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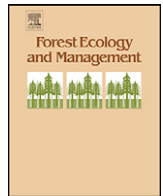
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## Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change—Range, abundance, genetic diversity and adaptive response

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## ABSTRACT

We explored impacts of climate change on the geographic distribution of European beech by applying state of the art statistical and process-based models, and assessed possible climate change impacts on both adaptive capacity in the centre of its distribution and adaptive responses of functional traits at the leading and trailing edge of the current distribution. The species area models agree that beech has the potential to expand its northern edge and loose habitat at the southern edge of its distribution in a future climate. The change in local population size in the centre of the distribution of beech has a small effect on the genetic diversity of beech, which is projected to maintain its current population size or to increase in population size. Thus, an adaptive response of functional traits of small populations at the leading and trailing edges of the distribution is possible based on genetic diversity available in the local population, even within a period of 2–3 generations.

We conclude that the adaptive responses of key functional traits should not be ignored in climate change impact assessment on beech. Adaptation to the local environment may lead to genetic and phenotypic structured populations over the species area already in few generations, depending on the forest management system applied. We recommend taking local differentiation into account in a future generation of process-based species area models.

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### 1. Introduction

Profound changes in the geographic distribution of European beech (*Fagus sylvatica* L.) are projected both by advanced statistical and process-based modeling techniques (Sykes and Prentice, 1996; Koca et al., 2006; Rickebusch et al., 2008). Exploring further the effects of climate change on such widespread species requires also an assessment of whether trees have the potential to adapt, as climate change is likely to exert strong evolutionary pressure (Parmesan, 2006). Some authors have expressed concern: that trees will be unable to adapt to such changes because the rate of climate change is rapid relative to the longevity of individual trees (Davis and Shaw, 2001); trees may not have adequate genetic diversity to adapt to the changing environmental conditions (Davis and Kabinski, 1992); and trees may not be able to disperse to newly available habitat fast enough, as the landscape they have to cross is

highly fragmented (Jump and Penuelas, 2005). Other authors, however, point to characteristics that allow trees to withstand environmental changes (Hamrick and Godt, 1996); trees have high phenotypic plasticity that allows them to withstand large environmental fluctuations during their lifetime (Rehfeldt et al., 2002); there are high levels of genetic diversity for allozymes and nuclear markers within – rather than between – populations (Buiteveld et al., 2007; Leonardi and Menozzi, 1995); and gene flow – especially of pollen – can occur over large distances, thereby exchanging favourable genetic variants between isolated stands (Petit and Hampe, 2006).

The aims of this study are the following: (i) to explore impacts of climate change on the distribution and abundance of European beech as projected by an ensemble of statistical models and a process-based dynamic vegetation model, (ii) to explore impacts of climate change on the adaptive potential of beech, expressed as genetic diversity, in the centre of the geographic distribution of European beech, and (iii) to explore the adaptive response of functional traits at both the leading and trailing edge of this distribution using a process-based dynamic tree model coupled with a quantitative genetic sub-model.

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Statistical species distribution models have been widely used in predictive biogeography for more than two decades (Austin et al., 1984; Busby, 1991), for reviews see Guisan and Thuiller (2005); Thuiller et al. (2008). There is recently renewed interest in this approach to analyze the likely impacts of global change on species distributions and biodiversity (Araújo et al., 2004; Erasmus et al., 2002; Midgley et al., 2003; Thuiller et al., 2006a, 2006b). Statistical models relate the observed presence/absence or abundance of a given species (or population) to a relevant set of limiting environmental variables (typically climatic variables for plants). The multidimensional envelope created by the models is usually described as an approximation of the realized niche described by Hutchinson (1957). The geographic representation of the estimated realized niche is then projected into the future according to some climate change scenarios (see Heikkinen et al. (2006) for a review). The main drawback of the approach lies in its correlative nature, which makes it not causal and not based on real processes. These approaches usually ignore factors such as biotic interactions, transient dynamics, migration, and nitrogen deposition. Although extensively used and also criticized (Bahn and McGill, 2007), some analyses having thoroughly tested their predictive power have shown relatively good performance to predict the current distribution based on independent data (Araújo et al., 2005).

Process-based dynamic vegetation models include biotic interactions and some also migration, so that transient responses to climate change can be simulated. For forests, the models are often based on the 'gap dynamics' concept: establishment, growth and survival are modeled for individual trees or cohorts in a number of replicate patches, each corresponding in size to the maximum influence of one large adult tree (Bugmann, 2001). If a large tree dies, the canopy is opened up and light-demanding trees can establish. Under beneficial environmental conditions and in the absence of disturbance, pioneer species get eventually out-competed by more shade-tolerant species. Establishment, mortality and disturbance (e.g. wind throw) are often simulated stochastically. The average vegetation simulated in the replicate patches (normally about 200) represents a certain forest stand or the forest in a larger region with the same environmental conditions (Bugmann, 2001).

Genetic diversity has not been explicitly represented in these models. A reduction of population size may cause a reduction of genetic diversity, and changes in tree densities can cause changes in the mating system and gene flow. The genetic composition of tree populations results from complex genetic systems that include processes and mechanisms of organization, expression, reproduction, combination, and temporal and spatial distribution of genetic information (Darlington, 1939). In comparison to other organisms, trees have a relatively high level of genetic variation (Hamrick and Godt, 1990; Nybom, 2004). This high level of genetic diversity guarantees high adaptability to diverse environments. This is particularly important for trees with long life spans. So far only a few applications modeling the potential genetic adaptability and adaptation of tree populations to climatic changes have been done. In most cases, statistical models have been used to make predictions based on quantitative genetic data from provenance tests (Matyas, 1994; Rehfeldt et al., 2002), progenies in common garden experiments (Beuker, 1994) or data from international phenological gardens based on clones (Chuine et al., 2000; Kramer, 1995).

