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Growing evidence for the existence of glacial refugia of European beech (*Fagus sylvatica* L.) in the south-eastern Alps and north-western Dinaric Alps

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Abstract

Background and Purpose: *It is widely accepted that south-European peninsulas were major refugial areas from where European beech,* Fagus sylvatica *L., spread to the rest of Europe in the Holocene. The aim of this paper is to review and evaluate all the available data and present different types of evidence, some of them new or overlooked until now, to support the hypothesis on the existence of glacial refugia of European beech further to the north, in the south-eastern Alps and north-western Dinaric Alps in the Pleistocene, and on rapid development of these populations in the Holocene.*

Material and Methods: *Numerous published pollen diagrams and palynological research as well as reports of macroscopic plant remains, mainly charcoal from Paleolithic sites, were analyzed to examine the presence of European beech in the late Pleistocene and Holocene. Data on genetic variation of beech populations from central and southeastern Europe were analyzed to investigate their genetic structure and differentiation. Additionally, the distribution of several taxonomically rather isolated herbaceous species, characteristic for mesophilous beech communities from the studied area, was analyzed.*

Results and Conclusions: *In the south-eastern Alps and north-western Dinaric Alps, the presence of beech in the Early and Late Pleistocene is confirmed by pollen records, and macrofossils, such as beech charcoal dating up to 70 ka BP, which have been excavated in several Paleolithic sites. Genetic investigations have revealed larger genetic diversity in the north-western populations, including those from the south-eastern Alps, while levels of genetic multiplicity and differentiation were highest in the Balkan Peninsula. Presented data support the hypothesis that some microrefugia in this area were inhabited with beech continuously through the last glacial period. These populations must have played an important role in the colonization of central and western Europe in the Holocene, and possibly spread southeast toward the Balkan Peninsula. This scenario is supported by the specific local distribution of several herbaceous species, which are character- and diagnostic species of recent beech communities from this area. This demonstrates that phytogeographical and phytosociological characteristics of herbaceous plants can indirectly support the reconstruction of the history of a tree species.*

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INTRODUCTION

In the last decades, numerous studies have investigated the glacial and post-glacial history of tree species. A better understanding of the past events and factors that influenced the distribution and genetic structure of tree species can improve management of their present and future populations, especially in the context of changing climatic conditions. European beech (*Fagus sylvatica* L.), the most economically important European broadleaf, is one of the most thoroughly investigated tree species. There is growing knowledge on the geographic extent of its glacial distribution, and further evidence including nongenetic data would be especially useful to help precisely identify and/or confirm possible beech glacial refugia.

The genus *Fagus* L. spread from Asia to Europe in the Tertiary by the late Early Oligocene (ca. 30 Ma ago) as the species *F. castaneifolia* Unger, and was already distributed in Europe in the Late Oligocene *(1)*. Based on rich fossil material, such as fossil leaf and fruit remains, and the latest revision of the *Fagus* genus from the Cenozoic of Europe *(2)*, two highly polymorphic and geographically clearly distinct species were present in Europe and south-western Asia during the Neogene, one of them resembling a number of modern species, including European beech (*Fagus sylvatica* L.). The evolution of *Fagus sylvatica* is not well known, but the Pleistocene glacial and interglacial periods, when repeated expansion and contraction of beech populations occurred in response to changing climate conditions, are considered as key periods for its present distribution in Europe.

European beech populations survived the last glacial period in several refuge areas. For a long time the mountainous regions of south-European peninsulas, primarily the southern Balkan and southern Apennine Peninsula, were considered as major refuge areas from where beech spread to the rest of Europe in the Holocene *(3, 4, 5, 6, 7, 8, 9, 10)*. The longest European pollen records show that beech has been a minor component of the vegetation or a dominant tree in southern Europe (Valle di Castiglione – Italy, Ioannina and Tenaghi Phillipon – Greece, Lago Grande di Monticchio, Italy) during most of the last 500 ka *(11, 12, 13)*, and beech has been detected continuously in palynological sequences spanning the last ice age in Greece *(14)*. Possible secondary refugia existed in south-western Europe *(15, 16, 17)* or in the South Carpathians *(8, 18)*.

