

# Extra-Mediterranean Refugia, Post-Glacial Vegetation History and Area Dynamics in Eastern Central Europe

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**Abstract** Evidences from fossil records and genetic research suggest that the arboreal refugia were not restricted to Southern Europe and in particular to the Mediterranean peninsulas during the full-glacials. Fossil pollen data and macrofossil remains indicate that several tree species have survived also at the Southern edge of the cold-dry steppe-tundra area in Central and Eastern Europe. Recent results of surveys on the Late Pleistocene Mammalian fauna clearly contradict to the “*tree-less tundra*” models for Europe North of the transverse mountain ranges of the Pyrenees, Alps and Carpathians. It was pointed out that the carrying capacity to feed the herds of large herbivores demands a rather productive environment. The presence of Northern temperate refugia is also supported by the “non-analogue” assemblages of small mammals discovered from the Late Pleistocene of unglaciated areas of Eastern Central Europe. The assembly of species today typifying the tundra, steppe and semi-desert habitats seems to include also species from deciduous woodland. Extra-Mediterranean core areas were identified also in widely dispersed cold-tolerant frogs and reptiles. Some of their core areas had been at least near the Carpathians and/or marginal areas of the Carpathian Basin. The close faunal connections of the Carpathians suggest the existence of highly dynamic contacts and exchanges with mountains of the Balkan Peninsula during the climatic fluctuations of the Upper Pleistocene. The Eastern and Southern Carpathians, together with the mountains of Western Transylvania, can be considered as core areas of survival and autochthonous evolution in some invertebrate groups with limited mobility. The post-glacial re-population of the Carpathian Basin from different directions has been supported by Illyrian versus Dacian vicarious pairs of sister species/subspecies. In mobile insect groups, peripherically isolated sibling species/subspecies have only been evolved, which display manifold biogeographic connections, e.g. to the Balkan Peninsula, Asia Minor or Southern Russia. The organisation of community-complexes of the Pannonian forest-steppe

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connected by habitat ecotones resulted in the overlap of several different faunal types, e.g. Mediterranean, Balkanic, Siberian, Ponto-Caspian, Ponto-Pannonian, Turano-Eremitic and Xeromontane elements.

## 1 Introduction: Refugia and Core Areas of Dispersal

### 1.1 *The Basic Components of the European Fauna*

Traditional biogeography has been loaded with a seemingly endless discussion on the principles and methods of the biogeographical characterisation of species. In the geobotanical literature, the purely chronological (*geoelements*) and the historical approaches (*geno-*, *migro-* and *chrono-elements*) have regularly been clearly disentangled (e.g. Walter and Straka 1970). In the zoogeographical literature, the term “faunal element” or “faunal type” has repeatedly been used for both approaches, often with a mixture of points of view. Faunal types have often been differentiated on the basis of the shape and the extension of the ranges (e.g. the “Central European”, “Palearctic” or “Holarctic”, etc. faunal elements in many faunistic publications). Quantitative methods of biogeography based on large databases have only rarely been used. Dennis et al. (1991) differentiated some types of endemic versus “extent” (i.e. widespread) species of butterflies, and have outlined some “*faunal structures*”, based on multivariate methods. As opposed to these methods, the European fauna has traditionally been subdivided into a “*holothermic*” refugial and a “*holopsychric*” invasion types (Rebel 1931). In addition, these faunal types have been characterised by some “*core areas*” (in German: *Arealkerne*, *chorologische Zentren*: Reinig 1950; de Lattin 1957, 1967) and interpreted as areas of survival (refugia) and, consequently, as “*centres of dispersal*” (“*Ausbreitungszentren*” in the German tradition).

The “*holothermic*” type was differentiated according to the secondary subdivision of the large Mediterranean refugial area (de Lattin 1949, 1957, 1967; Reinig 1950). Recently, this view was strongly confirmed and modulated by the growing molecular results and re-formulated as repetitive patterns of the generalised “paradigms” of core areas and tracks of post-glacial re-population. A general conclusion was that temperate species mainly derive from Mediterranean refugial populations that underwent range expansion in the late glacial and early post-glacial periods (Hewitt 1996, 1999, 2000, 2001, 2004; Taberlet et al. 1998; Schmitt and Hewitt 2004; Schmitt 2007). The other main group, the “*holopsychric*” type has been considered for a long time as a result of the “Siberian” invasion, suggested by some “classical”, monoglacialisitic biogeographical works (Hofmann 1873; Scharff 1899) and despite the evidences which have revealed the taxonomical differentiation of North-Eastern “boreal” and Southern European montane populations, especially in some butterfly species (Varga 1975, 1977; Nève 1996). Several authors (e.g. Schmitt and Seitz 2001; Steward and Lister 2001; Surget-Groba et al. 2001; Babik et al. 2004;

Ursenbacher et al. 2006; Saarma et al. 2007), however, have suggested an additional mode of colonisation of central and Northern Europe by *non-Mediterranean* populations, coming from one or more “continental” refugia: central Europe, Southern Ural, Caucasus and Western Asia. Other species exhibit mixed patterns, where different parts of Europe have been colonised both from Mediterranean and/or non-Mediterranean refugia (e.g. Fumagalli et al. 1996; Deffontaine et al. 2005; Kotlík et al. 2006).

