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ORIGINAL ARTICLE

# The Balkans: a genetic hotspot but not a universal colonization source for trees

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## Abstract

In the context of Europe, the southern peninsulas including the Balkans are considered hotspots of diversity. They preserved substantial parts of tree species and genera occurring in Europe during the Tertiary, as the effects of the Quaternary glaciations on species richness were not as severe here as in more northerly regions. The Balkans also harboured glacial refugia of most European trees, and this was probably the reason for a premature suggestion that this region was the main source for the Holocene recolonization of Central and Eastern Europe. However, studies based on a combination of paleobotanical and genetic evidence showed that this was an exception rather than a rule. In most tree species, the Balkan refugia have not effectively contributed to current gene pools. In spite of this, empirical studies have documented that genetic diversity in the Balkan region is generally higher than elsewhere in Europe, which can be attributed to a high number of refugia in this area harbouring differentiated genetic lineages, and high environmental heterogeneity. This makes the Balkans an important source of genetic material for forestry, especially in the light of the ongoing climate change.

**Keywords** Genetic diversity · Glacial refugia · Holocene recolonization · Species diversity

## Effects of the Quaternary climate oscillations on tree vegetation

Compared to the other temperate regions of the northern hemisphere, tree taxonomical richness in Europe is low, especially at the level of genera (Huntley 1993; Svenning 2003; Birks and Tinner 2016). This lack of tree diversity results primarily from extinctions during the Quaternary (Mai 1995). Diversity of temperate trees in Europe was high during the whole Neogene and remained so into the Pliocene (Kovar-Eder 2003). However, a large proportion of the temperate tree genera disappeared already in the Early Pleistocene (Martinetto 2001; Magri 2010; Popescu et al. 2010). Diversity of temperate tree genera became severely reduced already with the first strong glaciation in Europe in the Late Pliocene (e.g. *Liquidambar, Meliosma, Pseudolarix, Stewartia* disappeared at this stage), and continued to decrease into the Middle Pleistocene (extinction of *Liriodendron, Magnolia, Taxodium, Sequoia, Phellodendron, Tsuga, Carya*), while only few genera became extinct in the later stages, with *Zelkova* or *Pterocarya* surviving until the last glaciation (Follieri et al. 1986; Lang 1994; Svenning 2003; Birks and Tinner 2016; Magri et al. 2017). Some genera became extinct on the continent but preserved relictual occurrences on the Mediterranean islands (*Cedrus, Morus, Zelkova*: Svenning 2003; Fineschi et al. 2002). The reason for the severe Plio-Pleistocene extinctions in Europe is not fully clear. Migration barriers were most frequently mentioned as the explanation for the reduction in generic richness: the East-to-West orientation of the major European mountain ranges (Pyrenees, Alps, Carpathians) restrained several temperate trees from migrating south during the Pleistocene cold stages, and southern bordering of the continent by the Mediterranean Sea prevented further southbound retreat (Huntley 1993). Alternatively, climate of the southern refugial areas may have been responsible for the extinctions, as since the end of the Pliocene, and especially during the

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glacial periods, the Mediterranean region suffered from dry climate (Tzedakis et al. 2002).

Whatever were the reasons for disappearing of trees, the process did not take place everywhere. A few boreal tree species (e.g. Norway spruce or silver birch) survived even far in the North, as the ice sheet did not cover the northern part of the continent entirely (Allen et al. 2010; Binney et al. 2017). However, temperate trees were mostly restricted to refugial areas located more in the South, especially in the three southern European peninsulas—the Balkans, the Iberic and the Apennine peninsula (Taberlet et al. 1998; Taberlet and Cheddadi 2002). Even though many tree species have succeeded to repeatedly spread back and recolonize their former ranges during the Holocene, the massive southward retreat during the last glacial is still reflected in the geographical distribution of species richness. In addition, high diversity is a result of the fact that the territory of today's Balkan Peninsula with heterogeneous climate and complex physical geography provided a wide range of conditions for different species and vegetation types to evolve and also served as a crossroad for Asian lineages and taxa during east–west colonization of Europe since the Early Oligocene (Hewitt, 2011; Manafzadeh et al. 2014). Although the number of tree species in Europe varies depending on taxonomic concepts, the general trends clearly show that roughly 90% of all European trees can be found in the Balkans, 75% in the Apennine Peninsula, 70% in the Iberian Peninsula, while only about 35% in Scandinavia. A similar pattern applies to genera: out of 27 European tree genera, the Balkans harbours 26, while only 17 occur in Scandinavia (Svenning and Skov 2007; San Miguel-Ayanz et al. 2016; Caudullo et al. 2017). Nevertheless, also these data document that the Balkan Peninsula is the European hotspot of tree taxonomic richness, both on the species and the generic level.