Until recently, it seemed improbable that beech would have survived glaciations as far north as southern central Europe, and the area of the south-eastern Alps and north-western Dinaric Alps, mainly the area of present-day Slovenia and western Croatia, has not been considered an important glacial refuge for beech. However, the survival of small groups of beech trees in this area was previously suggested by Šercelj (*19*), and possible local post-glacial development of beech in the area of present-day Slovenia was discussed *(20)*. It is now known that Italian and Balkan beech populations have increased very slowly in their respective peninsulas in the post-glacial period *(21)*. Recent investigations combining genetic and fossil data across the entire species range have confirmed the probable existence of beech glacial refugia in Slovenia and the eastern Alps (and possibly in southern Moravia and southern Bohemia), which should be considered as the main source areas for the colonization of central and northern Europe by beech *(22)*.

The aim of this paper is to review and discuss all the available data and present different types of evidence, some of them new or overlooked until now, to support the hypothesis on the existence of glacial refugia of European beech in the south-eastern Alps and north-western Dinaric Alps in the Pleistocene, and on rapid development of local European beech populations in the Holocene.

PALEOBOTANICAL REMAINS

Pollen records

Fossil remains, mainly leaves, found in Oligocene marl layers in several Slovenian coal mines, including Zagorje, Trbovlje and Novi Dol *(23),* and numerous samples from nearby Croatian locations such as quarries in Planina gornja and Planina donja, Sveta Nedelja near Zagreb and possibly Radoboj near Krapina *(24, 25)* unequivocally demonstrate the Tertiary distribution of beech in this area. There are no reliable data on the presence of beech in the south-eastern Alps and north-western Dinaric Alps through most of the Neogene, but its continuous and high pollen concentration from the Velenje site in north Slovenia at the end of the Pliocene and beginning of the Pleistocene suggests that beech was still an important component of the vegetation of the south-eastern Alps; according to Šercelj *(26)* it was the dominant species in the late Pliocene in Velenje with pollen concentrations up to 30%. Beech was also present in sediments from a site near Ilirska Bistrica *(27)* which were, based on the floristic composition of the sediments, estimated to originate from the Donau-Günz Interglacial, a period of relatively moderate climatic conditions. During glaciations in the Early Pleistocene, beech pollen was still continuously present in sediments, but its concentration began to decrease, which may be a response to cooler climatic conditions. This is well exemplified at a site near Novo mesto where very low amounts of beech pollen could still be found in pollen assemblages estimated to originate from the Günz-Mindel interglacial period *(28)*. In the Mindel-Riss interglacial strata in the Middle Pleistocene, beech pollen was not recorded in the south-eastern Alps and north-western Dinaric Alps *(29, 30)*. This can be interpreted as either the complete absence of beech in this area in the Middle Pleistocene, or as the survival of only very small isolated groups or single trees in protected sites that produced only limited quantities of pollen difficult to trace. However, as reported by Šercelj *(31)*, beech pollen reappeared in sediments in Ljubljansko barje, though very scarcely, at the period of the Riss interstadials and Riss-Würm interglacial (> 51 ka

^{14}C BP, based on radiocarbon dating of the sediment), and became more abundant at the end of the Würm, possibly interstadial Brörup (> 48 ka ^{14}C BP, radiocarbon dating of the sediment). Pollen of similar age was also found in Bovec (estimated between 59 and 53 ka BP, second Würm interstadial, concentrations up to 40%) and in Mlino near Bled (early Würm, concentrations 5–8%) *(19)*. High pollen concentrations recorded as far back as the Würm glacial that remained high in interstadial periods support the hypothesis of the permanent and continuous presence of beech in the area long before the Holocene, when its strong expansion started. In the Bölling interstadial (12.5–13.3 ka BP), high concentrations of beech pollen were again recorded in several locations in the Ljubljansko barje, such as in Rudnik, Notranje Gorice and Log by Vrhnika *(32)* and Na mahu, where a marked increase of beech pollen was recorded in the zone which is ^{14}C dated between 14.3 and 11.9 cal ka BP *(33)*. In Sečovlje near Koper, beech pollen dated 9.16 ± 0.12 ka ^{14}C BP has also been found *(34)*.