## 1.2 *The Geographical Projection of the Faunal Type Frequency Data*

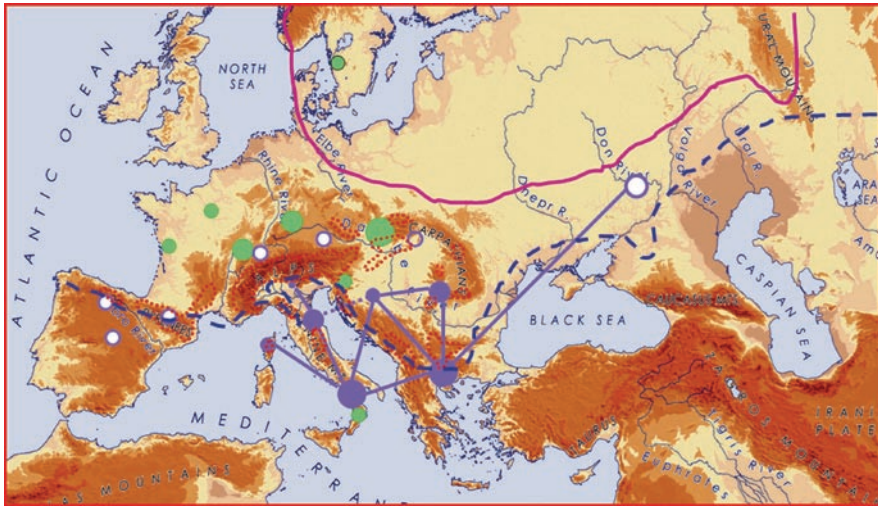
The faunal composition of formerly glaciated and therefore, nearly exclusively post-glacially re-populated Northern Europe is practically identical with North-Eastern Europe and Western Siberia which were considered as a main argument for being re-populated mostly from the East (Rebel 1931; de Lattin 1957, 1967). This major part of Europe clearly shows a high percentage of the “Siberian” faunal type in all mobile groups of animals such as birds (Stegmann 1932, 1938; Voous 1960, 1963) and butterflies (Reinig 1950; de Lattin 1964, 1967, see: Fig. 59, in Kostrowicki 1969; Fig. 1). This faunal type is also strongly represented in Central Europe, North of the Alps, being the prevailing faunal type mostly in the mountainous regions (e.g. Harz Mts., Bavarian and Bohemian forest, Sudetic Mts., etc.). In contrast, South of the large transversal chains of the Pyrenées, the Alps and the Northern Carpathians, the pre-dominance of the Mediterranean faunal type *sensu lato* has been demonstrated, with a decreasing gradient into Northern direction being extremely steep at the Pyrenees and partly North of the Alps and the Carpathians, but much more gently sloping from the Balkan peninsula to the Carpathian Basin. As a consequence of the overlapping of the different biogeographical influences, there is a transitional belt in Southern Central Europe including a large part of the Carpathian Basin where the proportions of the different faunal types are rather balanced (de Lattin 1967; Varga and Gyulai 1978; Varga 1995, 2003b, 2006).

Several consequences follow from this general biogeographical setting of Europe.

- In Europe, the highest number of endemic species is confined to some, mostly mountainous parts of the Mediterranean peninsulas (e.g. Williams et al. 1999; Finnie et al. 2007). These areas, more or less, regularly overlap in the different taxonomical groups; thus they can be considered as hotspots for endemism, and at the same time, they were the main areas of survival during the Quaternary glaciations. These areas often show also a high level of “multi-species genetic divergence” (Petit et al. 2003).
- On the other hand, there are ecologically transitional regions with high numbers of species, but without a high proportion of endemism (Williams et al. 1999). These are characterised by an overlap of the ranges of species of different

geographical origins caused by dispersal processes along gradients, e.g. the overlap of species belonging to different zonobiomes and azonal communities in the forest-steppe areas of the Carpathian Basin (Varga 1995). Recently, these areas have been identified as “melting pots” of genetic diversity (Petit et al. 2003) due to the secondary accumulation, re-distribution and re-combination of genotypes.

Another important observation was made by de Lattin (1957, 1964) who indirectly defined the “Siberian” species by their absence in the supposed Mediterranean refugial areas. These species show a peculiar “crowding” (de Lattin’s “*Stauungslinie*”) at the Northern boundary of the Mediterranean region. The re-interpretation of this biogeographical line subsequently followed in two steps. First, it was recognised that accumulated occurrence of marginal sub-species of continental species was shown around this line (Varga 1975, 1977), and later on, they were confirmed as multiple extra-Mediterranean refugia of continental species (Schmitt 2007; Schmitt et al. 2007) (Fig. 1).



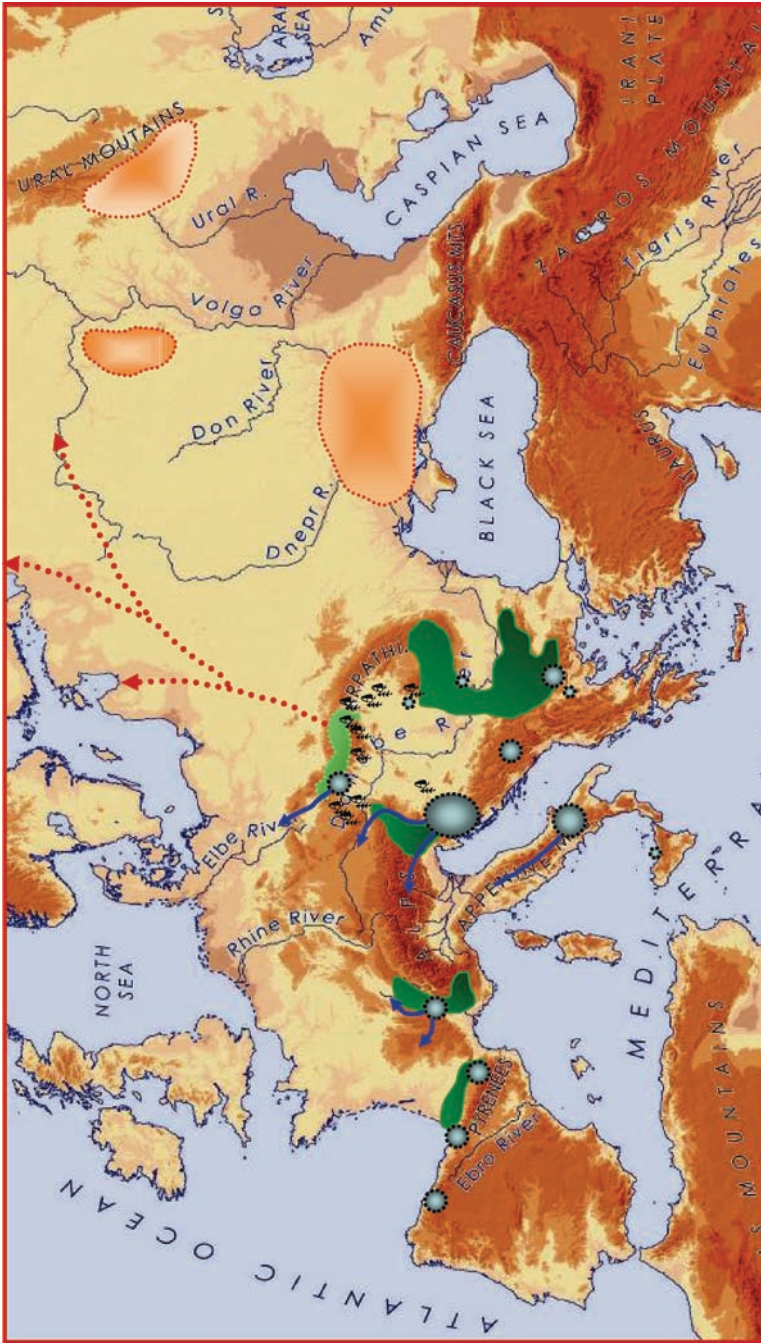
**Fig. 1** Important characteristics of biodiversity in Europe, compiled from various sources. *Purple line*: Southern and Western border of the high (>40%) representation of the Boreo-Continental (= Siberian) faunal elements (de Lattin 1967; Kostrowicki 1969). *Blue line*: Southern border of the expansion (“*Stauungslinie*”) of the Boreo-Continental (= Siberian) faunal elements (de Lattin 1967). *Red dots*: important mountain arboreal refugia (compiled from different sources). *Light blue circles*: core areas of the multispecies genetic divergence of the 25 European forests. *Full circles*: divergence higher than average, *empty circles*: lower than average. *Continuous lines* indicate high divergence, *dotted lines*, intermediate divergence (re-drawn and simplified from Petit et al. 2003). *Green circles*: mean number of haplotypes per forest, averaged across species. Diversity is highest at relatively high latitudes, North of the three European peninsulas (re-drawn and simplified from Petit et al. 2003)