More recent approaches include adaptive traits with defined genetic controls into mechanistic tree models (see Savolainen et al., 2004; Kramer et al., 2008). Adaptive responses of trees are particularly important at the edges of the geographic distribution of trees because as demographic processes at the leading edge differ from those at the trailing edge of a species area (Hampe and Petit, 2005; Thuiller et al., 2008). At the leading edge, *i.e.* the

northern edge of the distribution of tree species of the northern hemisphere, the timing of the onset of the growing season is an important adaptive trait, as it balances the effect of frost and the effective use of the available growing. At the trailing edge, *i.e.* the southern edge of the distribution, it is rather water limitation and successful recruitment that determines the rate of adaptive response of traits related to water availability. As Hamrick (2004) points out, the rate of adaptation to environmental change depends largely on successful recruitment events during the lifetime of a tree, and less so on the longevity of individual trees. Indeed, trees have overlapping generations and produce large numbers of seeds at regular intervals. During the first few decades of forest development tree numbers decline from several millions per hectare to a few hundred or less, resulting in a strong genetic selection (Geburek, 2005). To explore the impacts of environmental change on the adaptive potential of trees, the functional phenotypic traits as described in the process-based model need to be linked to a genetic model. The genetic model then characterizes selected parameters using a multi-locus/multi-allele genetic system for individual trees. The individual tree model then includes gene flow by seed and pollen dispersal and tree mortality, in addition to the processes related to growth described above for process-based vegetation models (Kramer et al., 2008).

## 2. Materials and methods

To explore impacts on the geographic distribution of beech we used a general process-based dynamic vegetation model, which also includes bioclimatic limits and can be applied over large areas, and a statistical species distribution model. Considering the genetic aspects, we estimated the changes of genetic diversity in the centre of its distribution and of changes of phenotypic values of adaptive traits at both the leading and trailing edge of its distribution. The connections between these approaches are that the adaptive response at the leading and trailing edges were derived with a process-based dynamic vegetation model including evolutionary changes, but only applicable at local scales. Each of the modeling approaches compromises between generality, reality and precision (Sharpe, 1990). Statistical modeling emphasizes precision, at the expense of reality; process-based modeling emphasizes reality at the loss of precision and classical genetic modeling emphasizes generality (Levins, 1966). We feel that a joint presentation of several established approaches provides a better understanding of future exploration of possible climate change on European beech than any single modeling approach can in itself.

Below we present an outline of the different approaches used. Details on the climate data used for both the statistical and the process-based species area models are presented in Appendix A.

### 2.1. Statistical species area modeling

We used the BIOMOD framework (Thuiller, 2003, 2004; Thuiller et al., 2009) implemented under the R-software. We fitted the following models relating beech distribution to the climate dataset: artificial neural networks, classification tree analysis, generalized additive model, generalized boosted model, generalized linear model, multiple adaptive regression spline, mixture discriminant analysis, and RandomForest. We fitted the models on a random subset (70%) of the data, the remainder being used to evaluate the models using Cohen's  $\kappa$  and the area under the curve (AUC) of a receiver operating characteristic (ROC) curve. Future beech habitat is obtained by applying these models to the two selected future climate datasets. We transformed the presence probabilities into presence/absence data, using both thresholds maximizing the percentage of presence and absence correctly predicted and maximizing the Cohen's  $\kappa$  statistic. From this binary

data, we calculated the species' habitat change (SHC), i.e. the difference between the number of presence points in the projection and in the original data. We also calculated the weighted average presence of beech under current and future scenario, i.e. the average of the presence/absence values, weighted by each the models' evaluation scores.

**Data and scenarios:** The presence and absence of beech in Europe were taken from the Atlas Florae Europaeae (Lahti and Lampinen, 1999) at a resolution of 50 km × 50 km. The bioclimatic data were derived from the climate data described below. We used the HadCM3 atmosphere-ocean general circulation models (AOGCMs), driven by the A2 and B1 greenhouse gas emission scenarios. We used mean annual temperature, mean winter temperature, growing degree-days up to April and August and the average fraction of plant-available soil water-holding capacity (fAWC) in the first (0–0.5 m) and second (0.5–1.5 m) soil layers, during the growing season (Schurgers et al., 2009; Rickebusch et al., 2008). The former two variables (fAWCs) were calculated using the LPJ-GUESS vegetation dynamics model (Smith et al., 2001), which accounts for hydrological effects of changes in vegetation structure and functioning, including the effect of increasing atmospheric CO<sub>2</sub> on stomatal conductance and transpiration (Hickler et al., 2009; Schurgers et al., 2009; see next section for more details on the LPJ-GUESS).

## 2.2. Process-based species area modeling

The process-based dynamic vegetation model LPJ-GUESS (Smith et al., 2001; Hickler et al., 2004; Koca et al., 2006) was applied for projecting future changes in the potential natural distribution and dominance of beech across Europe. As many other forest models, it adopts a gap dynamics approach for modeling population dynamics of a species, potentially in interacting with other species. A complete description of the baseline version is given in (Smith et al., 2001) and (Gerten et al., 2004), the latter describing updates of the hydrology scheme. A short summary is given below.

The model is driven by daily temperature, precipitation and cloudiness or radiation. It also demands information on the atmospheric CO<sub>2</sub> concentration and the soil texture class. Photosynthesis, canopy conductance, plant respiration, heterotrophic respiration, evapotranspiration, plant root-weighted uptake of water, and soil hydrology are simulated on a daily time step. Individual tree growth is implemented on an annual time step by allocating the annually accrued NPP to leaves, sapwood and fine roots based on a set of allometric rules (which are influenced by the level of water stress), and by simulating litter fall, fine root turnover and conversion of sapwood to heartwood. The vegetation dynamic processes of establishment, mortality and disturbance, including wildfires (Thonicke et al., 2001), are implemented each simulation year.