On a larger European scale, Huntley and Birks *(8)* compiled data from numerous sites and showed that the concentration of beech pollen was highest in the south of the Balkan Peninsula 9 ka BP, but did not exceed 5%. But only 500 years later (8.5 ka BP) concentrations in the south-eastern Alps and north-western Dinaric Alps far exceeded those in the Balkans, when they reached 25% 8 ka BP and remained high until 6 ka BP. This suggests a strong and very fast local expansion of beech, which led to the development of beech dominated forests during this period *(30)*. This rapid and extensive increase of beech populations in the eastern Alps and Slovenia in the early Holocene has also been confirmed by recent analyses of a large number of European pollen records *(21)*.

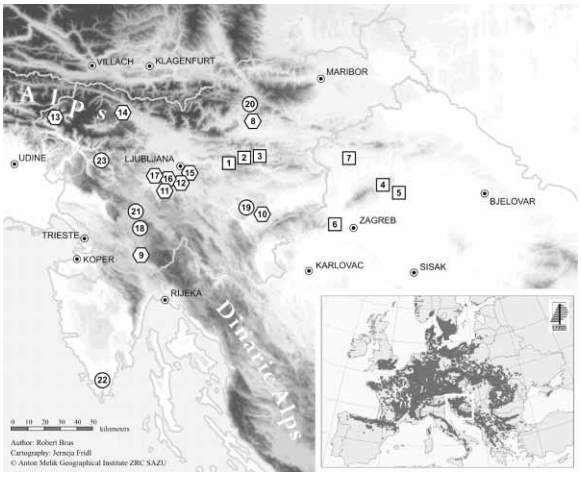

Figure 1. *A map of the south-eastern Alps and north-western Dinaric Alps (shaded area) and the location of the sites mentioned in the text: 1 Zagorje, 2 Trbovlje, 3 Novi Dol, 4 Planina gornja, 5 Planina donja, 6 Sveta Nedelja, 7 Radoboj, 8 Velenje, 9 Ilirska Bistrica, 10 Novo mesto, 11 Ljubljansko barje, 12 Črna vas, 13 Bovec, 14 Mlino, 15 Rudnik, 16 Notranje Gorice, 17 Log, 18 Loza, 19 Lukenjska jama, 20 Koprivška luknja, 21 Županov spodmol, 22 Šandalja, and 23 Divje babe I. Squares represent Tertiary fossil remains, hexagons pollen records, and circles macrofossils. The small image shows the natural distribution of European beech (*Fagus sylvatica *L.) (after EUFORGEN (62)).*

Macroscopic plant remains

Macroscopic plant remains such as wood, charcoal or seeds can be regarded as even more reliable proof of the actual presence of a particular tree species because long-distance transport is less likely than in pollen. In several Paleolithic sites in Slovenia and Istria (i.e. in the area of the south-eastern Alps and north-western Dinaric Alps), charcoal pieces of different tree species have been found, mostly in the remains of former fireplaces in caves. Beech charcoal was identified in several Paleolithic sites: in Loza near Postojna *(35)* and in Koprivška luknja near Velenje *(36)* from Gravettian culture but without radiocarbon dating while beech charcoal pieces of exceptional radiocarbon age (uncalibrated ^{14}C ages) were identified in Lukenjska jama near Novo mesto (12.58 ± 0.25 ka ^{14}C BP) *(37, 29)*, Županov spodmol near Postojna (between 12.46 ± 0.07 and 16.83 ± 0.15 ka ^{14}C BP) *(36, 30)* and Šandalja II (Istria, Cro) (21.74 ± 0.045 and 25.34 ± 0.17 ka ^{14}C BP) *(38)*. Beech charcoal from > 38 ka ^{14}C BP was found in the Paleolithic site Divje babe I near Idrija in the mountains of western Slovenia *(39)*, and the most recent paleobotanical research and analyses of layers in this site containing numerous charcoal samples unambiguously revealed a permanent presence of forest as early as the Middle Würm in the entire period from approximately 80 to 40 ka BP *(40)*. In addition to the different conifers that prevailed in vegetation, deciduous species including beech grew in the vicinity of Divje babe I site without any doubt. The presence of beech is always recorded in the warmer intervals of this period and absent in colder periods, but it again shows that it survived cold periods in close vicinity to the site. Its survival during severe climatic conditions of the cold Würm periods must have been enabled by particular adaptations, including late flushing and resistance to low winter temperatures. Indeed, the beech provenance Idrija from this area proved to be an extremely late flushing one, even on a European scale *(41, 42)*, but the relation of this unexpected behavior with plausible refugia in this area is yet to be explained and will need further research, including a long-term study of climatic and site conditions, testing of more provenances from this area, and studies of their genetic structure and adaptive traits such as flushing.

