Genetic adaptive response: missing issue in climate change assessment studies

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Abstract — Two misconceptions on the adaptive potential of forests occur in climate change impact assessments. The first is that forests would be unable to adapt genetically, as climate change occurs within the lifespan of trees. However, selection takes place continuously in the regeneration phase of the forest when the number of individuals are reduced from many thousands seedlings to several hundred trees per hectare. Thus, although an individual tree might face century or more changing climate, the population where this tree dies may already strongly deviate in its genetic make-up compared to the population in which the tree germinated. The second misconception is that differences between tree species or woody plant functional types are more important for climate change assessments than differences within a tree species. However, there is ample evidence that provenances have adapted to their local environment and consequently differ in their response to climate change. The ForGEM model attempts to accommodate for both misconceptions by combining a classical process-based individual-tree model with a quantitative genetic model. The model parameters can be characterized by the genetic model and result in local adaptation. Key-results of the application of the ForGEM model in climate change assessment are that genetic adaptation is indeed possible within a few generations for important adaptive traits such as phenology and water use, and that the rate of response of adaptive traits to climate change is strongly affected by forest management. We argue that, based on: 1) observational findings of different responses of populations of the same species to climate change due to local adaptation, 2) the simulated findings of adaptive responses within the time frame of climate change, and 3) the vast technological development in genome wide association studies, it is necessary and feasible to include genetic adaptive processes in cross-sectorial climate change assessment studies.

Index Terms— adaptation, adaptive capacity, climate change, extreme events, genetic diversity

1 Introduction

Genetic diversity is the ultimate source based on which species adapt to climate change (Geburek and Turok, 2005). Evolution resulted in the adaptation of plant species to local climatological conditions and consequently they respond differently to climate change. Also within plant species, local adaptation has occurred over time. Transplantation trials of tree species throughout Europe have shown that provenances, transferred within the geographic range of the species, differ in degree and even in sign of their response to changes in precipitation and temperature (Mátyás, 1996). This genetic diversity within a species, as a result of adaptation to local environmental conditions, is important at the limits of species distributions (Hampe and Petit, 2005). Genetic diversity is typically lowest at the expanding front of the species' distribution and highest at the retreating limit, thereby affecting the survival of the individual trees and thus the rates of expansion and retreat, respectively (Petit and Hampe, 2006). In the centre of the species distribution, it is particularly the vulnerability to extreme events and the capacity to recover from these events, where genetic diversity within a species plays an important role (Parmesan et al., 2000, Bengtsson et al., 2000). Management can have a major impact on the genetic diversity of perennial plant species (Valladares, 2008). Selection aiming at maximization of productivity of forest- and fruit trees and nut-bearing trees reduces genetic diversity. Also management measures to mitigate climate change impacts by means of assisted migration outside the existing species range, may decrease the capacity of the species to adapt to on-going climate changes because of a too low initial genetic diversity (Leech et al., 2011, McLachlan et al., 2007).

Current climate change assessment modelling ignores local adaptation of long living perennial plant species, such as trees. In this paper we argue that genetic diversity is an important issue that needs to be included in cross-sectorial climate change impact assessment studies. We indicate how adaptive capacity and adaptation, in a genetic sense, can be included in climate change assessment models to attain more useful local predictions.

2 Modelling adaptive capacity and adaptation

2.1 Quantitative genetics

Adaptation is the dynamic evolutionary process that leads to a trait becoming adapted to local environmental conditions by means of natural selection, i.e. differential survival as a consequence of differences in values of the trait under selection. Adaptive capacity in its genetic sense is potential of a population to respond to an environmental change by having its genetic composition modified and, as a consequence, also the phenotypic expression of functional traits. The population thereby becomes better adapted to the new environmental conditions.