### 1.3 The Geographical Projection of the Genetic Diversity Data

It is not only the number of the species, but also some characteristics of the genetic diversity that show the highest values in the “transitional” belt mentioned above. Based on the chloroplast DNA variation in 22 widespread European trees and shrubs, it was pointed out that despite their “individualistic” migration behaviour, diverse ecological requirements (from the Southern temperate to the Southern boreal zone) and different modes of seed dispersal, significant species of the woody flora of Northern Central Europe exhibited an essentially congruent pattern of genetic divergence (Petit et al. 2003; Fig. 1). Their genetically most unique populations are found in Southern and central Italy, Corsica, and the Balkan Peninsula extending into Northern Italy, the Northern Balkans and the Southern peripheries of the Carpathian Basin. However, this increased diversity is obtained mostly through the redistribution (“melting pot”) of the genetic information already present in the populations in refugia (the actual “hot spots”, i.e. areas where the diversity was evolved). Recent work on the genetics of oak populations has revealed that the existence of particular haplotypes in Romania resulted either from older indigenous relict populations or from crossing of populations originating from more than one refugium. There were several low or medium mountains North of the Balkan Peninsula that could have offered favourable climatic conditions during the Younger Dryas period to support viable populations of oak trees. At the beginning of the post-glacial times, the Carpathian Basin may have acted as a meeting point of several colonisation routes (Bordács et al. 2002; Petit et al. 2002). These genetic data are also supported by recent fossil findings of tree remains from the last full glacial period, North of the Mediterranean peninsulas. Fossil pollen data and macrofossil remains such as charcoals from the time of the last glacial maximum, i.e. 25,000–17,000 years ago, indicate that several tree species remained in small favourable pockets not only within the Mediterranean region, but also at the Southern edge of the cold and dry steppe-tundra area in Eastern, central, and South-Western Europe (Willis et al. 1995, 2000; Carcaillet and Vernet 2001).

Research on small-mammal mtDNA has also questioned the universality of Mediterranean refugia as the areas from which all temperate taxa colonised central and Northern Europe at the beginning of the present interglacial period. It was suggested that the Mediterranean “sanctuaria” (Widmer and Lexer 2001) in general were *not* also core areas of post-glacial expansion into deglaciated areas. Thus, a need for new paradigms for the phylogeography of cold-resistant arboreal species has been formulated, as well (Steward and Lister 2001). It was shown that Mediterranean populations of the shrews *Sorex minutus*, *Sorex araneus* and bank voles (*Chlethrionomys* spp.) did not contribute to the present-day gene pools in Central Europe (Fumagalli et al. 1996; Bilton et al. 1998). Instead, populations in Central Europe and Western Asia have participated suggesting the existence of glacial refugia in these regions. The central European evidences fit well with the botanical results from Hungary and the records of temperate mammals within cold-stage assemblages of central and Northern Europe (Fig. 2).





**Fig. 2** Important extra-Mediterranean refugia, compiled from various sources. *Dark green fields*: European coniferous forest refugia as revealed by Schmitt and Haubrich (2008). *Light green field with brown arrows*: the Northern Carpathian arboreal refugium with expansion routes of boreal species (coniferous trees, brown bear, etc.). *Light green field with blue arrows*: from various sources. *Grey circles with black outlines*: refugia of the beech (*Fagus sylvatica*) with important post-glacial expansion routes (re-drawn from Magri et al 2006; Magri 2007). *Light brown patches*: Eastern European boreal forest refugia during the LGM (from various sources)

## 2 The Basic Types of Zonal Setting in Europe: Glacial Vs. Interglacial

### 2.1 *The Notion of the Boreal Forest-Steppe as the Macro-Ecotone of the Mammoth Steppe and the Boreal Forest*

The Pleistocene glacial-interglacial cycles have resulted in the “*antagonistic dynamics*” of biota belonging to contrasting macrohabitats (de Lattin 1967, p. 356). Thus, principally, two basic types of zonal setting can be distinguished. The inter-/post-glacial (but also interstadial!) type can be characterised by the expansion of the *Arboreal* and regression of the “*non-Arboreal*” macrohabitats. As a result, the “open” macrohabitats (tundra, steppe, semi-desert and high mountains) have been separated by wooded zonobiomes, such as boreal and nemoral forests. Significant belts of macro-ecotones have been developed at the edges of the forested belts, e.g. forest-steppe as a transitional habitat type between the nemoral and steppic zones, subdivided into a sub-mediterranean (Pannonian) and a continental sub-type (Zólyomi 1949; Sjors 1963; Walter and Straka 1970; Varga 1995; Fekete and Varga 2006).

Thus, the glacial periods (stadials) have been characterised by a regression plus fragmentation of wooded habitats and consequently, by a broad contact of the tundra and the steppe zonobiomes with some forested “pockets” North of the refugial belt of the Mediterranean area. The transitional “macro-ecotones” developed at the forest-belt fringes: tundra-taiga and boreal forest-steppe (e.g. in Pannonian region). Recently, cold steppe vegetation with scattered boreal coniferous forests have been revealed during the cold stages in S Moravia, the SE margin of the Alps, E Hungary, parts of Romania (Carpathians), etc. (Rybnicková and Rybnicek 1991; Willis et al. 2000; Pokorný and Jankovská, 2000; Sümegei and Rudner 2001; Wohlfahrt et al. 2001; Björkman et al. 2003; Tantau et al. 2003; Willis and Andel 2004; Feurdean et al. 2007a,b). The presence of these Northern temperate refugia justifies the arguments for the so-called *non-analogue* assemblages of mammals described from the Late Pleistocene in unglaciated areas of the Northern hemisphere.