Genetic data

With the use of isozyme gene markers, a large number of beech populations from south-eastern and a large part of central Europe were analyzed to investigate their genetic structure and differentiation *(20, 43, 44, 45)*. These studies revealed differences in allele frequencies among regions in several marker loci. Some alleles were specific for one or a few adjacent regions and most alleles were found in the south-eastern part of the Balkan Peninsula. Some rare alleles such as *Mdh-B*^{109} were more frequent in the south-eastern Alps, north-western Dinaric Alps and central Europe, while extremely rare in the Balkan

Peninsula, and several rare alleles (e.g. *Px-B*^{52}, *Mnr-A*^{52}, *Mdh-A*^{135}, *Mdh-A*^{101}, *Mdh-A*^{88}, *Mdh-B*^{78} and *Pgi-B*^{126}) showed geographical trends and were exclusively or predominantly present in the central and/or eastern Balkan Peninsula *(43)*. Comparing allelic profiles, the southern-Balkan populations showed more similarities to Calabrian populations than to those from central Europe including the south-eastern Alps and north-western Dinaric Alps. This also supports the independent post-glacial development of central European populations. In the studied area of central and south-eastern Europe, the clinal course of genetic variation becomes clearly apparent in the direction from north-west to south-east. The highest levels of genetic multiplicity and differentiation were found in the populations from the southern Balkan Peninsula, whereas genetic diversity was largest in the north-western populations *(43)*. Based on genetic distances, a rough combination of studied populations into two groups is indicated: the first and larger group comprises populations from the north-western part (south-eastern Alps and north-western Dinaric Alps) and that more similar to those from central Europe; populations from central Bosnia and Herzegovina show an intermediate position; and the second group comprises populations from the central and eastern part of the Balkan Peninsula *(20, 44, 43)*, which, to a large extent, coincides with the area of the putative taxon *Fagus moesiaca* Czeczott. However, a neighbor-joining tree based on pairwise F_{ST} failed to clearly separate these two clades and the transition between the Balkan Peninsula and central Europe populations was interpreted as clinal and formed through isolation by distance *(45)*. In another study, the populations from the north-western Dinaric Alps and low Pannonic mountains, having all the characteristics of central European beechwoods, were found to be clearly separated from the south Balkans, but also from Biokovo and Istrian populations *(7)*. These findings indicate possible local and independent post-glacial development of beech populations in the south-eastern Alps and north-western Dinaric Alps, as well as populations from the central and southern Balkans. More recently, across the whole beech range three main groups of haplotypes were detected with the use of cpDNA markers: one in the Apennine Peninsula, one in the southern Balkan Peninsula, and the third throughout the rest of Europe including the south-eastern Alps. In this study, the area of the south-eastern Alps was recognized as a very important refugial area of beech *(22)*.