Quantitative genetics is the part of genetics that studies polygenic traits, *i.e.* traits that are under the influence of many loci (i.e. the location of the genetic information of a trait on the DNA string), each locus with two to many alleles (i.e. variation in the genetic information for that locus in the population). As there are many loci and potentially many alleles, the contribution of a single locus and allele on the phenotypic expression of the trait is only small. The contribution of the alleles and loci to the phenotypic values of a trait can be partitioned into additive, dominance (allele x allele interactions), epistasis (locus x locus interactions) and a remaining non-genetic component (Falconer and Mackay, 1996). Quantitative genetic studies are often restricted to additive effects because this is the component being inherited, and the determination of dominances and epistasis requires extensive experimental designs. As the additive allelic effects are considered constant, a particular combination of alleles over the loci determine the genotypic value of the traits, which, enlarged with the environmental component, defines the phenotypic value of a trait for an individual organism. Differential survival as a consequence of climate change, results in changes in the frequency of the alleles and thereby a change of the distribution of phenotypic values of a population. Thus, the population adapts to local environmental conditions. As a consequence of adaptation, some alleles will be lost from the population, either because these allelic effects are unfavourable under the new conditions or because of genetic drift. This loss in genetic diversity results in a reduced adaptive capacity to future environmental changes. Genetic processes to increase genetic diversity of adaptive traits are immigration of genetic material by gene flow from other populations, and mutation. In case of perennial plants, gene flow means input of pollen and seeds, or planting of new genetic material. Considering mutation, the low natural rate of mutation makes that this is in a time frame of a few generations relevant only for very large randomly mating populations.

2.2 Bridging eco-physiology and quantitative genetics in plant models

Dynamic global vegetation models assume a unique set of parameter values to characterise a plant functional type. At the global scale, the interest is in predicting shifts of the boundaries between plant functional types. It is unlikely that genetic processes determine the rate of change of boundaries between major vegetation zones under the influence of climate change, however, it is affected by adaptive capacity of the species. Also in the centre of the species area, adaptive capacity may have an important effect on the rate of adaptation of resource acquisition and therefore competitive ability of the species, and on the response to extreme events.

An individual-plant model in which process-based modelling is connected to a quantitative genetic representation of eco-physiological parameters is the ForGEM model (Kramer et al., 2008, Kramer and van der Werf, 2010). In principle each of the model parameters can be characterized by the genetic model and evolved due to environmental change. The genetic system can be initialised (determining initial allele frequencies and assigning allelic effects) either by taking a statistical approach or by using observed allele frequencies and allelic effects for Quantitative Trait Loci (QTLs) or Candidate Genes (CGs) determined in experimental populations (Brendel et al., 2008). As the initial distribution of allele frequencies has a strong effect on the simulated rate of the adaptive response, we currently assume on theoretical considerations that initially the allele frequency distribution follows a U-shaped beta distribution, *phi*. (Fig 1.) The allele frequency distribution is a function of the heterozygosis of the traits (H) and the number of alleles (k) (Nei, 1987). Inverting the cumulative distribution of *phi* leads to the initial allele frequencies (Fig. 2, see (Kramer et al., 2008) for details). Reasonable values for quantitative traits are: number of loci, *nLoci* =10, H=0.25 and k=2 (Kramer et al., 2008).

