate is predicted to change (Fig. 2). When comparing birch and pine in terms of the speed of their predicted adaptation, birch has a slight advantage due to its lower maturation age (which shortens generation time) and better long-distance dispersal ability (which promotes gene flow) (Fig. 3). However, the effect of these two factors on adaptation speed is small compared to that of established tree mortality (Table 1). Our study therefore stresses that in addition to genetic variation also local demography plays a substantial role for the climatic adaptation of trees, with increased mortality promoting adaptation of forests to warming climate.
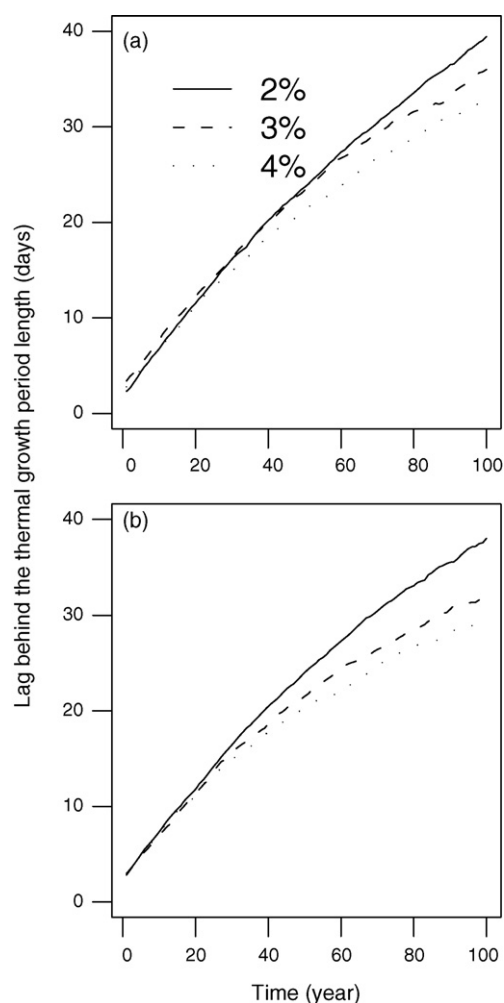
Fig. 2. Evolutionary lag between the mean genotypic growth period length and the climatic optimum (thermal growing season length). The lag is given as a function of time for (a) pine (pine dispersal, age at maturation 20 years) and (b) birch (birch dispersal, age at maturation 13 years). Results for different rates of mortality are indicated by different line types.

Our model includes detailed descriptions of long-distance dispersal and the genetic basis of growth period length. Yet, our simulations indicate the relative importance of different demographic factors rather than providing precise quantitative forecasts. This is because our model neglects complex interactions such as the interplay of temperature and day length (Bradshaw and Holzapfel, 2008), age- and size-specific fecundity (Sarvas, 1964) as well as environmental and demographic stochasticity that may affect the growth, competition, reproduction and spread of tree genotypes (Kuparinen and Schurr, 2007; Kellomäki et al., 2008; Schurr et al., 2008; Kuparinen et al., 2009). We had to ignore these complexities in order to derive a generic understanding of the relative roles of different factors affecting the adaptation of forests to warming climates. However, we do not expect the inclusion of these complexities to alter the qualitative outcome of our study. For instance, the consideration of age- (and size-) dependent fecundity would further slow down adaptation, since old maladapted trees would contribute more genes to the next generation. Including a more complex fecundity submodel would thus cause mortality to play an even stronger role for adaptation. A second aspect to bear in mind is that climate change alters not only the length of the thermal growing season, but also other environmental conditions that may affect the adaptation process. In particular, reductions in
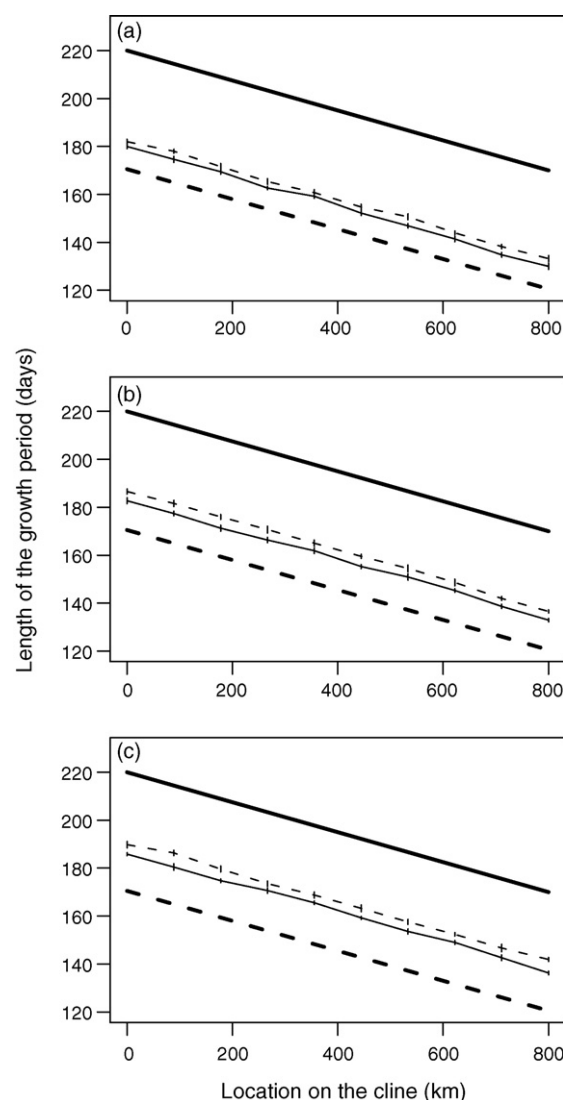
Fig. 3. Spatial distribution of genotypic growth period length along a climatic cline after 100 years of climate change. Thick lines indicate current (dashed) and future (solid) thermal growing season lengths, whereas thin lines describe the mean genotypic growth period length of pine (solid) and birch (dashed), with vertical lines encompassing 95% interquantile ranges (based on 10 replicate simulations). Considered mortality rates of established trees are (a) 2%, (b) 3%, and (c) 4%.