Phytogeographical and phytosociological data

The post-glacial migration patterns of European tree species are mainly inferred from pollen and plant macroremains and sometimes supported by genetic data. For European beech, a combination of paleobotanical and genetic data across the species range was first used by Magri *et al*. *(22)*. There are, however, other important types of data that can indirectly support or confirm the reconstruction of the glacial and post-glacial history of certain tree species. Until recently, phytogeographical and phytosociological data from other plant species were widely overlooked and not considered in studies of post-glacial development of beech. In this study, the species richness and the distribution of several taxonomically isolated and stenochorous herbaceous species abundant in the beech forests of the studied area were analyzed. Recent Illyrian beech forests, which are to a large extent distributed in the area of the south-eastern Alps and north-western Dinaric Alps, are characterized by high species richness. It is highest in Croatian beech forests, and decreases in all directions. Compared to approximately 450 species in Central European beech forest they contain around 700 species (*46, 47*). Of special interest is a separate group of herbaceous species of mesophilous Illyrian forests which have been classified into Illyrian floral elements, but are further differentiated within this group based on genetic, ecological, and chorological characteristics *(48, 49, 50, 51, 52)*. They are taxonomically rather isolated and often endemic to the area of the south-eastern Alps and north-western Dinaric Alps, and are only occasionally present in other parts of Europe. Trinajstić *(49)* defines and designates these species as Illyricoid species and lists 26 forest herbaceous species with such distribution. It is important to note that many of these Illyricoid species are tightly connected with beech, including character-species and diagnostic species of recent beech associations (e.g. Anemono trifoliae-Fagetum, Hacquetio-Fagetum, Vicio oroboidi-Fagetum, Lamio orvalae-Fagetum, Omphalodo-Fagetum) from the Illyrian beech forests, classified into the alliance Aremonio-Fagion (Ht. 1938) Borhidi *(53)*. Such species are *Aremonia agrimonioides* (L.) DC., *Lamium orvala* L. (Figure 2), *Epimedium alpinum* L. (Figure 3), *Vicia oroboides* Wulfen (Figure 4), *Anemone trifolia* L., *Euphorbia carniolica* Jacq., *Hacquetia epipactis* (Scop.) DC., *Omphalodes verna* Moench. (Figure 5) and *Scopolia carniolica* Jacq. The taxonomical and biogeographical status of these species indicate not only their probable Tertiary origin as supposed by Meusel *et al. (54)* and Turill (*55*), but in our opinion their specific and similar distributions, their concentration in the studied area and their tight connection with beech also indicate the possibility that, in the area of their present range, they have been an important component of mesophilous beech forests of whatever type, form or composition for a very long time. However, drawing conclusions from these biogeographical similarities requires some caution. While Borhidi *(56)* supposed the continuous survival of the hypothetical Fagion illyricum alliance (today's accepted name Aremonio-Fagion) from the Tertiary through the Pleistocene, Šercelj *(30)* argued that Fagion illyricum could not have survived the Pleistocene in the present phytosociological species composition. In this context, the evolution of plant communities is a very important issue. According to Whittaker *(57)*, the species are not commited in their evolution to particular communities and they change their associations with other species in evolutionary time. As a consequence of individualistic response of taxa to temporal environmental changes, com-

munities and vegetation units only merge as temporary assemblages of species, and past climates resulted in communities unlike any modern community *(58)*. From this it seems quite clear that beech associations that occurred in the Pleistocene were compositionally different than the recent communities which are classified into the Aremonio-Fagion alliance. On the other hand, many members of present-day phytocenoses have been associated for a long time, which is contradictory to a purely individualistic concept; according to Deil *(59)*, the reality lies in between 'co-evolved communities' and 'short-term assemblages'. In their site demands, the Illyrian species do not comprise a homogenuous group *(60)*, but individual Illyricoid herbaceous species are closely bound to the contemporary occurrence of beech. They often find their niche in the same habitats as beech and are adapted to the rhythm and site conditions which are crucially determined by beech as dominant species.

Moreover, Illyricoid herbaceous species are absent or very rare in other types of forests where beech is not present. Even if we know that during glacial stadials of the Pleistocene the ecological conditions were different from those in interstadials or early Holocene and if we assume that species evolve toward difference in both niche and habitat *(57)*, we can still expect some degree of such co-existence of these species as far in the past as the Pleistocene or during colonization, as supposed for other tree species such as silver fir *(61)*. Beech has likely only survived in multiple small areas in isolated populations forming different plant communities which were probably species-poor and certainly differed substantially from those today, but containing individual Illyricoid species as well. The likely variation of these communities is supported by the fact that beech is a very plastic species that occupies many different forest sites; in Slovenia, it is part of numerous associations with completely different floristic compositions. It is therefore possible that the communities from the Aremonio-Fagion alliance, which include Illyricoid species, only developed during the Holocene, much later than during the Pleistocene.

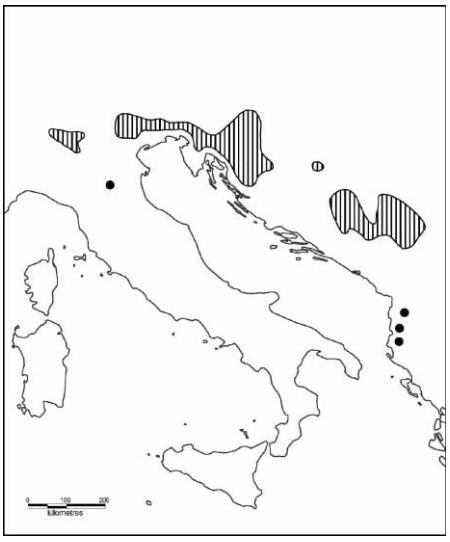

Figure 3. *The distribution of* Epimedium alpinum *L. (after 49).*

High species richness of recent beech forests of the studied area, the characteristics of Illyricoid species and the fact that most of the species which are particularly tightly connected to beech forests are found among Illyrian species *(60)* in our opinion speak in favor of the hypotheses that beech has indeed survived the Pleistocene in the area of south-eastern Alps and north-western Dinaric Alps.

