

Table 2 Relative posterior probabilities (p) and Bayes factor (BF) for the four historical models compared by approximate Bayesian computations. The models are described in Fig. 1

Model	p	BF
<i>a</i>	0.81	4.37
<i>b</i>	0.19	0.23
<i>c</i>	$2.3e^{-12}$	$2.3e^{-12}$
<i>d</i>	$1.0297e^{-56}$	$1.03e^{-56}$

for gene flow between recolonizing refugia and for the simultaneous divergence of the three populations.

Ecological niche modelling

Model performance, as assessed from the AUC (Area Under the receiver operating characteristic Curve), was high for all six algorithms (Table S6, Supporting information; $AUC = 0.98 \pm 0.01$), indicating that all six algorithms fit the data well (Monserud & Leemans 1992; Fieldings & Bell 1997; Allouche *et al.* 2006). With thresholds maximizing the True Skill Statistic (TSS), *M. sylvestris* had a good TSS value of 0.79 ± 0.04 . We ran ENM with both sets of past climate data, CCSM2 and MIROC, but only MIROC gave consistent results across Europe. We therefore present projections based on MIROC data (Figs 5b and S8b, Supporting information). The projection onto current climate layers identified a putative suitable climate area essentially located in Western Europe for *M. sylvestris* (Figs 5a and S8a, Supporting information). The MIROC model predicted that the areas suitable for this species during the LGM were limited to lower latitudes than those considered suitable today and were more fragmented, with in particular low probability of contact between Eastern and Western Europe, in agreement with the genetic data (Figs 5 and S8, Supporting information). The climatic model suggested that populations of the European crabapple may have been maintained in areas further north than the typical glacial refugia (Hewitt 2004), with possible continuity between the populations from Western Europe, Italy and the Balkans. The predicted distribution, however, does not show a refugial distribution in isolated places as expected if the species survived in nunataks in northern latitudes.

Discussion

Paleodistribution modelling and genetic data allowed inferences on the phylogeography of the European crabapple, an endangered species and valued genetic resource for apple breeding. The distribution predicted based on climatic data was overall consistent

with population genetic analyses, altogether suggesting population and range contractions of *Malus sylvestris* during the last glaciation with a fragmentation between Eastern and Western Europe followed by postglacial recolonization of Europe.

Glacial refugia for *Malus sylvestris*

Malus sylvestris displayed a clear geographical pattern of population structure, with three differentiated populations in Europe: (i) a western population (W) spanning a huge area from France to Norway, and an eastern group subdivided into (ii) a north-eastern (NE) population around the Carpathian Mountains and (iii) a south-eastern (SE) population located at the north-east edge of the Balkan Peninsula. The strong differentiation between the three populations and the decreasing allelic richness at increasing latitudes suggest that the European crabapple contracted its range to southern glacial refugia, one of which probably was in the Iberian Peninsula or in the south of France, and another one in the Balkans.

The NE population growing around the Carpathian Mountains displayed a low level of genetic differentiation from the SE population, but had a high level of allelic richness. There were two possible origins for this population: a refugium from north-eastern Europe that came into secondary contact with the SE population and a wave front from the Balkan refugium during the recolonization of Europe. ABC analyses evaluating the fit of various demographic models to microsatellite data showed that the most strongly supported scenario was the simultaneous divergence of the three populations, with gene flow between all population pairs. The NE population, therefore, probably originated from a glacial refugium rather than during the postglacial recolonization of Europe.

The geographical pattern of population structure uncovered in *M. sylvestris* is consistent with those found in other animal, plant and fungal taxa (Hewitt 2004; Lascoux *et al.* 2004; Schmitt 2007; Vercken *et al.* 2010) and, in particular, with the patterns commonly found in temperate forest trees (Petit *et al.* 2002; Heuertz *et al.* 2004, 2006; Magri *et al.* 2006). Indeed, the existence of a large western European population and differentiated eastern populations in the Balkans Peninsula has been reported in *Quercus* sp., *Abies alba* and *Fraxinus excelsior*. In some other tree species, such as *Alnus glutinosa* (King & Feris 1998) and the common beech *Fagus sylvatica* (Magri *et al.* 2006), the existence of additional refugia in the eastern part of Europe, particularly in the Carpathian Mountains, has been suggested on the basis of the high level of genetic diversity in cpDNA and pollen fossil records (Magri *et al.* 2006). Our microsatellite