The Würm glaciation had at least six maxima, the last one taking place about 22.000–18.000 years BP. The Last Glacial Maximum (LGM) was extremely continental and ended in rapid climatic fluctuations. The late Würm *kryoxerotic* period was characterised by the expansion of cold-continental *heliophyta* and steppic species (Iversen 1958; Tarasov et al. 2000; Velichko et al. 2002). Pollen-based “treeless tundra” models for Europe North of the transverse mountain ranges of the Pyrenees, Alps and Carpathians (e.g. Frenzel 1992; Huntley and Birks 1983; Huntley and Allen 2003) have repeatedly been questioned by researchers of the late Pleistocene mammalian fauna (Kretzoi 1977; Guthrie 1990, 2000; Guthrie and van Kolfschoten 1999; Simakova 2001; Yurtsev 2001; Steward and Lister 2001), because the carrying capacity sufficient to feed numerous large herbivores such as the

mammoth, the woolly rhinoceros, the reindeer, the giant deer, the bison or the aurochs demands a very productive environment (“steppe-tundra” or “mammoth steppe”, Guthrie 1990), like the cold-continental meadow steppes in Southern Siberia and Northern Mongolia (Varga et al. 1989).

Although the East-West faunal movements between the Western and Eastern temperate refugia (see: nemoral disjunctions!) were hindered during the last glaciation, the tundra-steppic areas of E Europe and the mountain belts of Central Asia were connected to each other. Thus, *non-analogue communities* were composed by mixing tundra, steppic and eremic-oreal elements (e.g. *Lemmus* and *Dicrostonyx* spp. together with *Citellus* spp. and *Allactaga*, *Sicista*, *Lagurus*, *Marmota* and *Ochotona*). This boreal forest-steppe habitat type appears to have included also cold-tolerant species of temperate habitats, e.g. *Clethrionomys glareolus*, *Apodemus sylvaticus* and *S. araneus*. Extra-Mediterranean core areas have also been revealed in several, widely dispersed cold-tolerant frogs and reptiles, as *Rana arvalis*, *Zootoca vivipara*, *Vipera berus* (Surget-Groba et al. 2001; Babik et al. 2004; Ursenbacher et al. 2006; Kotlík et al. 2006; Saarma et al. 2007).

### 3 European Refugia of Boreal Species

#### 3.1 Biogeographical Definition and Sub-Division of Boreal Species

The species of the boreal zone show a significant diversity of extension and taxonomical structure of ranges. Most boreal taiga-species are widely distributed from the Far East across Siberia to Scandinavia, often without significant geographical variations. They are partly inhabitants of forests but are often connected with peat bogs, e.g. due to the food-plant specialisation (e.g. the butterflies and moths *Colias palaeno*, *Boloria aquilonaris*, *Plebejus optilete*, *Anarta cordigera*, *Arichanna melanaria*). Vicarious taxa often occur in Southern Himalayan coniferous forests with dense scrub layer and undergrowth, rich in evergreen plant species (e.g. *Rhododendron*, *Vaccinium* spp.). Also, some boreal plant species complexes have a huge Holarctic or Eurasiatic range while their closest relatives are restricted to some Southern mountainous areas, as parts of the Himalaya, Tibet, etc., e.g. the boreal species complex consisting of the circum-boreal *Saxifraga hirculus* and the related spot-like Central Asiatic species: *S. diversifolia*, *S. przewalskii* and further species in Tibet. In other cases, the zonal boreal “taiga” distribution is combined with considerable disjunct ranges in the sub-alpine mixed coniferous forests of the Himalayas (e.g. several small passerine birds as *Dumeticola thoracica*, *Luscinia calliope*, *Muscicapa sibirica*, *Phylloscopus proregulus*, *Tarsiger cyanurus*) and/or with several larger or smaller spots in the European mountain coniferous belts, e.g. in many taiga-inhabiting birds, as *Tetrao urogallus*, *Tetrastes bonasia*, *Strix uralensis*, *Aegolius funereus*, *Picoides tridactylus*, etc. (Stegmann 1938; Voous 1963).



Such species are most richly represented in the coniferous zone of the South Siberian high mountains.

The number of (nearly) exclusively European boreal and boreo-montane species is relatively low. However, a molecular biogeographical analysis of such species can unravel the European coniferous forest refugia (Schmitt and Haubrich 2008). The existence of European coniferous forest refugia is also supported by the *Western-Eastern* sub-division of several boreal species with the Western populations obviously having European refugia during the last glaciations, e.g. *Picea abies* most probably in the mountains of the Balkans and in the Eastern and Southern Carpathians. The North-Eastern part of European Russia was populated from the East by the sister (sub-)species *Picea obovata*. In the catchment area of the Northern Dvina, a hybrid belt has been formed between them. The European *Pinus cembra* survived the LGM in Southern Alpine and Carpathian refugia (Willis et al. 2000; Wohlfahrt et al. 2001). Its sister species is the Siberian/Northern Mongolian *Pinus sibirica*, a dominant species of the light-penetrated mountain taiga, often mixed with *Larix sibirica* (Walter and Breckle 1986).

### 3.2 Carpathian–Balkan Boreo-Montane Arboreal Refugia

It is known since several decades that the Southern part of the Carpathian Mts. was a refugial area for temperate and mountain forest taxa during the last glacial period (Huntley and Birks 1983). The Eastern and the Southern Carpathians have been repeatedly pointed out as important glacial refugia, from which trees started to expand at the beginning of the Holocene (e.g. Huntley and Birks 1983; Bennett et al. 1991; Willis 1994). In particular, Willis et al. (2000) indicated that temperate refugia in Europe during cold periods might not have been restricted to the three Southern peninsulas (Iberia, Italy and the Balkans) because trees were undoubtedly present in Central Europe in areas such as the Carpathian Basin during the last cold stage. Radiocarbon data indicate the continuous presence of coniferous woodland not only during the relatively mild period from 35 to 25 kyr BP (thousands of radiocarbon years before the present), but also into the more severe last glacial maximum 25–17 kyr BP (Sümegei and Rudner 2001; Willis and Andel 2004).

The existence of full-glacial forests in Eastern Europe during the LGM (Willis et al. 2000) has often been questioned, but it has also been repeatedly confirmed by several macrofossil and palynological studies from the Carpathians (e.g. Farcaş et al. 1999; Björkman et al. 2003; Tantau et al. 2003; Willis and Andel 2004; Feurdean et al. 2007a) demonstrating the survival of most coniferous and cold-resistant deciduous trees or even the beech (Magri et al. 2006, Magri 2007) in refugial “pockets” in the hilly areas of the Carpathians or North of them. Similarly, forest refugia were also found in Southern Moravia, in the Eastern Alps, in the Dinaric Mountains and in the Eastern Balkans, etc. (Willis 1994; Willis and Niklas 2004).

