

**REPORT OF INTRASPECIFIC RESPONSE FUNCTION AND
DERIVATION OF CLIMATE TRANSFER LIMITS – D.T1.3.3**

**Conservation and sustainable utilization of forest tree
diversity in Climate change (Project n° CE614)**

The objective of the project is to improve integrated environmental management capacities
for the protection and sustainable use of natural heritage and resources

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INTRASPECIFIC RESPONSE FUNCTION AND DERIVATION OF CLIMATE TRANSFER LIMITS

Climate change is now a widely accepted phenomenon that has been studied for decades (Krupa and Kickert 1989; Rummukainen 2012; Stocker et al. 2013). Our knowledge on its present and potential future impacts on ecosystems is continuously expanding. Concerning forest ecosystems, trees are sessile individuals with a long life span and for these reasons tree species are particularly vulnerable to climate change. Shifts in temperatures and extreme climatic events patterns leads to direct or indirect impacts on trees' and forest ecosystem's viability, productivity and interspecific competitiveness. In this review, we will focus on the response of tree populations to climate.

Between 1880 and 2012, a 0.85 °C increase of global surface temperatures have been recorded according to the IPCC fifth assessment report (2013). These trends are expected to be reinforced in the future due to the further increase of greenhouse gases in the atmosphere; CO₂ has already increased from about 40% between the pre-industrial period and 2011 (Stocker et al. 2013).

If we consider only the rise in temperature, an overall positive effect on productivity with a longer growing season and photosynthesis rate is predicted within European forests, especially in the Northern latitudes (Saxe et al. 2001; Laubhann et al. 2009; Lindner et al. 2010). However, net photosynthesis reaches a threshold around 30 °C for major European tree species and this means that no biomass will be produced (Rennenberg et al. 2006). Moreover, adaptational lag may prevent an optimal increase of productivity with continuous changes in temperature. Additionally, a longer growing season may affect the interspecific competitiveness because tree species will not behave the same toward an increase of spring temperatures. Indeed pioneers species rely often only on temperature to break dormancy and thus will benefit from an earlier increase in temperatures. However late stage species rely on more complex factors with chilling requirement and photoperiod sensitivity to start the growing season and will need several generations to adapt the new conditions (Basler and Körner 2012).

About the increase of CO₂, while with uncertainties (Lindner et al. 2014), it is expected to play two roles: fertilization effect and an increase of water use efficiency (Keenan 2013), both of which would have positive effect on forest ecosystems.

In addition to the shift in temperatures, climatic extreme events occurrence (e.g. cold/warm days, droughts, precipitations, storms...) are expected to change. Already now, in Europe, an increase of warm days and a decrease of cold days have been observed with a likelihood above 90% according the fifth assessment report (Stocker et al. 2013). However, there are indications that while the frequency of cold days would decrease, intensity and duration may not (Rummukainen 2012). With a likelihood above 66%, both precipitation and droughts have increased, in Europe and in the Mediterranean regions respectively (Stocker et al. 2013). Trees are generally negatively affected by droughts and species such as European beach (Scherrer, Bader, and Körner 2011; Kint et al. 2012) and Silver fir (Lebourgeois, Rathgeber, and Ulrich 2010; Camarero et al. 2015) are found to be particularly sensitive; drought induced mortality in trees have already been observed in Europe (Allen et al. 2010).

Confronted with climate change, including both changes in temperature and extreme events regime, tree populations have to either persist via acclimatization and phenotypic plasticity, adapt or migrate to keep their fitness, competitive abilities and even survive in case of too substantial changes (Aitken et al. 2008; Bussotti et al. 2015).

Adaptation will depend on the genome of each species and the genetic diversity of the populations and it is shaped by natural selection and gene flow. From the genome perspective, the number of genes involved in the control of traits affected by climate change, such as height and bud burst, as well as their effect size and their repartition will have an impact on the local adaptation of populations. Results from previous studies emphasize that it is likely that several genes, each having a small overall effect, control these traits (Aitken et al. 2008). Moreover, it appears that linkage disequilibrium has a non-significant effect on natural populations (Brown et al. 2004; Neale and Savolainen 2004; Heuertz et al. 2006), which means genes will be mostly inherited independently. The genetic makeup of populations describes the diversity of alleles, a higher genetic diversity is regularly associated with a higher potential of populations to adapt in changing conditions. High genetic diversity within populations is supported by high gene flow among populations and large population size, the latter preventing allele's loss via drift and increasing the presence of rare alleles. However, extensive gene flow among populations under different selection pressures (Garcia Ramos

1997) as well as artificial unsuitable seedling plantation may slow down local selection process.