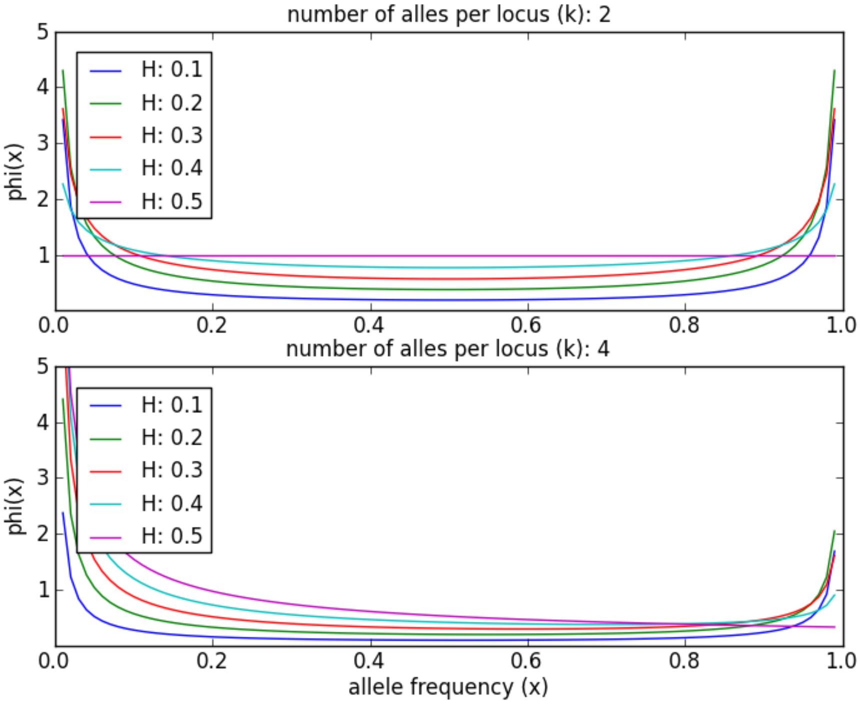

Fig. 1. Theoretical allele frequency distribution, *phi,* for different values of heterozygosis (*H*) and number of alleles per locus (*k*) (Nei, 1987). Most many alleles have either a very low or a very high frequency, and few alleles have a frequency around 0.5.

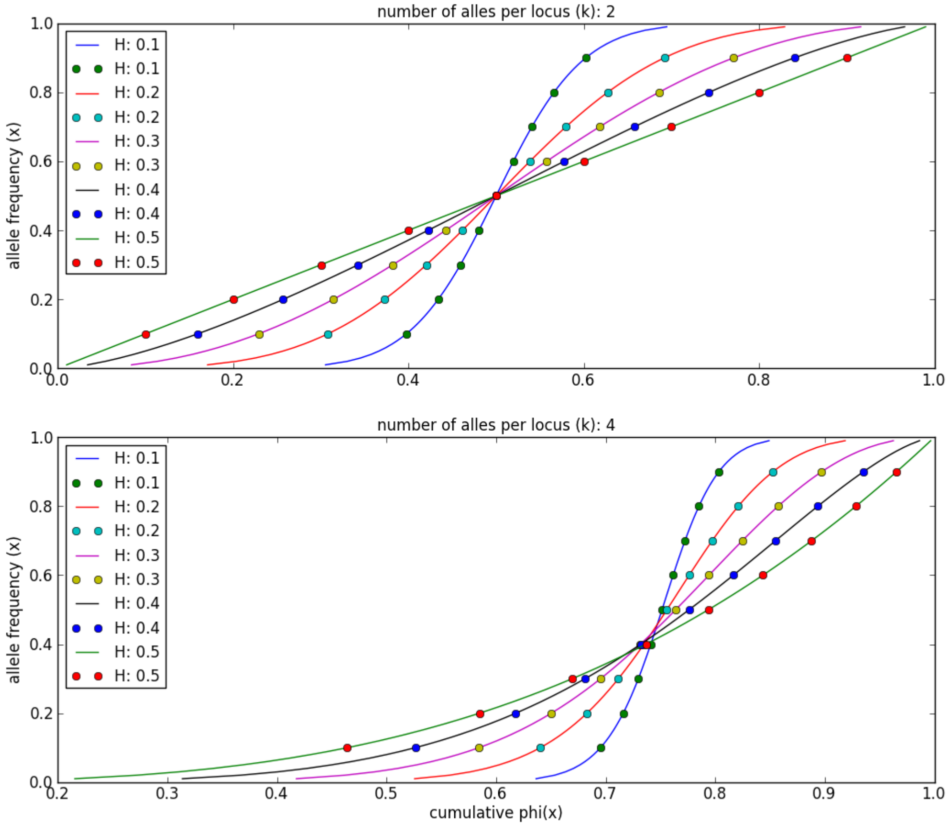

Fig. 2. Allele frequencies to initialise the ForGEM model for different values of heterozygosis (*H*) and number of alleles per locus (*k*). The dots indicate the allelic effects for a 10-locus trait evenly spaced over cumulative *phi(x)*. The same cumulative distribution of *phi* can be used if a trait is determined by another number of di-allelic loci.