The climatic conditions in some favourable localities of these regions could not have been as severe as those in Northern and central Europe during the LGM and during the beginning of the last deglaciation.

In the NE Carpathians (Mt Gutaiului), *Pinus mugo*, *P. sylvestris* and later on also *Larix* became established from 14,500 year BP onwards (Wohlfahrt et al. 2001; Björkman et al. 2003). Between 14,150 and 13,950 years BP, *P. cembra* have replaced *P. mugo* and *P. sylvestris*. At 13,950 cal year BP, the tree cover increased and *Picea* appeared for the first time, together with *P. cembra*, *P. mugo* and *Larix decidua*. The analysis of the sediments of the peat bog “Mohos” in the Eastern Carpathians (Tantau et al. 2003) has shown that an open boreal forest was dominated by *Pinus* during the last phase of the LGM. The presence of *Picea* pollen refers to its existence in a local refugium. The pollen data at the end of the late Weichsel indicate that beside the dominant *Pinus* and *Betula* species, *Alnus*, *Ulmus* and *Picea* also occurred in the area. The increased representation of *Alnus* at about 14,150 year BP and that of *Picea* and *Ulmus* between 13,750 and 13,200 years BP is interpreted as a consequence of nearby refugia of these trees. Beech pollen was dated in the North- Eastern Carpathians (Semenic Mts.) to 9,500 year BP while in most other diagrams for the Romanian Carpathians, it was registered between 7,500 and 8,000 years BP. From the late expansion of *Quercus*, *Tilia*, *Fraxinus*, *Acer* and *Corylus* between 10,750 and 10,200 years BP, it was concluded that these trees had to immigrate into the area from refugia further away. However, these refugia cannot have been situated very far from the Carpathians. It seems most likely that these refugia were located further to the South in Romania, or in lower hilly areas of the Carpathian Basin (Feurdean et al. 2007b). Several surveys across Hungary (Rudner and Sümegei 2001; Willis et al. 2001) from about 30 sites clearly demonstrate that cyclically recurring forested habitat developed in the Carpathian Basin during the late Weichselian, although this forest type might have been of an open forest or steppe forest/forest-steppe type. These forests or forest-steppes were of the boreal type mostly with cold-tolerant trees as *Picea*, *Larix*, *Pinus sylvestris* and *P. cembra*, *Betula*, *Carpinus*, *Salix* and *Juniperus communis*.

In Bátorliget, North-Eastern Hungary, a light-penetrated taiga forest and a cold steppe with *Artemisia* spp. dominated during the last cold phase of the Weichselian glaciation. However, it has also been demonstrated that some deciduous trees such as *Quercus*, *Ulmus*, *Alnus* and *Tilia* survived in meso/microclimatically favourable “pockets” of this mosaic landscape (Willis et al. 1995). Later, *Tilia* dominated woodland and a mixture of deciduous trees including *Ulmus*, *Corylus*, *Tilia*, *Fraxinus* and coniferous species (*Pinus* and *Picea*) (Willis et al. 1995, 2000; Magyari et al. 1999) were present in the early Holocene. In a neighbouring area of Romania (Turbuta), pollen of *Quercus* was not found before 12,000 year BP implying that *Quercus* did not survive in the proximity of the study site during the late glacial. Local stands of *Quercus* pollen became established between 12,000 and 11,000 years BP, but its local expansion did not occur until about 11,000 cal year BP and peaked between 10,000 and 8,500 years BP. This is generally simultaneous with the time of *Quercus* expansion in North-Western, Western and South-Western Romania, though in the Eastern Carpathians its expansion was dated to ca.

500 years later (Farcaş et al. 1999, 2004; Björkman et al. 2003; Tantau et al. 2003, 2006; Feurdean and Bennike 2004; Feurdean et al. 2007a).

The fossil and genetic data unanimously indicate that the beech (*Fagus sylvatica*) also survived the last glacial period in multiple refuge areas. Recent publications (Magri et al. 2006; Magri 2007) clearly demonstrate that the central European refugia of the beech were separated from the Mediterranean ones. In addition, the Mediterranean core areas did not contribute to the colonisation of central and Northern Europe. The Illyrian-Slovenian population migrated only to a limited extent Northward to colonise the rest of Europe. This population proved to be genetically similar to the population in Southern Moravia–Southern Bohemia, which is considered to be a possible refuge area on the basis of fossil data. This core area might have been the source for the colonisation of the Carpathians. From a genetic point of view, the populations in the Apuseni Mts. have been characterised by rather high allelic richness (Gömöry et al. 2003). Thus, it is possible that a secondary refugium of the beech was located in this area, which, however, did not significantly contribute to the colonisation of the Carpathian arc.

### ***3.3 Refugia of Cold-Tolerant Invertebrates and Exothermic Vertebrates in Eastern Central Europe***

Vertebrate and Mollusc remains show that the lowest Weichselian loess layers in the Carpathian Basin were formed during the first cool/dry phase of the last glacial, between 50,000 and 70,000 years BP (Hertelendy et al. 1992). The dominance of woodland species decreased, but the tree cover was able to survive the unfavourable environmental changes because, as a result of the mosaic-like environment, some mild and humid micro-climatic areas developed in the foothill zone. On the Tokaj hill, for example, a coniferous forest-steppe was revealed with wildfires in a taiga-like environment during the LGM. Charcoal from *Picea* and podsollic soils were identified (Sümegei and Rudner 2001).

Between 22,000 and 20,000 years BP, a decline of thermophilous gastropod species and expansion of a kryo-xerophilous, *xeromontane* element were observed (Sümegei and Krolopp 2002; Füköh et al. 1995). The occurrence of *Vallonia tenuilabris* was shown together with the boreo–Alpine/montane *Columella columella*. The dominance of the kryptophilous land snails reached values of 80% in the Northern parts of the Carpathian Basin while the occurrence of the same group was about 40% in the Southern parts. Data of mollusc analysis refer to a large-scale heterogeneity in both palaeogeographic and palaeobiogeographic conditions for the area examined, creating some sort of a meeting point of faunal elements adapted to different environmental conditions in the region. The “gastropod-thermometer” developed by Krolopp and Sümegei (1995) showed a mean July temperature about 11–12°C in the Northern and 13–14°C in the Southern part of the basin during the LGM. Several further land snails and slugs (*Arianta arbustorum*, *Trochoidea geyeri*, *Arion fuscus* and *Arion* spp.) were also able to survive harsh climatic conditions in

small spots in the central European periglacial (Haase et al. 2003; Pinceel et al. 2005) or even within the Alpine permafrost area. DNA and allozyme data on *A. fuscus* show that its glacial survival was possible in or at the periphery of the Alps as well as in other European mountain ranges (e.g. the Tatra Mountains and Southern Balkans).