mortality due to improved growth conditions (Rehfeldt et al., 2002; Persson, 1994) might, according to our findings, substantially slow down evolutionary adaptation. Such reductions in mortality are predicted for the northern part of the range of Scots

Table 1
Relative impacts of mortality, age at maturation (AM) and dispersal on the lag between mean genotypic growth period length and the climatic optimum (thermal growing season length) after 100 years of climate change. The table shows estimates of a linear mixed-effect model fitted to simulated results.

Factor	Lag (days)	SE (days)
Intercept (AM 13, birch dispersal, 2% mortality)	38.20	0.53
Pine dispersal	+2.17	0.67
AM 20	−0.04	0.67
3% mortality	−6.23	0.71
4% mortality	−8.68	0.71
Pine dispersal × AM 20	−0.73	0.67
Pine dispersal × 3% mortality	+1.32	0.82
Pine dispersal × 4% mortality	+1.49	0.82
AM 20 × 3% mortality	+1.22	0.82
AM 20 × 4% mortality	+0.36	0.82

pine, whereas in the central and southern areas the warming climate results in reduced survival and growth (Rehfeldt et al., 2002; Reich and Oleksyn, 2008). On the other hand, adaptation might be sped up if mortality factors such as storms, fires, or insect outbreaks get more common in the future (Meehl et al., 2007; Bowman et al., 2009; Dukes et al., 2009).

The persistence of maladapted old trees preventing the establishment of seedlings better adapted to a changed environment has previously been suggested as a mechanism slowing down the evolutionary adaptation of forest trees (Savolainen et al., 2004; Kramer et al., 2008). Our finding that the role of mortality is, in fact, overwhelming compared to dispersal ability and maturation age implies that differences in the evolutionary potential of species might mainly arise from differences in their natural or human-induced mortality rates. Particularly, species with lower dispersal ability may not be in a substantially worse position in terms of their potential for evolutionary adaptation. Adaptation supported by high mortality can also arise because populations subject to regular disturbances such as storms or fires may adapt more quickly than those in less hazardous environments. In forestry management, such a pattern could be mimicked by thinning of old trees to speed up natural regeneration (e.g. Kramer et al., 2008). However, from a conservation perspective this management option seems questionable since it may negatively impact species that depend on old trees. Alternatively, the transplantation of genotypes from lower to higher latitude forests could aid the establishment of better adapted genotypes (Hoegh-Guldberg et al., 2008; Marris, 2009).

Climate change is anticipated to substantially alter geographic species ranges and plant diversity (Thomas et al., 2004; Thuiller et al., 2005). However, predictions of climate impacts on plant diversity are commonly based on correlative species distribution models which do not represent any demographic process, or on dynamic global vegetation models which currently neglect genetic differentiation within species ranges (Thuiller et al., 2008). Our study shows that tree species can easily lag more than 50% behind the possible increase in thermal growing season forecast to take place over the next 100 years. Therefore, evolutionary processes should be accounted for in analyses of the future performance, distribution and productivity of long-lived plants that show strong local adaptation for climatic conditions.

Acknowledgements

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