LPJ-GUESS has been extensively evaluated by comparison to observations, particularly from European and other temperate ecosystems. Studies include evaluation of the modelled forest stand structure, development and tree species distributions (Smith et al., 2001; Hickler et al., 2004, 2009; Arneeth et al., 2007; Koca et al., 2006), carbon cycling and productivity (Arneeth et al., 2007; Hickler et al., 2008; Wramneby et al., 2008) and leaf area index (Smith et al., 2008).

**Data and scenarios:** We applied the model with two atmosphere-ocean general circulation models (AOGCMs): HadCM3 and NCAR-PCM, and one emission scenario (A2). These two climate scenarios were selected to be representative of larger ensembles of temperature and precipitation projections for Europe. Using HadCM3 with the B1 emission scenario (lower emissions than A2), for example, yields stronger impacts on vegetation and more

warming than using the colder NCAR-PCM with the high emission scenario A2. Nevertheless, the chosen climate scenarios span only part of the uncertainty range (Fronzek et al., 2010). Model input in terms of soil texture was derived by disaggregating a 0.5° global soil texture dataset (Sitch et al., 2003). Historical CO<sub>2</sub> concentrations for 1901–2000 were taken from McGuire et al. (2001) and TRENDS (<http://cdiac.esd.ornl.gov/trends/co2/contents.htm>) for the years 1999 and 2000.

## 2.3. Modeling genetic diversity at the landscape level

In the present study we used the landscape version of the simulation model Eco-Gene (Degen et al., 1996; Degen et al., 2006) to analyze on a regional scale the impact of demographic changes caused by changing climate on the genetic composition of beech at its distribution center. The abiotic environment is homogeneous within each grid cell and is defined by fixed and dynamic environmental parameters (altitude, annual rainfall, mean annual temperature). The model can incorporate several different tree species. Each species for which the model is run is represented by another layer. At the species level the landscape model is an individual tree model. Thus, the grid cells contain trees with spatial position, diameter, and multi-locus-genotypes. Eco-Gene Landscape provides a detailed representation of the transmission of genetic information first from one generation to the next and second across the landscape. The realized mating system and the characteristics of flowering events of a tree species govern the extent of recombination and segregation. These determine the potential and realized combinations of alleles (genetic states at a specific gene) in multi-gene systems. The distribution of produced gametes (pollen) and zygotes (seeds) across a geographic region results in spatial patterns of multi-locus genotypes. This spatial genetic structure in turn determines the diversity of multi-locus genotypes that can arise from mating in future generations. In Eco-Gene Landscape implemented mating systems range from selfing to obligate outbreeding. Pollen and seed dispersal follow negative exponential or normal dispersal functions, respectively, and thus provide the connectivity between grid cells. Suitability of local habitats (grid cells), i.e. the maximum possible population size in a grid cell, is governed by the species specific carrying capacity for each species at that locality. The carrying capacity hereby is a function of mean annual temperature and annual rainfall. Based on climatic envelopes adapted to tree species in Germany by Kölling et al. (2007) we assigned the maximum carrying capacity to grid cells that have rainfall and temperature values in the centre of the climatic envelop. Thus, the carrying capacity of the species changes in time depending on the climate change scenario applied. We assumed linear decreasing carrying capacities towards the borders of the climatic envelopes. The species goes extinct locally, if either the future annual rainfall or the mean annual temperature of a grid cell falls outside the climatic envelop. Description of the implementation of other processes like growth, and mortality in simulations, as well as detailed information on mating system and phenology modeling are found in the documentation of the single-plot Eco-Gene model (Degen et al., 1996).

**Data set and scenarios:** The simulated landscape covered a 10 km × 10 km area in the northern part of the Solling (Germany). The area was subdivided into a grid of 400 cells, each 500 m × 500 m in size. The distribution of naturally occurring beech forests, fir plantations and non-forested lands within the study area was assigned based on the CORINE Land Cover 2000 data (German Federal Environmental Agency (DLR-DED, 2004)). Elevation data from the CIGAR-CSI SRTM 90 m database (Jarvis et al., 2008) was used to represent altitude within the study region. Climate data of current conditions represent the time period from 1950 to 2000 and were obtained from WOLRDCLIM (Hijmans et al., 2005).

The starting data set was created by distributing *F. sylvatica* to all grid cells classified as “Forest”. In order to reach an equilibrium structure we simulated 300 years of pollen and seed dispersal without changing mean temperature and rainfall. A maximum carrying capacity of 100 reproductive trees ha<sup>-1</sup> was assumed for beech. Based on average allele frequencies obtained at eleven allozyme loci and three microsatellite loci from a recent research project on 4 beech populations (Maurer et al., 2008) in Germany we generated initial genotypes for the beech trees.

The regional climate model “WETTREG” (Spekat et al., 2006) predicts for the B1 emission scenario an increase of mean temperature of 2 °C and for the A1B scenario of 2.6 °C by the year 2100 for the Solling region (Germany). The predictions for precipitation in the Solling region are such that for the B1 scenario the area sees an increase of 10–30% during winter month and a stable or slight reduction up to 10% during the summer months. Thus, the overall effect on the annual precipitation might be an increase or a decrease.

In our simulations we ran three scenarios:

(A) 100 years of constant mean temperature and mean annual rainfall representing the averages observed in the period 1950–2000; (B) 100 years with a linear increasing temperature of 2 °C and linear decreasing annual rainfall by 20%; (C) 100 years with linear increasing temperature of 2 °C and linear increasing annual rainfall by 20%.

In addition to population sizes, we computed the mean effective number of alleles (El Mousadik and Petit, 1996) in the 1st and last simulated year to measure the potential impact of demographic changes on the genetic diversity of neutral traits.

#### 2.4. Modeling adaptive response of functional traits at the stand scale

We used the model ForGEM (Kramer, 2004; Kramer et al., 2008; Schelhaas et al., 2007; Schelhaas, 2008) to explore the adaptive response of functional traits to changes in temperature and precipitation. ForGEM is a physiologically based model that simulates growth and development of individual trees at a scale of several hectares in case of a closed forest (several millions of seedlings) (Kramer, 2004; Kramer et al., 2008). Many processes are described similarly to those used in the SORTIE model (Pacala et al., 1996, 1993; Pacala and Deutschman, 1995) and LPJ-GUESS (see above).