## Balkans: a hotspot of genetic variation of trees

During the whole Quaternary, climatic conditions in the Balkans remained at least moderately favourable for the survival of temperate forest trees, in contrast to more northern regions. Of course, not permanently and not everywhere in the Balkans. Locations, where a tree species has continuously persisted since the Tertiary, were exceptions even in the Balkans (Médail and Diadema 2009). Both during the glaciations and the interglacials, the climate varied dramatically temporally as well as spatially (Holm and Svenning 2014). Consequently, the areas suitable for tree survival were probably small and variable: they expanded during warmer periods and became fragmented again during the glacial maxima (van Andel and Tzedakis 1996), and harboured different tree communities in different periods (Cheddadi et al. 2005). Therefore, the concept of a single continuous and homogeneous refugium in the Balkans harbouring all tree species across the whole Quaternary is an oversimplification; even the idea of multiple unconnected refugia does not adequately reflect the complexity of the processes that shaped the current genetic and species diversity (Nieto Feliner 2011). Most of the Balkans was occupied by xeric *Artemisia*-Gramineae-Chenopodiaceae steppe-like vegetation, while favourable conditions for survival of trees remained preserved only in a relatively narrow belt around 500–800 m a. s. l., below the tundra-like vegetation at higher elevations (Birks and Willis 2008). A continuous presence of both coniferous and deciduous tree taxa is documented by pollen diagrams from southeast Europe, while their presence and abundance varies from site to site. The populations of thermophilous and mesophilous deciduous taxa were most likely located at favourable microsites such as south facing slopes and more humid higher ground, but high proportions of conifer pollen (spruce in the eastern and pines in the western part of the Balkans) suggest a more massive presence of conifers (Willis 1994). Médail and Diadema (2009) identified three types of refugia for the Mediterranean region, each type suitable for a different set of tree species: moist mid-altitude refugia allowing altitudinal shifts in response to climate changes or the in situ persistence of species, deep gorges and closed valleys around rivers or creeks with continuous moisture, and low-altitude areas representing locally moist and warm sites such as valley bottoms, coastal plains and wetlands. All these vegetation types have their analogies in the modern vegetation of western Eurasia (Birks and Willis 2008). The Balkans, covered by rugged high mountain ranges alternating with broad river valleys and lowlands, potentially offered suitable conditions for at least the former two types.

Such a complex history is expected to have promoted formation and persistence of multiple genetic lineages of most species in the refugial areas including the Balkans, reflected in high levels of allelic and haplotypic richness. Empirical studies do not fully confirm this expectation, however; it must be emphasized here that in contrast with the Iberian and Apennine peninsulas, south-eastern Europe is generally underrepresented in studies examining genetic variation of trees at the Europe-wide scale. For example, a complex study of 22 woody species in 25 forests across Europe (Petit et al. 2003) included only one population from the Balkan refugial area (excluding the Romanian Carpathians). Expectedly, this population showed a high divergence but a generally low haplotypic richness, which contradicts with other studies based on larger sample sizes. For instance, the study of Magri et al. (2006) on European beech revealed the highest number of haplotypes of the maternally inherited chloroplast DNA just in the southern and south-western Balkans. The same applies to the study of Hatziskakis et al.