In the group of continental species, the woodland ringlet (*E. medusa*) represents a particularly interesting and well-studied case. Good evidences have been found based on allozyme data that this specie had multiple Würm ice-age differentiation centres around the glaciated Alps, in the Carpathian region and in the Balkan Peninsula (Schmitt and Seitz 2001; Schmitt et al. 2007). This glacial distribution pattern of *E. medusa* shows several parallel features with cold-tolerant vertebrates such as the adder, the bank vole, etc. (Deffontaine et al. 2005; Kotlík et al. 2006; Ursenbacher et al. 2006), most probably due to the particular climatic conditions of Eastern Europe during the last ice-ages. Supposedly, the decline of the temperature was, especially in the summer period, less dramatic as in the Atlantic part of Europe. This was combined with a decrease in the precipitation causing a transitional climate and mosaic-like vegetation similar to the recent conditions in the cold-continental forest-steppe belts of Southern Siberia and Northern Mongolia. Three of the four groups of *E. medusa* confined to the Carpathians most probably had their differentiation centres at the low elevations of the Southern-South-eastern Carpathians. The fourth lineage, composed of populations from the Western Carpathians and the North-Eastern Carpathians, might have had a core area of larger extent near to the Northern Carpathians or in the Carpathian Basin. The genetic diversity values of these populations suggest that the differentiation centre in the Carpathian Basin was as large and stable as the ones in the Southern Carpathians (Schmitt et al. 2007). Evidence for Central European refugia was also found for several other woodland species (Steward and Lister 2001). Recently, Schmitt and Haubrich (2008) indicated several Eastern European refugia of the large ringlet (*Erebia euryale*), a butterfly species strictly restricted to the European mountain coniferous forest zone. They concluded that the mountains of South-Eastern Europe were the most important reservoirs of the coniferous forests in Europe.

The Pleistocene glacial refugia of the European *Bombina* toads were located both in the “classical” refugial areas of the Appenins and the Balkans (core areas of *B. pachypus* and sub-species of *B. variegata*, Szymura et al. 2000; Canestrelli et al. 2006) as well as more to the North, in the Carpathians and the adjoining lowlands (Vörös et al. 2006; Hofman et al. 2007). Strong genetic evidences have been provided that *B. variegata* survived the LGM in the Carpathians. The mtDNA and allozyme data suggest two separate refugia. One clade probably had its refugium in the Southeastern edge of the Carpathians while the most likely refugium of the other clade was in the Southern Carpathians, where the haplotype diversity is the highest. However, the deep genetic divergence among European *Bombina* lineages suggests their pre-glacial origin.

The European populations of the moor frog are subdivided into three genetic lineages from which two are exclusively found in the Carpathian Basin. They, most probably, survived the LGM in the Carpathian Basin and have expanded to the

North to a rather limited extent only (Babik et al. 2004). The survival of *R. arvalis* in the Carpathian Basin was also demonstrated with fossil records (Venczel 1997). This view is supported by further recent data suggesting that this region might have been an important LGM refugial area in other amphibians and reptiles, as well. In the lizard *Z. vivipara*, a haplotype restricted to Northern Hungary and Austria was found in a species-wide survey of mtDNA variation (Surget-Groba et al. 2001). This ovoviviparous form shows peculiar karyotypic characters and demonstrates that the ovovivipary independently evolved in the Western European and Pannonian (*Z. vivipara pannonica*) populations (Kupriyanova et al. 2006; Surget-Groba et al. 2006). The suggested refugia of the adder (*V. berus*) would be in the Southern pre-Alpine lowland (Italian clade), in the “Illyrian” core area in the Western Balkan peninsula (Balkan clade) and several core areas of the Northern clade: in the Carpathian region (Carpathian sub-clade), East of the Carpathians (Eastern subclades) and in a location between Great Britain and Poland (Central European subclade). The survival of two mitochondrial lineages in the Carpathian Basin throughout the LGM was postulated in this species, one East of the Alps, and the other in the North-Eastern part of the basin or even in the Eastern Carpathians (Carlsson 2003; Ursenbacher et al. 2006).

### **3.4 Refugia of Boreal Birds and Mammals in Eastern Central Europe**

Comparison of phylogeographic structures in several Eurasiatic boreal species has shown that species associated with the taiga forest revealed essentially similar patterns. In the wood lemming (*Myopus schisticolor*), and also in most other boreal forest species, no substantial phylogeographic divisions across Northern Eurasia have been reported (Zink et al. 2002; Fedorov et al. 2008). The contraction of the range of these species to a single, probably Southern Siberian refugial area during the late Pleistocene followed by demographic expansion seems to be a general background for their shallow phylogeographic structure. The most important genetic discontinuity has usually been observed between the “Northern” Eurasiatic and the “Far East” clades. The limited distribution range of the South-eastern lineages suggests that their core areas (“Manchurian refugium” of de Lattin 1967) could not play an essential role in the post-glacial colonisation of Northern Eurasia by boreal forest species. A weak phylogeographic structure was also discovered in the flying squirrel (*Pteromys volans*), in which the divergence between the Far Eastern and Northern Eurasian groups may have been initiated during the Weichselian glaciation (Oshida et al. 2005). Mountain ranges in Southern Siberia and North-Eastern China may have isolated the Far Eastern group. Although the largest part of North-Eastern Europe and Siberia was not covered with ice during the last glaciation, most parts were overgrown by cold tundra-steppe (“mammoth steppe”) under extremely cold and dry conditions (Svendsen et al. 1999, 2004; Simakova 2001; Schirrmeister et al. 2002). At that time, multiple isolated refugia of *P. volans* could be formed in



Eurasia. After the last glaciation, *P. volans* might have expanded throughout Northern Eurasia, along both sides of the Ural mountains.

Other boreal species show clear phylogeographical structures with well-differentiated populations in the coniferous forest zone of the South European mountains. They belong to rather different taxonomical groups. The brown bear complex can be mentioned as a classical example, (e.g. Taberlet and Bouvet 1994; Valdiosera et al. 2007). The discovery of 18,000-year-old charcoal of yew (*Taxus baccata*) and Scots pine (*P. sylvestris*) in Western Slovakia (Litynska-Zajac 1995) indicates that the climatic conditions at the Western Carpathians might have been suitable for the brown bear. The Eastern Carpathians served also as a refuge area for brown bears during the last glacial phase. Nevertheless, recolonization from the Eastern Carpathian refuge appears to have been less effective compared to the migration that began from the North-Western Carpathian refuge. This recolonization pattern can be explained by the more Northern position of the North-Western Carpathians (leading edge).