For this study, we used two phenotypic plastic traits, i.e. the timing of bud burst to explore the adaptive response to temperature near the leading edge of the distribution of European beech (i.e. the Netherlands), and the relation between stomatal conductance and soil water availability near the trailing edge of the distribution of beech (i.e. south of France). The adaptive response of both traits is constraint by balancing selection, i.e. frost damage and expansion of the growing season for budburst, and soil water depletion and carbon uptake for stomatal conductance, and the evolution of both traits is described mechanistically.

For the bud burst case study, we used the sequential model to simulate the date of bud burst (Hänninen, 1990; Hänninen and Kramer, 2007; Kramer, 1994b). In this model, the date of bud burst is simulated based on the sequential attainment of a tree's critical chilling – and subsequent forcing requirements (Sarvas, 1974). After initial sensitivity analyses (results not shown), we selected the critical chilling requirement as the model parameter to explore the impact of global warming on the timing of bud burst. We used –2 °C as temperature threshold of damaging frost (Kramer, 1994a; Kramer et al., 1996; Sakai and Larcher, 1987; Yoshie and Sakai, 1982). It is assumed that for adult trees after budburst, all foliage and flowers are lost and that seedlings (<0.5 m) are killed if ambient temperature is below this threshold. The assumed effect of frost on plant fitness was that if ambient temperature drops

below –2 °C within 5 days after budburst, seedlings (<50 cm) are killed and both leaves and flowers of adult trees are dropped. The foliage of adult trees can be restored from a reserve pool, but the trees are assumed not to flower again the same season.

For the stomatal conductance case study, we used a spatially explicit water balance model (see (Groen et al., 2000) for the description of the sub-model). This model was converted into an individual tree model by dividing the soil into ‘pockets’ from which the tree obtains water depending on available water and amount of roots in a pocket. After initial sensitivity analyses (results not shown), we selected the exponent of the soil water modifier (Landsberg and Waring, 1997) (their Eq. (2)) to explore the adaptive response of stomatal conductance to soil water availability. This is an empirical logistic relation that is related to the general van Genuchten–Malem equation (Genuchten, 1980; Wösten et al., 1999) and depends on both soil texture and plant species. Thus, here we assume that genetic variation exists in the tree population enabling an adaptive change of this function with changing environmental conditions.

To explore the impacts of environmental change on the adaptive potential of trees, the functional phenotypic traits as described in ForGEM were combined with a quantitative genetic model. This means that allelic effects were assigned to alleles of a 10-loci and 2-allele system for each selected parameter. Allelic effects were statistically determined such that: (i) the distribution of bud burst dates in an observed forest stand coincides with that of the simulated beech population, and (ii) initial allele frequencies followed a theoretical skewed distribution (see (Kramer et al., 2008) for details). The latter is important because the initial distribution of allele frequency has a strong impact on the rate of the adaptive response. Narrow sense heritability is used to initially determine the genetic and environmental variance of a trait based on the observed total variance. The ratio of the genetic and environmental variance will change during the course of the simulation as consequence of selection. Thus, heritability is not a model parameter but varies dynamically. This model includes gene flow through dispersal of pollen and seeds. The frequency of alleles changes during the simulation as seedlings are killed or trees contribute less to the next generation than other trees depending on their genetic make-up.

Mortality is based on an empirical approach, in which the probability of mortality increases with decreasing growth rate, expressed as 5-year average of the diameter increment (see (Kramer et al., 2008) for details).

*Data and scenarios:* To explore the adaptive response of the date of bud burst of beech to change in temperature at the leading edge of its distribution, we used the observed time series of the Dutch Royal Meteorological Institute at De Bilt (52°06'N, 5°12'E, 2 m a.s.l.) from 1901 to 1990. Annual time series were sampled at random from this population of 90 meteorological time series. A temperature offset of 3 and 6 °C was daily superimposed on this time series. To explore the adaptive response of stomatal conductance to change in precipitation at the trailing edge of the distribution of beech, we grouped observed time series at Ventoux (44°10'N, 5°16'E, 1450 m. a.s.l.) into a dry, normal and wet population and sampled from these meteorological sub populations. The characterisation of the simulated stands was obtained from the DynaBeech site database (Kramer, 2004).

Both forest management and gene flow from the source population may affect the adaptive response of a functional trait to changes in a climate driver. We therefore compared three management regimes, namely, a group conversion system, a shelter cut system and no management (Matthews, 1999) (see Kramer et al., 2008; Schelhaas, 2008 for details for the implementation of these management systems in ForGEM). As we aimed to simulate adaptive responses at both the leading and

trailing edge of the distribution of European beech, we simulated small pure beech stands, 2 ha in size, with and without external gene flow from the source population. The genetic make-up of external gene flow is simulated with the initial genetic make-up of the newly founded stand. This means that no adaptive responses were assumed in the source population. In case of external gene flow, it was assumed that a tree within the simulated stand receives 20% of its pollen from the source population.