Allelic effects are determined in the ForGEM model by first assigning +1 and -1 values to the two alleles of di-allelic multi-locus traits and subsequently normalising the allelic effects (mean of zero, variance of unity) under the constraint of the U-shaped distribution of allelic frequencies as indicated above. Fig. 3 shows the decline in allelic effect with increasing number of loci for a di-allelic genetic system with symmetric allelic effects. Genotypic values for a model parameter are attained by adding the observed mean and multiplying with the observed variance of the parameter. Phenotypic values are attained by enhancing the genotypic values with an environmental deviate based on the heritability of the trait.

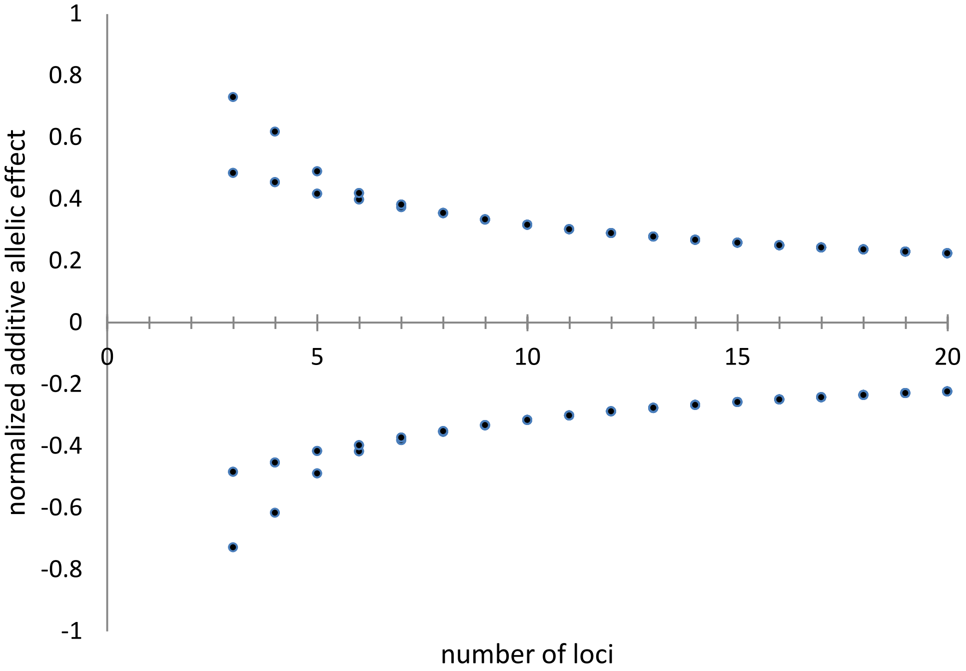

Fig. 3. Normalised additive allelic effects assigned to di-allelic multi-locus traits, under the constraint of the distribution of allelic frequencies as indicated in Figs. 1 and 2 with k=2 and H=0.25. With a low number of loci ($nLoci$ < 7) two symmetric allelic effects are attained. At higher values for the number of loci per trait, all alleles have virtually the same effect on the genotype.