DISCUSSION AND CONCLUSIONS

Certainly, caution is needed when drawing conclusions from paleobotanical remains including pollen data and attention should be paid to the choice of the paleodata used. Such data may be locally affected by several factors, including the heterogeneous quality of pol-

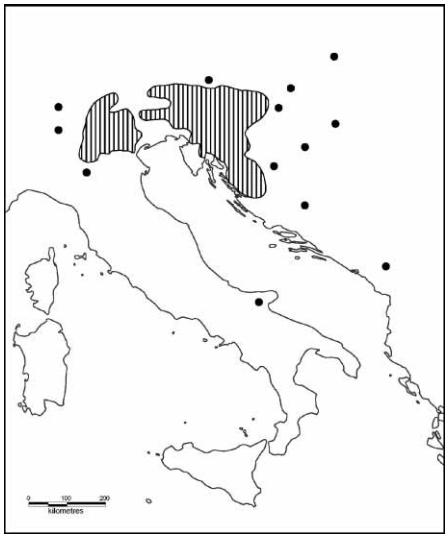

Figure 2. *The distribution of* Lamium orvala *L. (after 49).*

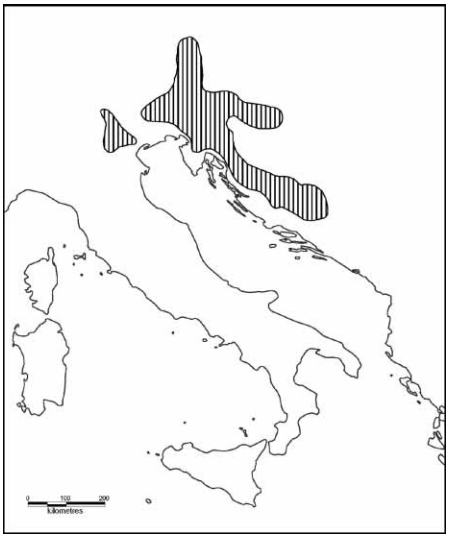

Figure 4. *The distribution of* Vicia oroboides *Wulfen (after 49).*

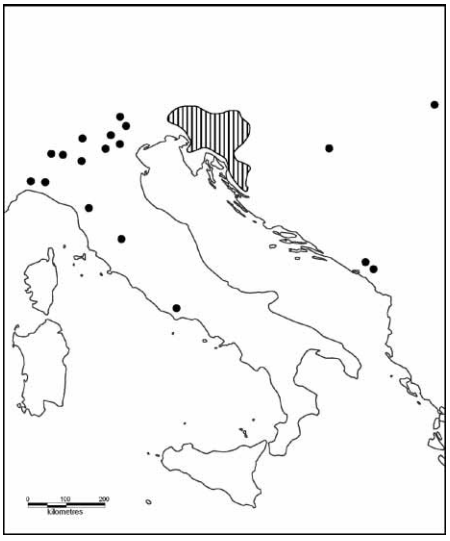

Figure 5. *The distribution of* Omphalodes verna *Moench (after 49 and 63).*

len data, sampling methods, pollen sums, determination criteria, taxonomic nomenclature, and the heterogeneous quality of chronological control *(64)*. The only reliable chronological guide is radiocarbon dating. Unfortunately, most of the Late Pleistocene sediments from the studied area are mineralogenic and unsuitable for radiocarbon dating *(29)*. In this review, most of the records where the ^{14}C dating of the wood, charcoal or organic substance in the sediment was possible, were included; however, in some cases only estimation is cited. Despite these general limitations, the large number of different paleobotanical remains and their good agreement suggest the presence of at least small isolated beech populations that might have survived the Pleistocene glaciations. Due to the geographic position of this area and a range of geological, geomorphological, and climatic conditions where Mediterranean, alpine and continental climates converge in a very small area, the existence of protected, south-facing microsites could well have enabled the survival of small populations or groups of beech. The continuous occurence of beech pollen throughout the middle and late Würm in the location Azzano Decimo in the plain of Friuli *(65)* and in Euganean Hills near Padova *(66)* in north-eastern Italy indicates the continuous survival of reduced and sheltered beech populations relatively close to the south-eastern Alps and north-western Dinaric Alps. Since the see level is presumed to have been about 100 m lower in Pleistocene than today *(30)*, these two areas were not separated from south-eastern Alps by the Adriatic see as today and formed a more united area of mid-altitudes which are believed to have offered the warmest conditions in the Pleistocene.