### 3. Results

#### 3.1. Future projections of geographic distribution of *F. sylvatica* based on statistical species area modeling

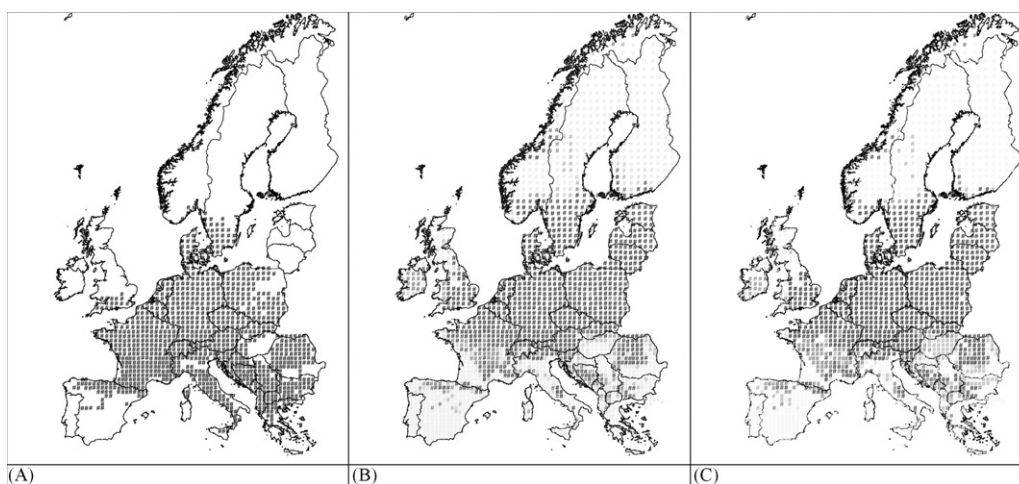
The results show a northward shift of the southern limit of the distribution of beech and a northward extension of the northern limit (Fig. 1). The predictive accuracy of the statistical niche-based models onto the evaluation data was high with an AUC of 0.94 and a Cohen's  $\kappa$  of 0.78 demonstrating an almost perfect fit. Under the two climate change scenarios, the beech could lose about 29% of its current suitable habitats. If we assume an unlimited dispersal strategy, the beech could gain 12% of additional new suitable habitats in Northern Europe under the A2 scenario and only 8% under the B1 scenario. Most of the current habitats which could

become unsuitable by 2050 are located in the South of France, Italia, ex-Yugoslavia, and Greece. Alternatively, the regions which could become favourable in the future for beech are located in Scandinavia and the Baltic states (Fig. 1).

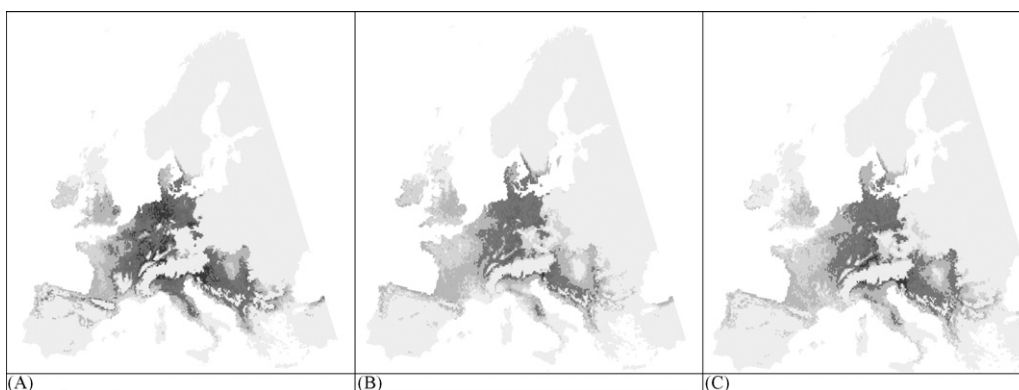
#### 3.2. Future projections of geographic distribution of *F. sylvatica* based on process-based species area modeling

As with the statistical approach, the model shows range expansion in the north, and contraction or reduced dominance in the south (Fig. 2). According to LPJ-GUESS, dominance also decreases in Western Europe. The magnitude of range shifts, however, is substantially less in the transient simulations. Both climate models give similar changes in the projected distribution and dominance of beech by the end of the century (Figs. 1 and 2). Projected equilibrium changes are much more similar to those from the statistical model, but the reduced dominance in Western Europe is more pronounced in the process-based model (Fig. 3).

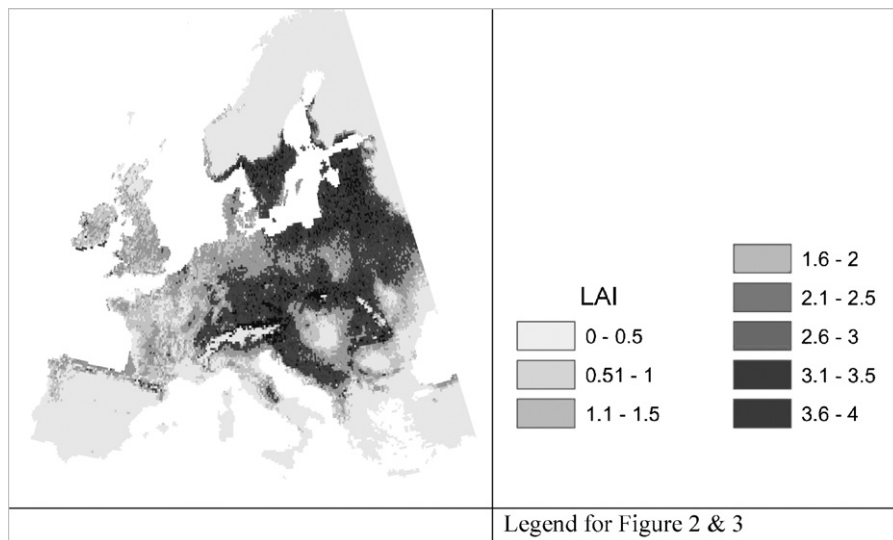
The simulated present-day distribution has some important deviations with the observed distribution of beech: the simulated north-eastern border is too far to the west, in particular in central Europe, where the model does not predict the existing beech forests in the Czech Republic. In north-western Europe, the modeled beech range expands too far on the British Islands.



**Fig. 1.** Simulated current and future (scenario A2 and B1) potential distributions of beech in Europe using statistical distribution models. The maps indicate the average presence value across models, evaluation methods and scenarios (A2 and B1), weighted by the models' evaluation scores: 1 (black) = suitable, 0 (light grey) = unsuitable according to all models. (A) Current climate, (B) A2 climate change scenario, and (C) B1 climate change scenario.