(2009), which found 13 haplotypes in the beechwoods of Greece, whose distribution indicates the presence of at least 4 refugial populations in this area. Even more striking: a study in the Greek Mt. Paggeo revealed the presence of 8 chloroplast haplotypes structured in three highly divergent areas within a territory of 10 km length (Papageorgiou et al. 2014). High haplotype richness in the south-western Balkans contrasting with a relative homogeneity in central Europe was documented in other tree species as well (*Alnus glutinosa*: Havrdová et al. 2015; *Fraxinus angustifolia*: Papi et al. 2012). Nevertheless, areas with high haplotypic diversity often occur also in more northern regions, usually in contact zones of postglacial colonization routes: *Quercus* sp. is an excellent example (Petit et al. 2002).

In the case of pollen-dispersed genes (nuclear, but also chloroplast genes in the Pinaceae) the situation is a bit more complicated, as such genes can often be transferred over large distances (Liepelt et al. 2002). However, even gene flow cannot completely wipe-out diversity patterns resulting from glacial survival and postglacial recolonization. Studies allowing a direct comparison between the Balkans and the more northerly regions are by far not as numerous as one would expect after more than 20 years of genetic inventories of trees using various types of genetic markers (which again might be a tribute to the emphasis on Western Europe in large international projects); an overview of them is presented in Table 1. It shows that with few exceptions, the intrapopulation allelic richness is generally higher in the Balkans, irrespective of the marker type. Gene diversity (expected heterozygosity, effective number of alleles) is also mostly higher in the Balkans; empirical data thus do not confirm the richness/diversity contrast expected between refugial and colonizing populations (Hewitt 1996; Comps et al. 2001). However, the diversity excess in the Balkans seems to result from excessive allelic richness rather than increased evenness of allelic frequencies expected in recently bottlenecked populations. Data about genetic differentiation are too scarce to allow generalization; however, where available, $F_{ST}$-values indicate higher genetic divergence among populations in the Balkans than in central Europe.

## Recolonization of Europe in the Holocene: What was the contribution of the Balkans?

Both paleobotanical and genetic data indicate that the concept of "refugia within refugia" (Nieto Feliner 2011) perfectly fits with the situation in the Balkans during the Quaternary. The presence of a plenty of highly divergent lineages at locations sometimes separated by only few kilometres or tens of kilometres is a footprint of a complex history, when fragmented tree populations became differentiated due to both neutral processes associated with limited population size and isolation (bottlenecks and founder effects) and adaptation.