Currently all information is available to initialise the ForGEM model at the European scale, though such model runs have yet to be made. Daily meteorological parameters are obtained from the ISI-MIP database. The initialisation of forest stands is based on a database containing the abundance of 20 tree species at a 1x1 km resolution over Europe (Brus et al., 2012). Using species abundance at a location, a plot with observed stand information from a National Forest Inventories (NFI) database is selected with approximately the same species abundance. The statistics of the NFI plot are then used to generate a forest stand with statistically the same characteristics (Fig. 4). Soil characteristics required are those to determine water availability according to pedotransfer functions (Wösten et al., 1999, Wösten et al., 2001). For forest management, we follow the classification of Forest Management Approach (Table 1, (Duncker et al., 2012)), projected to the European scale (Fig. 5, (Hengeveld et al., 2012)). This approach can accommodate scenario assumptions on changes in forest management due to policy and market developments. As simulations at the European scale for each km^2 grid cell is too calculation intensive, a stratified sampling scheme is used based on the Global Environmental Stratification (Metzger et al., 2005, Metzger, in press).

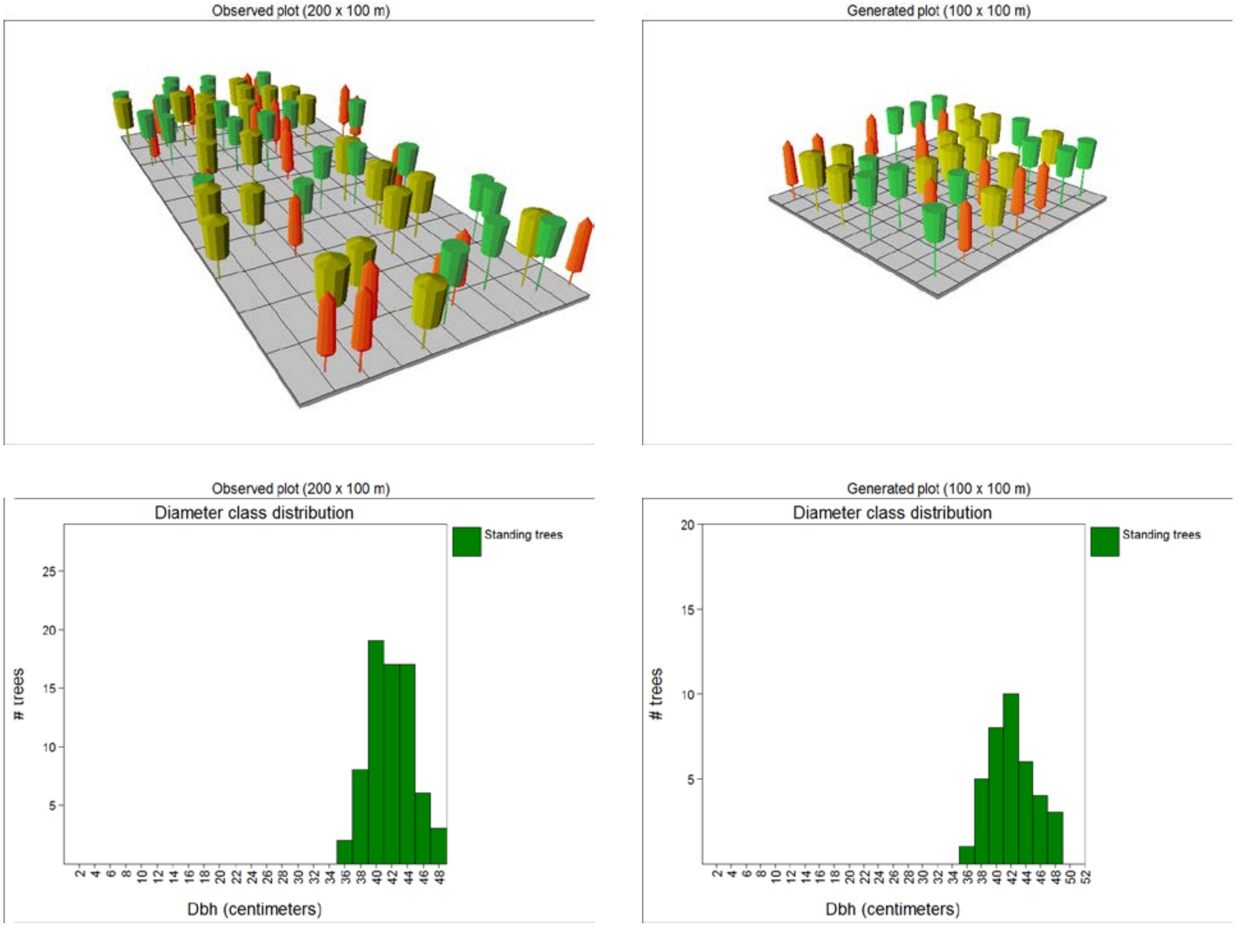