**Fig. 2.** Current and future leaf area index (LAI) of beech in Europe using a process-based dynamic vegetation model. Two AOGCMs were used with one emission scenario (A2) (see Fig. 3 for the legend of these figures and Appendix A for the explanation of the climate change scenarios). (A) Current climate (averaged for 1961–1990). (B) HadCM3 scenario (averaged for 2071–2100). (C) NCAR-PCM scenario (averaged for 2071–2100).



**Fig. 3.** Long-term LAI of beech in equilibrium with 2071–2100 climate according to process-based model LPJ-GUESS under the A2 HadCM3 climate scenario. Long-term LAI of beech in equilibrium with 2071–2100 climate according to process-based model LPJ-GUESS under the A2 HadCM3 climate scenario.

3.3. Future projection of genetic diversity at the centre of the geographic distribution of *F. sylvatica*

The spatially explicit population genetics approach as implemented in Eco-Gene Landscape (Degen et al., 1996) showed a limited impact of changing temperature and rainfall on the number of reproductive trees and the genetic diversity of beech at the center of its distribution range in the mountainous region Solling (Table 1). The scenarios B and C caused only a slight reduction of reproductive trees for beech. The simulated climate change scenarios in the Solling region went along with an increase of beech in higher areas and a small decrease in lower altitudes.

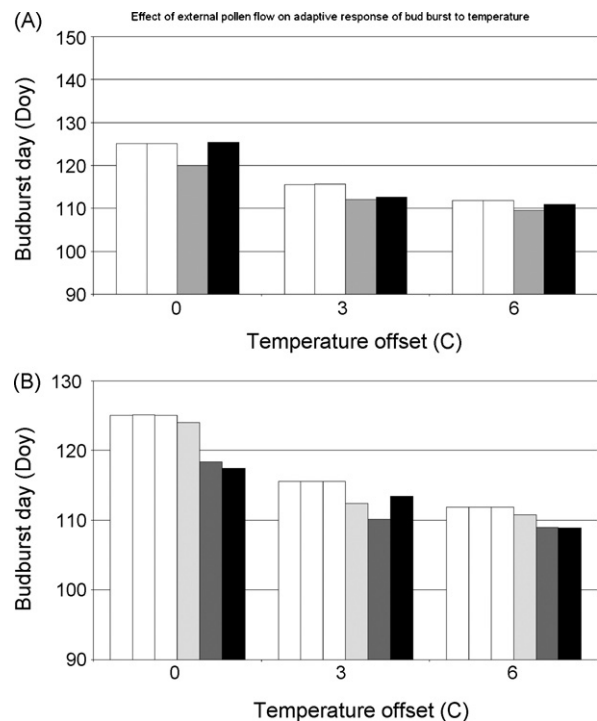
3.4. Future projection of adaptive response of functional traits at the edges of the geographic distribution of *F. sylvatica*

There is a strong effect of temperature on the average day of budburst in the simulated population (Fig. 4A and B). This is partly a phenotypic plastic response and partly genetic adaptation. The phenotypic plastic response can be seen in Fig. 4A and B by comparing the date of bud burst at different temperature scenarios at the start of the simulation ( $t = 0$ ). The adaptive response can be seen in Fig. 4A and B as the difference between the date of bud burst at  $t = 0$  and 300 at the same temperature scenario. Fig. 4A shows that for the simulated population also an adaptive response is possible under the current climate (temperature offset 0). The effect of external pollen flow from the source population is a reduced adaptive response (difference in date of bud burst at

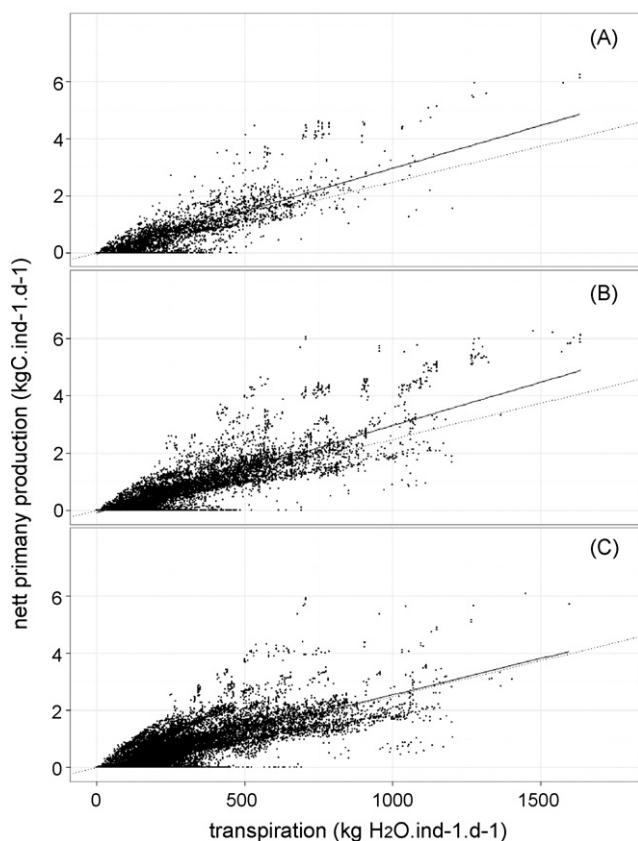
$t = 300$  with external pollen flow = 0.0 and 0.2). It is assumed in the model the source population is very large and does not adapt to the temperature scenario. The shelter cut management system results consistently in a faster adaptive response than the group selection cut system (Fig. 4B). The effect of the no management system on the adaptive response does not give a consistent pattern compared to the other 2 management systems (Fig. 4B). This is probably due to a larger stochasticity of the no management system compared to the other systems.

**Table 1**  
Results on the number of reproductive trees (A) and the effective number of alleles (B) of simulations with the model Eco-Gene Landscape for the Solling region (Germany).