Southern European montane refugia have also been revealed in the capercaillie (*T. urogallus*). It was suggested that the Southern European *aquitanus* lineage had expanded throughout Europe before the LGM, and the Eastern, *urogallus* lineage expanded in Asia and North-Eastern Europe. During the LGM, the two lineages were restricted into separate refugia (*aquitanus*: Iberia and Balkans, *urogallus*: Southern Siberia). During the post-glacial re-forestation, the *urogallus* lineage replaced *aquitanus* in Europe and forced them to the South-west into their refugia in the Pyrenees and Cantabrian Mts. (Duriez et al. 2007).

Different phylogeographical structures have been revealed in the root voles (Brunhoff et al. 2003), lemmings (Fedorov et al. 1999), collared lemmings (Fedorov and Stenseth 2002), and common voles (Haynes et al. 2003; Fink et al. 2004). In these cases, the Ural Mountains separated the Northern European and Siberian lineages. Root voles in Europe form a Northern and a central mtDNA phylogroup. Fossil records from the last glaciation have demonstrated that collared lemmings (*Dicrostonyx*) and true lemmings (*Lemmus*) used to be the most common small mammals in the periglacial tundra-steppe of central Europe. These species were regularly accompanied by several vole species, including the root vole. These species assembly always remained North of the “classical” Southern European refugia. Thus, central European root vole populations can be considered the sources of Northward expansion during the deglaciation. This model is corroborated by the data demonstrating that the fragmented populations in the Netherlands, Slovakia and Hungary all belong to a single mtDNA phylogroup. Consequently, the threatened populations in Hungary, Austria, Slovakia and the Netherlands represent glacial and post-glacial relicts (van de Zande et al. 2000).

Bilton et al. (1998) show that the Mediterranean populations of *S. minutus*, *S. araneus* and *Clethrionomys* spp. did not contribute to the present-day gene pools of the Central and Northern European populations. This view has also been supported by the high rate of endemism in the Mediterranean bank vole phylogroups. In contrast with some forest rodents (*A. sylvaticus*, *A. flavicollis*), bank voles would not be restricted to

the Southern forest refugia during the last glaciations. Therefore, bank vole populations might have survived the Quaternary glaciations in their Northern refugia. This may have resulted in their present complex phylogeographic pattern including multiple glacial refugia in central Europe, in the Mediterranean mountains and possibly also in several Eastern regions. Based on fossil records, the Carpathian region has been suggested as a glacial refugia area for this species. These refugia were most likely to be located near the Alps or in the Carpathians and possibly at the network of streams in the marginal areas of the Carpathian Basin. Phylogeographic analyses of the bank vole have already suggested that glacial refugia located in central and Eastern Europe made a major contribution to the modern population of this species in Europe (Deffontaine et al. 2005; Kotlík et al. 2006). The analysis of nucleotide diversity also demonstrates that these Eastern Central European regions acted as core areas of expansion for the Western lineage of the bank vole. Another refugial area was proposed in the regions of Eastern Romania, Western Azov Sea and the Crimea (Jaarola and Searle 2002).

## **4 Area Dynamics, Evolution and Diversity Patterns in the Carpathian Basin**

### ***4.1 Endemic Taxa and Autochthonous Evolution in the Carpathian Basin***

The level of endemism generally correlates with the geological age of the refugia where relict-like taxa have been evolved and/or could survive. The Carpathian Basin belongs to the geologically young areas of Europe. Its relief developed under the influence of the Alpine orogenesis and by retreat of the Paratethys and the Pannonian inland sea. Moreover, the phylogeography of some freshwater invertebrates (e.g. Neritidae snails, see: Bunje 2007; Fehér et al. 2007) is clearly connected with the evolution of the Ponto-Pannonian water basin and of the Danube catchment area. In addition, there are several taxonomical groups with considerable proportion of endemic species, e.g. the land gastropods (Soós 1943) the earthworms (Lumbricidae: Csuzdi and Pop 2007) or some soil arthropods (e.g. Opiliones, Diplopoda: Korsós 1994; Collembola: Dányi and Traser 2007). Their core areas clearly coincide with the younger tertiary land masses within and near the Carpathian Basin.

Most endemic species are narrow specialists, inhabiting extreme habitats, such as thermal springs, karstic caves and karstic springs (Table 1). Several endemic troglobionta have been described in gastropods, pseudo-scorpions, harvestmen, spiders and springtails, often occurring within a single or a few caves of karstic mountains. Several species of earthworms, millipedes, centipedes and assels can be considered as holo-endemic species of the Western Transylvanian (Apuseni) mountains (Csuzdi and Pop 2007; Varga and Rakosy 2008).

Endemic terrestrial insects of the Carpathians are, as a rule, short-winged, flightless species such as the bush-crickets *Isophya*, *Poecilimon* spp.; some stenotopic relict grasshoppers (*Capraiuscola ebneri*, *Podismopsis transsylvanica*, *Uvarovitettix transsylvanica*, *Zubovskia banatica*; Kis 1965, 1980); numerous species of the

**Table 1** Examples of stenotopic species of extreme habitats endemic to the Carpathians and the Carpathian basin

Taxonomic group	Species	Habitat type	Occurrence
Gastropoda	<i>Melanopsis parreysi</i>	Thermal springs	Baile Felix (Oradea)
Gastropoda	<i>Theodoxus prevostianus</i>	Thermal springs	Hungarian Middle Range
Gastropoda:	<i>Paladilhia hungarica</i>	Karstic water in caves	Mecsek Mts. (Abaliget)
Gastropoda	<i>Paladilhioipsis transsylvanica</i>	Karstic water in caves	Mți. Apuseni
Gastropoda:	<i>Paladilhioipsis leruthi</i>	Karstic water in caves	Mți. Apuseni
Amphipoda:	<i>Niphargus tatrensis</i>	Karstic water in caves	Calcareous mts. in the Northern Carpathians
Gastropoda	<i>Bythinella (Sadleriana) pannonica</i>	Karstic springs	Calcareous mts. in the Northern Carpathians
Palpigradi:	<i>Eukoenia vagvoelgyii</i>	Karstic caves	Aggtelek karst, Slovakian karst
Araneae	<i>Centromerus chappuisi</i>	Karstic caves	Mți. Apuseni
Araneae	<i>Troglolyptantes racovitzai</i>	Karstic caves	Mți. Apuseni
Araneae	<i>Nesticus biroi</i>	Karstic caves	Mți. Apuseni
Diplopoda	<i>Haasea hungarica</i>	Karstic caves	Mecsek Mts. (Abaliget)
Diplopoda	<i>Hungarosoma bokori</i>	Karstic caves	Mecsek Mts. (Abaliget)
Isopoda	<i>Mesoniscus graniger</i>	Karstic caves	Aggtelek karst, Slovakian karst
Collembola	<i>Pumilnura dudichi</i>	Karstic caves	Aggtelek karst
Collembola	<i>Protaphorura kadici</i>	Karstic caves	Aggtelek karst
Collembola	<i>Arrhopalites dudichi</i>	Karstic caves	Aggtelek karst
Collembola	<i>Arrhopalites hungaricus</i>	Karstic caves	Aggtelek karst
Collembola	<i>Arrhopalites bueckensis</i>	Karstic caves	Bükk Mts. (N. Hungary)
Coleoptera, Carabidae	<i>Duvalius bokori</i>	Karstic caves	Slovakian karst
Coleoptera, Carabidae	<i>Duvalius gebhardtii</i>	Karstic caves	Bükk Mts.
Coleoptera, Carabidae	<i>Duvalius microphthalmus</i>	Karstic caves	Calcareous mts. in the Northern Carpathians
Coleoptera, Carabidae	<i>Duvalius hungaricus</i>	Karstic caves	Aggtelek karst, Slovakian karst
Coleoptera, Carabidae	<i>Duvalius redtenbacheri</i>	Karstic caves	Mți. Apuseni
Coleoptera, Carabidae	<i>Duvalius biroi</i>	Karstic caves	Mți. Apuseni

