



Review and synthesis

Evolutionary consequences of historic anthropogenic impacts on forest trees in Europe

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ABSTRACT

Throughout history, man has strongly utilized and affected forest genetic resources in Europe. From an evolutionary perspective deforestation/fragmentation (→genetic drift), transfer of seeds and plants to new environments (→mainly gene flow) and selective logging (→selection) are most relevant and have been particularly addressed in this review. In contrast to most conifers, broadleaved tree populations have been especially reduced by historic fragmentation, and consequently, the related genetic effects have been possibly more pronounced. Widespread wind-pollinated species with wind/animal dispersed seeds appear to be more resilient to fragmentation than species with e.g. small geographic ranges and gravity dispersed seeds. In addition, naturally fragmented populations in the range margins may be more vulnerable than central populations as conditions for gene flow are generally impaired in peripheral areas. Traits important for adaptation (e.g. bud burst, bud set) are controlled by many genes, and as a corollary of fragmentation such genes are lost at a low rate. Large scale commercial translocation of seeds and plants for forestry purposes applies mostly to conifers and dates back about two centuries. Although many translocations have been successful in a forestry perspective, exposure to new selective regimes has sometimes challenged the adaptive limits of populations and caused setbacks or even diebacks of populations, as well as influencing neighbouring populations with maladapted genes (e.g. Scots pine, maritime pine, larch). Many tree species have substantial plasticity in fitness-related traits, which is vital for survival and viability following translocations. Selective logging has been practiced in Europe over the last two centuries and implies removal of superior trees with respect to growth and quality. Such traits are partly under genetic control. Consequent removal of superior trees may therefore have negative effects on the remaining gene pool, but this effect will also be counteracted by extensive gene flow. Although humans have strongly affected European forest trees over the last millennia, we argue that they are still resilient from an evolutionary perspective.

1. Introduction

Mesolithic foragers opened up the forest in Europe probably not before 6000 BP. Early human impact was certainly locally restricted on a very small scale (Williams, 2003) and had no significant effect on the gene pool of forest trees. However, this picture changed drastically over time. It is well documented that vast forest areas in Europe have been converted into agricultural land, populated areas and various infrastructures (Spiecker, 2003). Today Central Europe is one of the most heavily populated regions on earth with the most severe human-caused forest fragmentation (Wade et al., 2003) and virgin forests can hardly be found (Parviainen, 2005). Environmental air pollution in Europe especially since the early 1980s put additional strain to forest ecosystems and contributed to forest decline and also changed the gene pool

of remnant forest tree populations (Geburek, 2000). Introduced pest and pathogens drove certain plant species to the brink of extinction. For instance, *Fraxinus excelsior* is facing a severe die back since the early 1990s and this species threatening disease is now present across whole Europe (Pautasso et al., 2013). Transfer of exotic tree species to Europe such as *Populus deltoides* or hybrids *P. x canadensis* have caused hybrid swarms with *P. nigra* (Fossati et al., 2003) decreasing ranges of the local species. Global warming alters environmental conditions causing longer vegetation periods and changing optimal time and intensity for reproductions in forest trees. Genetic changes in forest tree populations are plausible but complex to study. These genetic effects are experimentally much more difficult to quantify in tree species compared to short lived organisms (but see Prunier et al., 2011). Moreover global warming has increased fire frequencies in the Mediterranean area and

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since the mid-1970 the annual area burned for example in eastern Spain more than tripled (Pausas, 2004) causing additional fragmentation effects.

Due to the extensive European-wide deforestation peaking at the end of the 18th or early 19th century (Williams, 2003), genetic losses due genetic drift are likely. On the other side the distribution area of conifers was artificially enlarged when countermeasures were taken to satisfy the high demand for timber and other wood products by establishing new productive forests. In consequence, conifers were used far beyond their natural range, and conversely, the area of broadleaved species was reduced. Scots pine (*Pinus sylvestris*) and spruce (*Picea abies*) have been particularly used (Spiecker, 2003), but also the translocation of relatively rare species such as mountain pine (*Pinus mugo*) and bog pine (*Pinus uncinata*) from Central Europe, for instance, to Scandinavia (Øyen, 1999) increased the species' ranges and exceeded the natural gene flow by several orders of magnitude. In the wake of such translocations plant material has been exposed to different environments and thus new selective regimes. Additionally gene flow from translocated populations may also have altered the gene pool of conspecific forests in dependence of the ratio between translocated vs. local population (Ellstrand, 1992).

The objectives of our paper are to review and exemplify the effects of fragmentation, translocation and selective cutting on the gene pool and evolutionary potential of European forest trees particular from a historic perspective. We collated several historic examples and discuss the impact in light of the genetic and ecological characteristics of forest tree species and how this may vary across regions. While we will focus on historic effects and have tried to target also non-geneticists, the interested reader is kindly advised to pay attention also to previous papers tackling human impacts on the gene pool of forests (Lefèvre, 2004; Bradshaw, 2004; Finkeldey and Ziehe, 2004).