(A) Total number of reproductive trees of <i>Fagus sylvatica</i>			
	Scenario A	Scenario B	Scenario C
Year 1	130,204	130,204	130,204
Year 100	128,770	111,498	127,755
(B) Mean effective number of alleles of <i>Fagus sylvatica</i>			
	Scenario A	Scenario B	Scenario C
Year 1	1.47	1.47	1.47
Year 100	1.46	1.46	1.46



**Fig. 4.** (A) Effect of fraction external pollen flow on adaptive response of budburst to increased temperature. (□)  $t = 0$  (pollen flow 0, 0.2); (▣)  $t = 300$  yr, external pollen flow 0; (■)  $t = 300$  yr, external pollen flow 0.2. Averaged over all 3 management regimes (Group selection, Shelter cut, No Management). (B) Effect of management regime on adaptive response of budburst to increased temperature. (□)  $t = 0$  yr, (▣)  $t = 300$  yr, Group selection; (▤)  $t = 300$  yr, Shelter cut system; (■)  $t = 300$  yr; No management. Averaged over both pollen scenarios (0.0 and 0.2).



**Fig. 5.** Transpiration rate ( $\text{kg H}_2\text{O tree}^{-1} \text{d}^{-1}$ ) and net primary production ( $\text{gC tree}^{-1} \text{d}^{-1}$ ) simulated by the model ForGEM in the (A) Dry, (B) Average and (C) Wet scenario. Dots: individual tree values in the simulation period 200–300 yr. Continuous line: linear regression through the presented data. Dotted line: linear regression through the individual tree values for the simulation period 25–50 yr. An increased slope of the continuous line relative to the dotted line indicates an increase in the water-use efficiency of the population after 2–3 generations of population dynamics relative to the initial situation.

Fig. 5A–C shows the relationship between transpiration rate and net primary production (NPP) of individual trees for the period 200–300 simulated years for the dry, average, and wet scenarios, respectively. The linear regression through the data represents the water-use efficiency (amount of NPP per unit water transpired) of the initial stand. The thin line in each figure represents the water-use efficiency for the period 25–50 years since the start of the simulation, so that initialization effects are ignored. During that period the lines for the different scenarios coincide (results not shown) as no adaptation can have taken place yet in response to the precipitation scenarios. The results indicate that there is a change in the response of stomatal conductance to soil moisture availability in the beech population under the dry and average scenarios such that the water-use efficiency increases, whereas the water-use efficiency did not change in the wet scenario (Fig. 5A–C). Table 2 presents the water-use efficiencies for the management-, and the pollen flow scenarios. The very low value of the scenario (indicated in italics): dry – group selection – 0.2 external pollen flow is because in one of the simulation runs only very few trees remain. For the other dry scenarios appears pollen flow appears to enhance water-use efficiency. There is no clear pattern of the effect of management on water-use efficiency for this period. The selection of the output interval to smaller sections of the simulation period that 200–300 years did affect the estimates of the water-use efficiencies. However, the broad trend remains that there is an adaptive response in the dry scenarios, less response than that in the average scenario and no response in the wet

**Table 2**

Water-use efficiency ( $\text{gC kg H}_2\text{O}^{-1}$ , based on whole-tree diurnal NPP and transpiration rate) as determined by the ForGEM model for the period 200–300 since the start of the simulation. The 18 simulation represent: 3 climate scenarios (Dry, Average, Wet), 2 pollen flow scenarios (0 or 20 percent of the pollen that a tree receives comes from the source population) and 3 management scenarios (No management, Group selection, Shelter cut). The stand had initially a water-use efficiency of 2.503 (calculated for the simulation period 25–50 years since the start of the simulation, over all scenarios).

Forest management system	External pollen fraction	Dry	Average	Wet
No management	0.0	3.050	3.473	2.974
	0.2	4.429	3.207	3.029
Group selection	0.0	3.513	3.525	2.602
	0.2	<i>0.062</i>	3.534	2.728
Shelter cut	0.0	3.475	3.363	2.677
	0.2	3.821	3.632	2.688

scenarios, with very little effect of external pollen flow and no effect of forest management of the observed responses.

#### 4. Discussion

The predicted rapid climate changes may result in strong directional selection pressures. Selective sweeps, in addition to mortality, will furthermore reduce genetic diversity of regions linked to a selected locus (Hoekstra et al., 2001). The extent of linkage in the genome hereby will depend not only on the selection coefficient, but especially also on the mating system realized. Thus, modelling changes of genetic diversity based on neutral markers represents a conservative approach. One main advantage of only considering neutral traits in simulations of species evolutionary responses lies in limiting the number of assumption that have to be made during parameterization, since for many traits we have no or only a very limited knowledge of selection coefficients, dominance or epistatic effects (Reusch and Wood, 2007). A neutral approach thus provides a genome-wide, trait-independent view of genetic changes and their limits due to demographic factors, such as restricted gene flow or reproductive system in populations across a landscape due to changing environmental conditions. The landscape scale genetic model thus aims at a generic representation of genetic processes, thereby sacrificing realism by not explicitly including selection. By using the change in population size in the Solling region of beech due to climate change, it was possible to evaluate impacts of climate change on neutral genetic diversity. An increase of beech abundance at higher altitudes was projected using this approach. Efficient pollen dispersal and large population size went along with stable levels of genetic diversity. The limitation is that the model did not consider genetic selection. Genetic selection results in an increase of mortality (Gregorius and Degen, 1994) and may thus reinforce random genetic drift because of smaller population size.