Fig. 4. Visualisation of a stand used to initialise the ForGEM model. Spatial distribution of trees and diameter distribution of observed plot with individually measured trees and the same representation of a generated plot based on stand statistics (density per species, mean and coefficient of variation of height and diameter at breast height) of the observed plot. Note that spatial structure is not accounted for in the generated plot. Yellow trees – *Quercus robur*; Orange trees – *Fagus sylvatica*; Green trees – *Fraxinus excelsior*. Visualized with Stand Visualisation System SVS, (McGaughey, 1997).

Table 1. Characterisation of Forest Management Approaches (FMAs) (Duncker et al., 2012).

FMA	**title**	**management intensity**	**objective**
1	unmanaged forest / nature reserve	passive	to allow natural processes and natural disturbance regimes to develop without management intervention
2	close-to-nature forestry	low	to manage a stand with the emulation of natural processes as a guiding principle; any management intervention in the forest has to enhance or conserve the ecological functions of the forest
3	combined objective forestry	medium	a mix of different objectives, additional objectives to timber production can be water and soil protection, mushroom production, habitat protection, avalanche prevention, game management and nature protection, fire prevention and/or recreation, and are adapted to the local situation
4	intensive even-aged forestry	high	to produce timber
5	short rotation forestry	intensive	to produce the highest amount of merchantable timber or wood biomass