2. Two different types of genetic variation: Adaptive and neutral genetic variation

Sufficient genetic variation is vital for the adaptation of tree populations (Reed and Frankham, 2003). In this context it is important to emphasise that there are two principally different types: adaptive and neutral genetic variation. Adaptive genetic variation is under natural selection. Many genes encode the whole protein synthesis and affect a single adaptive trait. The effect of each gene is usually very small. Relevant adaptive traits in forest trees are, for instance, budburst, bud set, vegetative and generative growth. Adaptive traits are commonly studied in time-consuming quantitative genetic experiments under standardised environmental conditions, but more recently also genomic selection based on next generation sequencing have been successfully applied in forest tree breeding (Grattapaglia and Resende, 2011) very likely providing genomic tools for studying natural tree populations. By contrast, neutral genetic variation is not under selection and, therefore, does not directly affect plant fitness

(but see also Palazzo and Gregory, 2014) and hence has no direct influence on the evolutionary potential. However, this type of genetic variation is very useful in assessing gene flow and breeding system, and can be easily studied applying various molecular techniques. Thus, adaptive and neutral genetic variation have complementary roles when evolutionary factors acting on a species are appraised (Eriksson and Ekberg, 2001). Neutral genetic variation is poorly correlated with the adaptive counterpart, and vice versa, adaptive variation is not a good predictor for non-selective evolutionary factors (Karhu et al., 1996). For the range of other genetic terms mentioned in this review we refer to the glossary.

3. Important characteristics when tree species are anthropogenically affected

It is obvious that a tree species which is barely genetically

structured across space such as *Pinus nigra* (Giovannelli et al., 2017) must be considered differently when the human impact is to be assessed compared to a species which is genetically well structured such as *Pinus sylvestris* (Rehfeldt et al., 2002). Generally, forest tree populations are highly genetically differentiated in adaptive traits (Savolainen et al., 2007), but knowledge about their response to certain environments (population response function) across major parts of their distribution range is very limited (but see Rehfeldt et al., 2002 for *Pinus sylvestris*).

When genetic data are incomplete or even completely missing, life history traits may give a valuable clue on genetic effects due to human impact. Several meta-studies (e.g. Hamrick and Nason, 2000) have shown that the geographic range is the best predictor of neutral genetic diversity in long-lived woody species and wind pollination in combination with wind or animal dispersal of seeds sustains a high gene flow. Other life history traits that may be helpful are the tree species' range during the last glaciations and the following recolonization. These characteristics affected the genetic spatial pattern and are relevant when human actions are to be genetically evaluated. The Carpathian Mountains, for instance, were not glaciated and offered sufficient living space for extended tree populations. It is very plausible that populations existing during that time were not or only very weakly affected by genetic bottlenecks contrary to tree populations of many other European mountains such as the Alps. Therefore, we can assume that the Carpathian Mountains harbor populations of high genetic diversity. This is indirectly supported by field data showing that Carpathian provenances for instance of Norway spruce *Picea abies* (König, 2005; Krutzsch 1974) and Scots pine (Magnesen, 2000) perform well both within and beyond the species' natural ranges. Populations originating from this mountainous range are expected to be more resilient to human impact due to their relatively high phenotypic plasticity (see below) than populations occurring in many other parts of the natural distribution.

Another relevant life history trait is the generation time. Probably forest tree species with long generation times such as oaks and beech evolve more slowly than species that are mature at an early stage such as poplar and willows (Aitken et al., 2008). However, it can only be speculated that adaptation of long-lived tree species relies more on phenotypic plasticity than is the case with species with short generation cycles, in which selection processes might be faster.

4. Forest fragmentation

Deforestation leads to fragmentation of forests and causes genetic changes associated with isolation and reduced population sizes (Jump and Peñuelas, 2006; Cubry et al., 2015). In Europe the intensity of historic deforestation has varied strongly among regions and over time. Initial anthropogenic effects on population structure of forest trees in temperate central Europe was probably connected to deliberate use of fire and date back to early postglacial times (10,000 BP) (Carcaillet 1998), and from the mid-Holocene forest fragmentation has been a major feature (Thompson, 2005)

4.1. Genetic effects of forest fragmentation

Specific local deforestation effects on genetic structure of forest trees have been hypothesised as an explanation of the observed genetic structure for instance in Mediterranean English yew (*Taxus baccata*) populations 4000 BP (González-Martínez et al., 2010) and Carpathian Norway spruce populations 2200 BP (Magyari et al., 2011). Simulations have suggested significant deforestation in Alpine Europe and Belgium-Luxembourg as early as 3000 BP (Kaplan et al., 2009). Pollen of cultural plant species was found already from around 3500 BCE in Denmark and northernmost Germany indicating deforestation in this area as well (Nielsen et al., 2012). Eventually, after the peak of the Middle Ages (11th to 13th century) until about the 19th century many parts of Europe were characterized by extensive deforestation (Williams, 2003).

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