**Table 1** Overview of studies of allelic variation at nuclear loci comprising both the Balkans and central Europe

| Species | Marker | Balkans[a] | | | | | Central Europe[b] | | | | | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $N_P$ | $A$ | $h_e$ | $n_e$ | $F_{ST}$ | $N_P$ | $A$ | $h_e$ | $n_e$ | $F_{ST}$ | |
| *Fagus sylvatica* | Allozymes | 43 | 2.29 | | 1.392 | 0.038 | 178 | 2.19 | | 1.473 | 0.032 | Gömöry et al. (2007) |
| | Allozymes | 3 | 2.44 | 0.197 | | | 3 | 2.25 | 0.243 | | | Harter et al. (2015) |
| | EST-SSR | 2 | 8.61 | 0.656 | 4.327 | | 4 | 7.50 | 0.592 | 3.517 | | Dounavi et al. (2016) |
| | SNP | 2 | 1.64 | 0.151 | 1.231 | | 3 | 1.25 | 0.044 | 1.063 | | Dounavi et al. (2016) |
| *Castanea sativa* | nSSR | 3 | 4.62 | 0.436 | | | 12 | 4.97 | 0.327 | | | Poljak et al. (2017) |
| *Alnus glutinosa* | nSSR | 8 | 5.72 | 0.669 | | | 23 | 5.17 | 0.626 | | | Havrdová et al. (2015) |
| *Fraxinus angustifolia* | nSSR | 5 | 3.78 | 0.538 | 2.726 | | 3 | 3.20 | 0.477 | 2.226 | | Gérard et al. (2013) |
| *Fraxinus excelsior* | nSSR | 17 | 15.82 | 0.736 | | 0.093 | 16 | 14.43 | 0.814 | | 0.027 | Heuertz et al. (2004a) |
| *Quercus petraea* | Allozymes | 1 | 3.37 | 0.353 | 1.782 | | 21 | 3.41 | 0.349 | 1.699 | | Zanetto et al. (1994) |
| | nSSR | 2 | 14.79 | 0.182 | | | 1 | 13.12 | 0.366 | | | Neophytou et al. (2010) |
| *Quercus robur* | nSSR | 2 | 14.60 | 0.822 | | | 1 | 14.53 | 0.814 | | | Neophytou et al. (2010) |
| *Sorbus domestica* | nSSR | 4 | 5.18 | 0.590 | 3.100 | | 4 | 4.93 | 0.548 | 2.592 | | George et al. (2015) |
| *Sorbus torminalis* | nSSR | 5 | 8.00 | 0.703 | 4.820 | | 4 | 6.93 | 0.631 | 3.941 | | Kučerová et al. (2010) |
| *Picea abies* | Allozymes | 3 | 1.68 | 0.020 | | | 4 | 1.75 | 0.021 | | | Kannenberg and Gross (1999) |
| *Pinus mugo* | nSSR | 5 | 5.18 | 0.450 | 2.640 | | 14 | 4.86 | 0.449 | 2.679 | | Żukowska and Wachowiak (2017) |
| *Taxus baccata* | nSSR | 12 | 4.13 | 0.736 | | | 53 | 4.47 | 0.773 | | | Mayol et al. (2015) |

$N_P$ number of populations, $A$ allelic richness, $h_e$ expected heterozygosity, $n_e$ effective number of alleles, $F_{ST}$ coefficient of differentiation

[a] Greece, Bulgaria, Macedonia, Albania, Montenegro, Serbia, Bosnia and Hercegovina, Dalmatia (Mediterranean part of Croatia)

[b] Slavonia (continental part of Croatia), Slovenia, Austria, Hungary, Slovakia, Czech Republic, Poland, Germany

Southern European peninsulas, and especially the Balkans, have traditionally been considered the main source of genetic lineages recolonizing Europe during the Holocene (Taberlet et al. 1998; Tzedakis 2004). For boreal species such as *Picea abies*, *Pinus sylvestris* or *Betula pendula*, the idea of northern refugia was accepted (Palmé et al. 2003; Pyhäjärvi et al. 2008; Tollefsrud et al. 2015; Tóth et al. 2017). However, for temperate tree species, the paradigm of the presence of effective refugia solely below 46° N latitude still persists (Tzedakis et al. 2013), although it has been gradually challenged by several large-scale studies.

European white oaks (*Quercus* subg. *Lepidobalanus*) represent an instance of a taxon, where the paradigm is valid. The Holocene migration of oaks was reconstructed based on a combination of genetic and paleobotanical evidence in probably the most extensive study of this kind (Petit et al. 2002). Although it revealed a very complex situation in central and eastern Europe with a plenty of partly overlapping distributions of haplotypes and genetic lineages of different origins, it confirmed an essential role of the southern European refugia (including the Balkans) in the recolonization (Fig. 1). All last glacial maximum (LGM) refugia were suggested to be located in the southern European peninsulas and only secondary refugia, harbouring oak populations during the Younger Dryas cold period were supposed to be located more northwards (e.g. in Istria and North-western Dinaric Alps). In *Fraxinus excelsior*, another temperate broadleaved species, the situation is already a bit different: although ash populations in the Western Carpathians and adjacent Polish lowlands immigrated from southern Balkans, Czech and German populations have their origin in a refugium located probably in the Eastern Alps or North-western Dinaric Alps (Heuertz et al. 2006). In *Fagus sylvatica*, a high chloroplast haplotype diversity and morphological variability in the south-western Balkans (which motivated local botanists to classify local beechwoods as a separate taxon *Fagus*