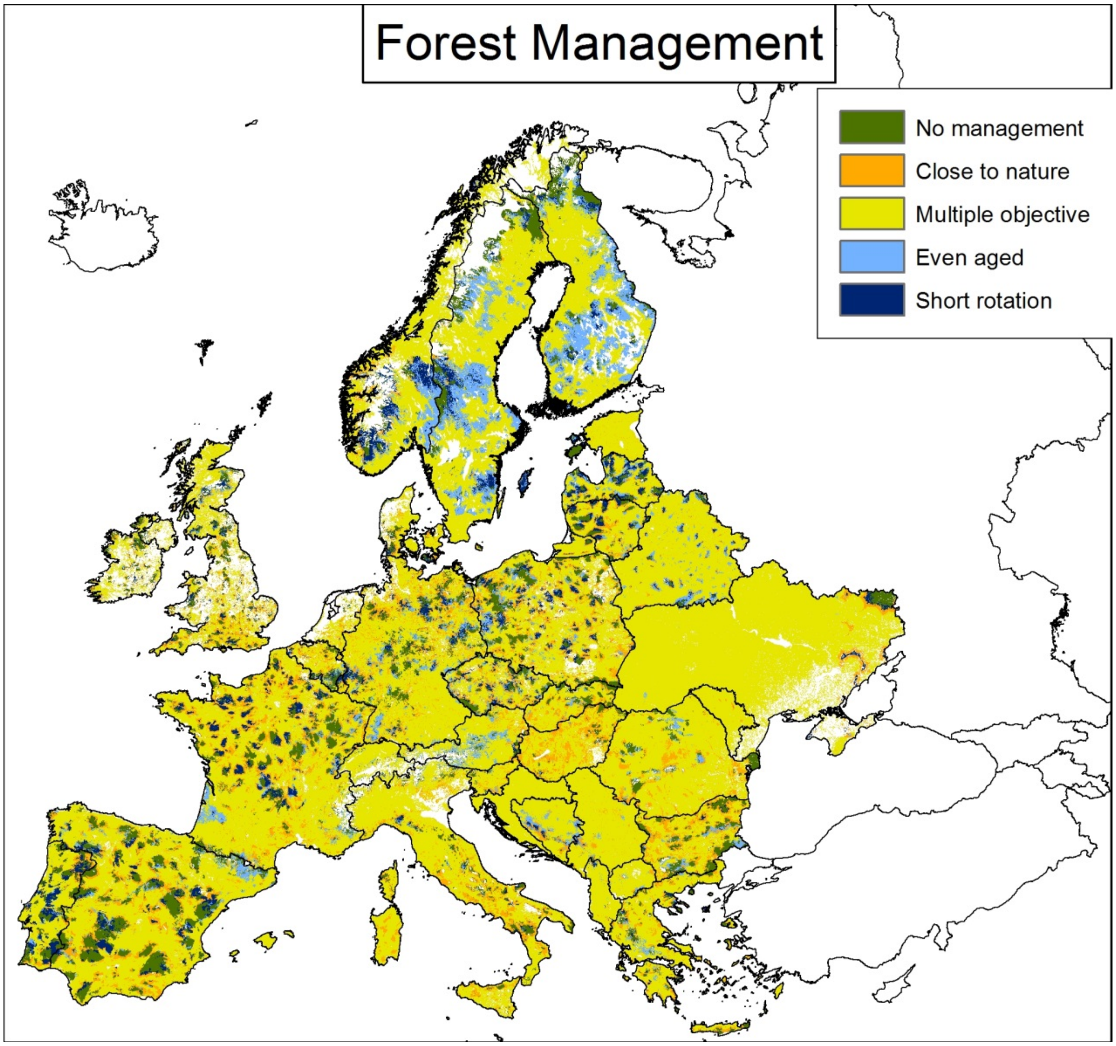

Fig. 5. Distribution of Forest Management Approaches (FMAs) over Europe (Hengeveld et al., 2012). See Table 1 for a characterisation of the FMAs.

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3 Discussion and Conclusions

The overall conclusions based on applications of the ForGEM model for climate change assessment studies at stand level are, firstly, that genetic adaptation of forest trees is possible within two to three rotations for important adaptive traits as phenology and water use; secondly, that the rate of response of adaptive traits to climate change is strongly affected by forest management (Kramer et al., 2010). The currently on-going whole genome studies will vastly increase the rate at which associations between QTLs and CGs and functional traits are found. Therefore,, a large amount of directly useable genetic information is likely to emerge in the near future for many economically important tree species (Neale and Kremer, 2011). That will improve the initialisation of the genetic system in ForGEM for local populations and thereby increase the accuracy of the adaptive responses to climate change. In combination with the observed findings that different provenances of the same species of trees can strongly differ in their response to a similar change in the climate (Mátyás, 1996), this means that it is necessary and feasible to include genetic processes in climate change assessment studies. Individual-based models are essential for such analyses, as both climate envelop models and process-based models that include parameters that can only be determined at the population level, may predict local extinction even if growing conditions improve (Kramer et al., 2012).(Kramer et al., 2012).

Cross-sectorial analyses can be performed with less uncertainty by including genetic processes in existing individual-, process-based climate change assessment models. In particular market sectors such as forestry, agro-forestry, and agricultural systems with fruit trees and nut-bearing trees can only respond with adaptation and mitigation measurements if uncertainties for alternatives of local trees are reduced. Overall, a stable environment in terms of perennial plant species is an essential requirement for human well-being, health, survival, migration and social stability. Genetic diversity of these species is an important aspect of environmental sustainability (Kremer, 2006) and resilience (Kramer, 2007) in the face of climate change, and needs to be taken account in cross-sectorial analyses and modelling inter-comparisons.

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