forest tree species, as for other temperate species, including mammals, reptiles and amphibians (Provan & Bennett 2008; Stewart *et al.* 2009). The existence of such a 'northern' glacial refugium is consistent with the results of ENM, suggesting that *M. sylvestris* may have survived at high latitudes. In some tree species, such as *F. sylvatica*, it has been suggested that such a northern refugium may have served as the main source population for the recolonization of Eastern Europe after the LGM, whereas a south-eastern population spread over a much more limited area during postglacial recolonization (Hu *et al.* 2008).

For ash, silver fir, oaks and beech, Italy has been identified as a possible additional glacial refugium, isolated from other lineages by the Alpine barrier (Taberlet *et al.* 1998). We detected no footprint of an Italian refugium in *M. sylvestris*. This may be due to the lack of pure *M. sylvestris* from this region. Our samples from Italy indeed were all introgressed by the cultivated apple *M. domestica*, which may be linked to the introduction of the cultivated apple in Europe by the Romans in Italy, probably 3000 years ago (Mabberley *et al.* 2001). For the W population, which probably expanded from an Iberian refugium, the level of allelic richness was high, but significantly lower than that in the eastern populations. These differences in genetic variability may be due to much more severe climatic episodes (i.e. arid and cold) during the Quaternary Period in this region than in other parts of Europe (Petit *et al.* 2003). Tree populations that survived successive ice ages in the Iberian Peninsula were restricted to a few small suitable areas and were thus smaller than those in other parts of Europe.

Suture zones and recolonization fronts for the European crabapple

There were two main waves of recolonization by *M. sylvestris* from the glacial refugia in Europe: Western Europe, right into the north, was probably recolonized by populations from the Iberian Peninsula or the South of France, whereas the population from the Carpathian Mountains spread, albeit to a lesser extent, northwards in Eastern Europe. The population from the Balkan refugium does not seem to have recolonized large areas.

Our microsatellite markers indicate some admixture in the three populations. The W population contained the smallest number of admixed individuals and displayed the highest level of genetic differentiation from the other populations. This pattern suggests higher levels of recent genetic exchange between the SE and NE populations. The lack of samples from Central Europe may have resulted in an underestimation of the number of individuals with admixed ancestry in the western and eastern populations, but ABC analyses provided a high level of confidence for the choice of the model assuming gene flow between populations.

The biogeographic scenario uncovered in our study, with two main recolonization fronts in Western and Eastern Europe, has been demonstrated for many other temperate tree species (Heuertz *et al.* 2004; Lascoux *et al.* 2004). Suture zones in Central Europe, as detected for the European crabapple, are also typical of other temperate tree species (Petit *et al.* 2002; Heuertz *et al.* 2004, 2006; Magri *et al.* 2006; Liepelt *et al.* 2009). However, a clear suture between SE and NE populations and evidence for admixture have not been reported before. These findings demonstrate the utility of nuclear microsatellite markers for retracing the ancient demographic history of populations and the extent of admixture in phylogeographic studies.

Historical gene flow and dispersal capacity in the European crabapple

The European crabapple is dispersed by animals, but the weak spatial genetic structure within each population at the European scale, weak IBD patterns and low Sp values suggest that this species may be dispersed over large distances. These results are consistent with those previously reported for scattered temperate tree species (Oddou-Muratorio *et al.* 2004; Oddou-Muratorio & Klein 2008). The high dispersal capacity of the European crabapple and its current wide distributional range extending into the northern-most parts of Europe characterize this species as a rapid colonizer (Svenning & Skov 2007), consistent with its high pioneering capacity (Larsen *et al.* 2006).

Ecological niche models

Ecological niche models projections onto current climate layers resulted in a current suitable habitat for the European crabapple covering most of Europe, except Southern Spain and Italy, consistent with the Euforgen map of actual distribution (http://www.euforgen.org/distribution_maps.html), although this extends further east than the region studied in this study. Predictions showed that the distribution of the European crabapple, like those of many other European tree species (Svenning *et al.* 2008), was affected by climate changes during the Quaternary Period, with a contraction and fragmentation of populations. The modelling results suggested possible refugia in the European crabapple in the northeast, southeast and west, concordant with the distribution of the three genetic clusters and ABC results. Despite the overall concordance between ENM and