The presented data also support the local development of beech forests after the glacial period. As indicated by early and very high pollen concentrations, the local expansion of beech populations in the early Holocene was very fast and must have happened in conditions similar to those today. At present, European beech still grows in optimal conditions in this area. In Slovenia, beech is the basic structural element of most forest associations, and the most widely spread tree species, found on 89% of the total forest area and presenting 32% of the total growing stock *(67)*. Some of the Illyricoid species are also conserved as a minor component of mesophilous beech forests in adjacent parts of Europe, such as northern Italy, Austria, Hungary, and the north-western Balkan Peninsula, but nowhere combined as in the south--eastern Alps and north-western Dinaric Alps, and are always much less abundant *(49)*. This distribution pattern indicates that they likely spread to these adjacent areas following beech in its postglacial migration, but with a considerably slower migration rate. Traditional palynology-based estimates of postglacial beech migration rates in Europe are estimated to 200–300 *(8)* and 150–500 *(58)* m/year, while more recent research suggests migration rates between 100 and 150 m/year *(68)*. On the other hand, the recorded migration rate for the studied herbaceous woodland species was less than 1.25 m/yr in extant forests of northern Europe *(69, 70)*. These figures demonstrate that the migration of tree species is many times faster than that of herbaceous species. This suggests that the Illyricoid herbaceous species have not had enough time to migrate to their present range from other areas such as the Balkan Peninsula and would certainly have not had sufficient time to expand locally after their arrival in the Holocene. Besides, at present these species are absent from most of the Balkan Peninsula and if they would have migrated north-west, there is no explanation why they would completely disappear from the areas which they originally occupied and where beech is abundant today. Instead, the local glacial survival and development of Illyricoid species within their present range seems to be a much more probable explanation. Phytosociological and phytogeographical characteristics of herbaceous species closely bound to beech communities can therefore indirectly support the continuous survival of beech in the area of the south-eastern Alps and north--western Dinaric Alps in the Pleistocene, as well as its local development in the Holocene.

In addition to this local development, it seems that these European beech populations have played an important role in the colonization of central and western Europe in the Holocene. Previously it was believed that beech spread in the postglacial period to parts of central Europe from the central and southern Balkan Peninsula. The migration from the Balkan Peninsula, where extensive beech glacial refugia certainly existed, to central Europe was most likely only possible along the slopes of the Dinaric mountain chain, and along the Carpathian Mountains. In comparison with the Carpathian arc, the Dinaric mountain chain offers a shorter way from the Balkan Peninsula to central Europe. It is mainly situated between the Pannonian plain, which had a continental climate and very likely cold and dry conditions in the early Postglacial, creating unsuitable conditions for the spread of beech, and today's Adriatic. Moreover, in the

area of Velika Kapela, between Rijeka and Karlovac, where the Dinaric mountain chain becomes very narrow, there was probably a bottleneck for massive south-east-northwest migration and the spread of beech in that direction could not have been very expansive. But as suggested earlier *(20)*, even if movement in this direction was possible, the area of the south-eastern Alps and north-western Dinaric Alps would already have been occupied with locally developed beech populations. Genetic differentiation of beech populations in the Balkan Peninsula, the distribution ranges of Illyricoid herbaceous species, and the open question of the south-eastern border of the distribution area of the fir-beech communities, classified into the association Omphalodo-Fagetum *(71)* even indicate the possibility that beech spread in the southeast direction to some extent and met with the locally developing or northwest migrating southern populations in certain parts of central Balkan Peninsula. The above presented evidence largely supports the conclusions in a study which combined genetic and fossil data across the whole species range *(22)*. Furthermore, this study shows that phytosociological and phytogeographical characteristics of herbaceous forest species can successfully support other datasets in reconstructing the history of a certain tree species, including beech.

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