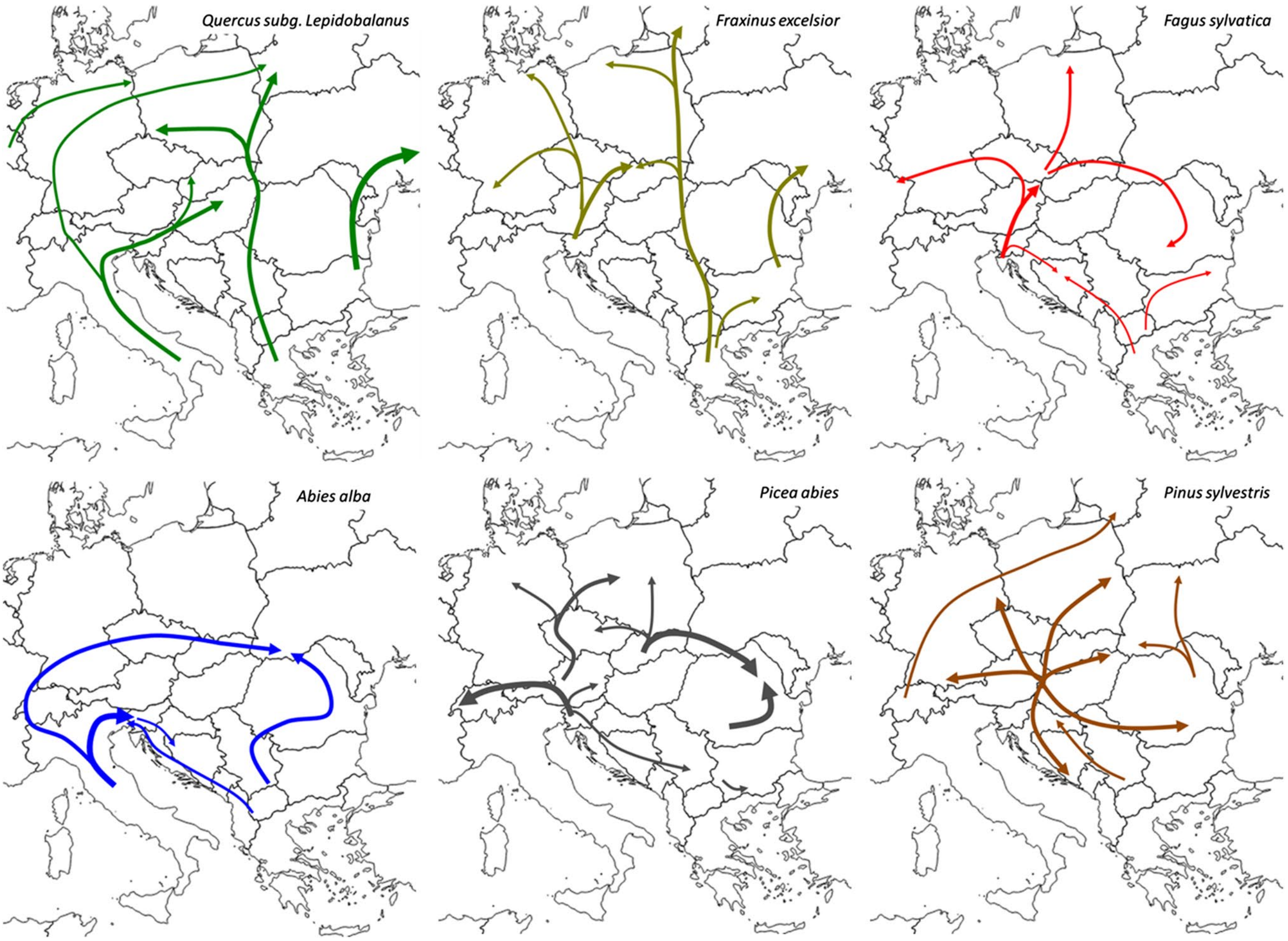

**Fig. 1** Schematic representation of postglacial colonization routes of six principal European tree taxa in the Balkans and central Europe reproduced after or reconstructed from published data: white oaks (Petit et al. 2002), common ash (Heuertz et al. 2004b, 2006), European beech (Magri et al. 2006), silver fir (Gömöry et al. 2004, Liepelt et al. 2009), Norway spruce (Tollefsrud et al. 2015) and Scots pine (Tóth et al. 2017)