The statistical species distribution model much better predicts the current distribution of beech than the process-based dynamic approach (Figs. 1 and 2). This is because the statistical model aims at the highest precision, whereas the process-based model aims at realism and understanding consequences of the mechanisms as indicated below. The discrepancies between the process-based model and the actual distribution of beech (Figs. 1 and 2) can be explained by its values of three bioclimatic limits: the temperature thresholds for survival and establishment, the duration of the growing season, and the chilling requirements for bud burst. At the eastern border of its range, the bioclimatic limits for survival ( $-3.5^\circ\text{C}$ ) and establishment ( $-2.5^\circ\text{C}$ ) are apparently too high. Using a lower value may give more realistic predictions. In the area near the Czech Republic, beech is further weakened in competition

with other species because growing season duration is close to the bioclimatic limit used here (1500 growing degree-days). In north-western Europe, the STASH model (Sykes and Prentice, 1996) reproduced the limit of beech based on high chilling requirement for beech relative to other species (Murray et al., 1989). Using the same chilling requirement in LPJ-GUESS delayed budburst of beech so much that it suffered unrealistically in competition with other species. Furthermore in central Europe, beech populations may not respond so strongly to chilling but rather depend on photoperiod (Doktor et al., 2005). In summary, with the current parameterization, LPJ-GUESS most probably overestimates future range expansions of beech in north-western Europe, and the model probably underestimates the expansion potential in north-eastern Europe. If the projected decline in LAI in Western Europe is realistic depends on the realism of the implemented chilling requirement.

The finding that a single parameter-value representation for bioclimatic limits over the entire range for beech leads to local over- or underestimation by the model indicates that in reality geographic variation, thus local adaptation, exists for each of these bioclimatic limits. With regards to chilling requirements, local adaptation may also explain why experiments on the effect of chilling requirements and photoperiod on the timing of bud burst of beech performed on beech seedlings have yielded conflicting results (Heide, 1993b, 1993a; Falusi and Calamassi, 1996; Falusi and Calamassi, 1990). Provenance trials show that the temperature sum required for flushing has large geographic variation (Wuehlisch et al., 1995), suggesting that the same may be true for temperature sum requirements for the duration of the growing season. Also for frost survival genetic variation has been found in the north-eastern range of beech in Europe (Bolte et al., 2007).

The ForGEM model addressed this aspect of local adaptation in the distribution of beech, and the role of both forest management and external pollen flow on the rate of adaptation. This is done using a realistic process-based modeling of both ecophysiological and quantitative genetic processes and a realistic representation of forest management. This requires detailed information which can be collected at the stand level. However, that information is not easily available at the scale of the geographic area of beech. The model results indicate that selection pressure exists towards earlier bud burst with increasing winter temperature at the northern edge of the distribution of beech. At the southern edge, the model indicates a selection pressure towards higher water-use efficiency if water availability during the growing season decreases. The rate of adaptation of bud burst is about 1–2 d °C<sup>-1</sup> temperature rise, whereas the phenotypic plastic response is about 3–4 d °C<sup>-1</sup> (Fig. 4, see also Kramer, 1994a). In comparison, in an experiment where seedlings from provenances of beech from the south-east and north-west of Europe were grown in the Netherlands, the difference in date of bud burst between the provenance from Bulgaria and the Netherlands was 4–6 days (Kramer et al., 2001; Wuehlisch et al., 1997). The average winter temperature in the Netherlands is about 3 °C and 0 °C in Bulgaria (WOLRDCLIM (Hijmans et al., 2005)). Thus, the simulated adaptive response of bud burst is about half the observed adaptive difference between these locations. See Matyas (1994) for more detailed analyses on provenance test data for climate change impact assessment. Our results suggest that forest management enhances the rate of adaptation, relative to forests without management (Fig. 4B).

The adaptive responses for bud burst and stomatal conductance are based on an additive 10-locus, 2 allele genetic model for the model parameter affecting these phenotypic traits (Kramer et al., 2008). We did not test the importance of interactions between alleles and loci on the rate of this adaptive response (Falconer and Mackay, 1996). However, based on the modeling results of Savolainen et al. (2004) and on the data- and theoretical analyses by Hill et al. (2008), the presented adaptive response are unlikely

to be very different if other quantitative genetic assumptions were used (Kramer et al., 2008). We conclude that the adaptive responses of key functional traits should not be ignored in climate change impact assessment on beech. Adaptation to the local environment may lead to genetic and phenotypic structured populations over the species area already in few generations. This agrees with the findings by Bolte et al. (2007) who conclude that the adaptation of European beech populations and provenances to drought and frost varies and that phenotypic plasticity and evolutionary adaptability of European beech appear to be underestimated. These characteristics may counteract a further contraction of the European beech range arising from climate change in the future (Bolte et al., 2007). Evolutionary changes leading to local differentiation may also be the reason why the species distribution model STASH was not able to reproduce the distribution of beech during the mid-Holocene (Giesecke et al., 2007), as derived from pollen data, even if driven with climate input from a number of different global climate models. Verification of these modeling results should be done both under field conditions with different forest management strategies, and under experimental conditions where the response of functional traits to a series of abiotic conditions of different genotypes is studied.

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### Appendix A. Climate data

For both the statistical niche and process-based species area modeling, we used a gridded climate dataset of mean monthly temperature, precipitation and cloud cover for the European land surface from 1901 to 2100 at 10' × 10' spatial resolution (about 16 km; Mitchell et al., 2004; New et al., 2002). The period 1901–2000 was constructed from interpolated observations. The climate scenarios, covering the period 2001–2100, were derived by combining interpolated data on historical climate (1951–2000) with changes in climate variables simulated by two AOGCMs (Mitchell et al., 2004). AOGCM-derived monthly climate anomalies were smoothed and the observed, linearly detrended interannual variability for 1951–2000 was superimposed onto this smoothed trend twice, to represent the periods 2001–2050 and 2051–2100. Thus, the AOGCM-based scenarios share the same climate variability, which is based on the observed variability of the 20th century, but they account for AOGCM-specific projected long-term mean change through time and space (see Mitchell et al., 2004 for details). We used two AOGCMs, HadCM3 (Gordon et al., 2000) and NCAR-PCM (Washington et al., 2000), and two greenhouse gas emission scenarios (B1 and A2). The climate data set has been developed with the integrated EU project *ALARM* (Settele et al., 2005).

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