At the trait level, several genes with high diversity combined with high seeds productivity will be the basis for high selection potential. Lynch and Lande (1993) found that species are able to adapt steadily if the rate of change is under a critical threshold. This threshold will depend on environmental factors (stochasticity and strength of selection), population factors (standing genetic variation and effective population size) and individual fecundity. For a higher rate of change however, adaptation rate will be too weak, leading to adaptational lag and eventually to extinction (Lynch and Lande 1993).

Because trees are sessile individuals, migration is restrained to seed dispersal. Migration is not deliberate, however: while seed dispersal occurs randomly around the parental trees, only seeds under favorable conditions will develop. With shifts in climate, directional migration to a better environment will then be observed at the leading edge of the species range. It will be associated with extirpations of populations at the rear-edge, in regions where conditions are not suitable anymore. Tree migration rates are critical in times of climate change. These rates have often been studied in relation with the last transition of glacial/interglacial periods. Pioneers studies based on pollen records and early genetic studies determined that species survived the cold period in Europe in South refugia (i.e. Iberian Peninsula, Italy and the Balkans) (Huntley and Birks 1983; Bennett, Tzedakis, and Willis 1991; Konnert and Bergmann 1995; Demesure, Comps, and Petit 1996; Dumolin-Lapègue et al. 1997). According to these results, postglacial migration rates in Europe were estimated up to 1000m/y. These rates were not matching the empirical migration rates (<100m/y). This mismatch was referred to as the Reid's paradox (Clark et al. 1998) and was explained by long distance seed dispersal events. These events are leading to the formation of small founder populations that can then increase their survivability via pollen long distance gene flow. More recent studies, based on species distribution modeling, pollen and genetic markers, support that small cryptic refugia populations survived in Central Europe in addition to the population in Southern refugia (Willis and Van Andel 2004; Aitken et al. 2008; Svenning, Normand, and Kageyama 2008; Tzedakis, Emerson, and Hewitt 2013) and this considerably decreases the estimated trees migration rates. Other studies in North America (McLachlan and Clark 2004; Gugger and Sugita 2010; Iverson et al. 2018) or more general studies (Aitken et al. 2008) also found these rates to be between 10 and 200m/y depending on the species and the study. In these conditions, it is likely that the natural rate of migration associated with rare long distance seed dispersal will

not be able to cope with upcoming temperature shifts considering that necessary migration rate are found to be at least 1000m/y and up to 5000m/y (Davis and Shaw 2001; Malcolm et al. 2002). The above-mentioned extreme events and other anthropogenic impacts such as forest fragmentation (Schwartz 1993; Resco De Dios, Fischer, and Colinas 2007) will further hamper natural migration of species.

Historically, artificial transfer of seeds from one location to another (assisted migration) was often associated with risk of maladaptation (Campbell 1979; Zobel and Talbert 1984). Maladapted seeds lead to an overall decrease in fitness and growth of the population and can even negatively affect surrounding locally adapted populations (McKay et al. 2005). However, if migration rates for natural populations are too slow or if seeds provenance used for reforestation remains the same we might also face a decrease in health and productivity of forests ecosystems (St Clair and Howe 2007; Bower and Aitken 2008). Moreover, local seed source can be less adapted due to factors such as population history (e.g. bottleneck, founder effect) and adaptational lag. With an increasing understanding of environmental factors, biotic (e.g. competition, diseases and pests) and abiotic (e.g. climate and soil conditions), genetic factors and their interaction (Genotype*Environment) responsible for tree populations performances we could decrease the risk of maladaptation. The study of tree populations in relation to climate has been an ongoing subject of research since the last decades. It notably aims to identify the best seed source for different climatic regions of several economically valuable species (e.g. which ref to choose here? (Hamann, Gylander, and Chen 2011)). This knowledge, in combination with predicted future climatic conditions may encourage us to reconsider traditional practices and approaches such as trans-boundaries assisted migration may be needed for species and populations the most vulnerable to climate change.

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