*moesiaca*: Czeczott 1933) is a strong hint for the presence of LGM refugia. However, as shown by Magri et al. (2006), southern Balkans refugia did not contribute to recolonization of Europe, as their expansion towards the North was blocked by the Wallachian and Hungarian lowland in the East and by the expansion of beech from the refugia located in Slovenia or Istria in the West (Fig. 1). Silver fir (*Abies alba*), a typical temperate conifer, is a similar case: genetic lineages originating from the Balkan refugia succeeded to invade the Carpathians until the Ukrainian border in the East and even penetrate north-eastern Italy (Tarvisio region) in the West but there their expansion was halted by counter-colonization from the Italian and maybe North-western Dinarian refugia (Liepelt et al. 2009). Piotti et al. (2017) even indicated a possible connection between the Balkan and south-Apennine refugia of silver fir; however, Calabrian populations are strongly differentiated from those in central and northern Apennine mts. and have not contributed to recolonization of Central Europe. *Picea abies* and *Pinus sylvestris* are considered boreal rather than temperate species; however, in addition to extensive ranges in Scandinavia and north-eastern European plains, they are broadly distributed across temperate regions of Europe as well. Both conifers were present in the Balkans during the LGM but these refugial populations have not substantially contributed to the colonization of central Europe (Tollefsrud et al. 2015; Tóth et al. 2017).

For commercially less important species, the studies are less abundant but exist, and again generally confirm just a secondary importance of the Balkan refugia for the colonization of the current ranges of temperate tree species. Hazel (*Corylus avellana*), which dominated the European landscape during the early Boreal period, probably spread from local refugia scattered across Central Europe or, alternatively, from a larger refugium at the Bay of Biscay. Balkan populations, strongly differentiated in chloroplast haplotypes, have not contributed to the colonization (Palmé and Vendramin 2002). Two lineages of *Carpinus betulus* with the origin in southern-Balkan mountain ranges colonized the Black Sea coast, Moldova, the Southern and Eastern Carpathians but the rest of the current distribution range seems to have been invaded by a lineage originated from the North-western Dinaric Alps (Grivet and Petit 2003; Postolache et al. 2017). In European crabapple (*Malus sylvestris*) there were two main waves of recolonization from the glacial refugia in Europe: Western Europe was probably recolonized by populations from the Iberian Peninsula or the south of France, whereas the population from the Carpathian Mountains spread northwards in Eastern Europe. Again, the population from the Balkan refugium does not seem to have recolonized large areas (Cornille et al. 2013). For alders (*Alnus glutinosa* and *A. incana*) the studies of Havrdová et al. (2015) and Mandák et al. (2016) suggested the Balkan Peninsula as the recolonization source, based on nuclear marker data. However, this contradicts the distribution of chloroplast haplotypes: A high haplotypic diversity in the Balkans is in contrast with the fixation for a single haplotype in the rest of the distribution range (especially true for *A. glutinosa*). As pointed out by Giesecke and Brewer (2018), such pattern may have resulted from a strong bottleneck at the outset of postglacial expansion but recolonization from a more northerly located refugium is a more plausible explanation.

The example of alders points to the risk of overrating one type of data (nuclear microsatellites in this case) in the reconstruction of the Holocene recolonization. Paleobotanical studies, which may rely on pollen spectra and macrofossils, may suffer from a similar risk. Pollen can be transferred over large distances (especial in wind-pollinated species). Recording pollen grains of a certain species in the pollen spectrum does not yet mean the presence of the species on the site. Usually, this problem is treated by setting a threshold, below which the presence is considered not guaranteed (e.g. 2% for *F. sylvatica* in the study of Magri et al. 2006). Nevertheless, any such threshold, even though backed by deep expert knowledge, is artificial and arbitrary. On the other hand, pollen data reflect dynamics of the local population, as they are determined across the whole profile. Macrofossils give undoubted evidence of the in situ presence of a certain species at a certain time but generally are rare and do not allow any inference on population size and its temporal change. Charcoal of temperate trees such as *Fagus*, *Abies*, *Ulmus* or *Taxus* dated to LGM was found at many sites across central Europe (Willis and van Andel 2004), documenting the unambiguous local existence of LGM populations of these taxa. Willis and van Andel (2004) reported charcoal of *Fagus*, *Abies*, *Ulmus* or *Taxus* from deposits pre-dating the LGM sensu stricto, which is dated around 26–18 ka BP. The fate of these populations and their genetic contribution to the present-day populations is a matter of question. Tzedakis et al. (2013) argued that there were no tree refugia north of 45°–46° N during the LGM and stated that the colonization of central-northern Europe started from the Mediterranean regions. On the other hand, specific local gene pools can sometimes be identified in the regions, where the LGM presence of a species is demonstrated by macrofossils. Beech in the Cantabrian and Basque ranges or in the Southern Carpathians can be an example (Magri et al. 2006). Both chloroplast and allozyme data indicate that the local refugial populations were invaded by beech coming from the main Central-European refugium. Limited population size is the most plausible explanation: in a bottlenecked population genetic drift may deplete the gene pool of beneficial alleles (Comps et al. 2001) and deprive the population of ability to expand even when environment improves. The strength of studies like that of Magri et al. (2006) or Tollefsrud et al. (2015) lies just in the combination of different types of evidence: macrofossil and pollen data, biparentally and maternally inherited markers, to make inference the Holocene history of a species, and even such combination may be not enough to resolve all open questions about the location of refugia and their contribution to Holocene colonization. In the future research, new types of evidence can be deployed to support other datasets in reconstructing the history of a certain tree species; an example are phytosociological and phytogeographical characteristics of herbaceous forest species as shown for beech (Brus 2010).

## Implications for gene conservation and forestry

Human-induced climate change has finally received attention of the society and the politicians that it deserves. However, it is not the sole threat to forest ecosystems and not the first one that appeared in the history. Tree populations have always been endangered by weather extremes, newly emerging pathogens and pests, and other factors. Although diversity does not necessarily guarantee resistance and flexible responses of a population, a community or an ecosystem to climatic and biotic hazards (Pennekamp et al. 2018), biodiversity loss has been demonstrated to alter the overall stability of a system (Donohue et al. 2013). Therefore, gene conservation programs focus on genetically rich regions such as refugial areas. Both high intrapopulation diversity and interpopulation differentiation make the Balkans an excellent candidate for gene conservation programs of trees. Unfortunately, the density and distribution of dynamic gene conservation units for forest trees do not fully reflect this fact, as there are countries without a single gene reserve (Albania, Montenegro; see http://portal.eufgis.org/maps/).

Mitigation of climate change effects on forest ecosystems is another relevant issue, where the information about the evolutionary past of local populations is useful. For forest trees, assisted migration, i.e. transfer of genetic material from populations, which in the evolutionary past experienced climatic conditions expected on target sites in the future, is an often-proposed adaptation measure (Williams and Dumroese 2013). The context of the postglacial migration needs to be taken into consideration in the recommendations for assisted migration. As populations in different refugia were exposed to different environments and their genetic structures became modified by neutral processes associated with small population size, they often exhibit non-identical adaptive properties, as demonstrated by Bošeľa et al. (2016) for silver fir. Lack of adaptedness and outbreeding depression are the risks associated with long-distance transfers of materials between regions colonized from different refugia. Unfortunately, Balkan provenances are underrepresented in large international common-garden experiments organized in Europe for principal tree species in the 1990s and 2000s. Therefore, even though Balkan tree populations are to be considered a valuable source of genetic material for future breeding programs and reforestation in central Europe in the context of climate change, exact data about the origin of the reproductive materials must be recorded and the performance of the established forest plantations in terms of survival, growth and physiology needs to be carefully monitored and evaluated.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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