**Table 2** Examples of endemic species of forest soils in Transylvania

Lumbricida	<i>Allolobophora dacica</i>	Forest soil + litter	Mți. Apuseni
Lumbricida	<i>Octodrilus</i> spp. (12 spp.!)	Forest soil + litter	Mți. Apuseni
Pseudoscorpiones	<i>Neobisium brevipes</i>	Forest soil + litter	Mți. Apuseni
Opiliones	<i>Ischyropsalis dacica</i>	Forest soil + litter	Mți. Apuseni
Diplopoda	<i>Trachysphaera biharica</i>	Forest soil + litter	Mți. Apuseni
Diplopoda	<i>Typhloiulus serbani</i>	Forest soil + litter	Mți. Apuseni
Myriopoda	<i>Monotarsobius paucioculatus</i>	Forest soil + litter	Mți. Apuseni
Myriopoda	<i>Monotarsobius spelaeus</i>	Forest soil + litter	Mți. Apuseni
Myriopoda	<i>Monotarsobius burzenlandicus</i>	Forest soil + litter	Mți. Apuseni
Myriopoda	<i>Lithobius dacicus</i>	Forest soil + litter	Mți. Apuseni
Isopoda	<i>Cylisticus major</i>	Forest soil + litter	Mți. Apuseni
Isopoda	<i>Trachelipus spinulatus</i>	Forest soil + litter	Mți. Apuseni
Isopoda	<i>Biharoniscus racovitza</i>	Forest soil + litter	Mți. Apuseni

ground beetles (*Duvalius*, *Trechus*, *Patrobus*, *Morphocarabus* spp.) and weevils (e.g. *Otiorrhynchus* spp.). A bulk of these endemic taxa is confined to the Eastern and Southern Carpathians, to the Apuseni Mts. and to the mountains of Banat, which could preserve relict species (e.g. the tertiary relict gastropods *Chilostoma banaticum*, *Pomatias rivulare*) or some narrow endemic species of Isopoda and Diplopoda (Table 2) in refugia without permafrost phenomena during the last glaciations (Bennett et al. 1991; Krolopp and Sümegi 1995; Willis et al. 1995).

In the more mobile insect groups, the proportion of endemism lies rather low (e.g. in *Odonata* no endemic taxa occur in the Carpathian Basin). Most endemic Lepidoptera of the Carpathian Basin belong to Microlepidoptera, which have flightless females and are strictly specialised to some food plants living on halophyta in the saline grasslands of the Fertő-Neusiedlersee area (Kasy 1965) and those of the Great Hungarian plain (Kiskunság and Hortobágy). Endemic subspecies of *Geometridae* and *Noctuidae* evolved as peripheric isolates of turano-eremic species from the late-glacial, *kryoxerotic* periods, e.g. *Narraga tessularia kasyi*, *Saragossa porosa kenderesensis* (on food plants: *Artemisia santonicum*, *A. pontica*) and *Hadula dianthi hungarica* (on *Gypsophila muralis*). Some endemic taxa in the sandy areas of the Pannonian lowland are specialised predators or parasitoids, e.g. the spider *Dictyna szabo*i and the pompilid wasp *Cryptocheilus szabopatayi*. Further species described as endemics later proved widely-dispersed steppicolous species. In their majority, the endemics of the lower, hilly parts of the Carpathian Basin, however, represent thermophilous post-(inter?-) glacial relicts with connections to the Balkan Peninsula, Asia Minor or Southern Russia (e.g. *Apamea sicula tallosi* in warm-humid alluvial areas, *Dioszeghyana schmidtii schmidtii* and *Asteroscopus syriacus decipulae* in Pannonian xerothermic oak forests, *Polymixis rufocincta isolata* in the Villányi Mts.; *Chersotis fimbriola fimbriola*, *Euxoa vitta vitta*, *E. hastifera pomazensis* and *Cucullia mixta lorica* in the dolomitic areas of the Transdanubian Middle Range, *Chersotis fimbriola baloghi* in the Aggtelek Karst). Balkanic connections have also been observed in butterfly species, which

are restricted to special, Pontic-Pannonian steppic food plants, e.g. *Plebeius sephirus* (feeding on *Astragalus exscapus*, *A. dasyanthus*), *Melitaea telona kovacsi* (on *Cirsium pannonicum*).

Several endemic Macrolepidoptera subspecies of the Carpathians belong to the genera *Erebia* and *Glacies* (Table 3). A few endemic taxa are only widespread in the Carpathians and in the neighbouring mountainous areas, e.g. *Aricia artaxerxes issekutzi*, *Photedes captiuncula delattini*, while others are confined to the Southern Carpathians, often with Balkanic connections: *Erebia cassioides neleus*, *Coenonympha rhodopensis schmidtii* (Varga 1975, 2003a). The subspecies of *Erebia melas* inhabit island-like, calcareous mountain stocks, *E. melas runcensis* in the Apuseni Mts., *E. melas melas* in the Cernei Mts. and *E. melas carpathicola* in the Eastern Carpathians). All these data clearly demonstrate that the Carpathians, especially the Eastern and Southern parts, together with the mountains of Western Transylvania (Apuseni Mts. and Banat) can be considered as core areas for the survival and autochthonous evolution in many invertebrate groups of limited mobility.

## 4.2 The Carpathian–Balkan Connections

The close geological and faunal connections of the Carpathians suggest the existence of highly dynamic contacts with the mountains of the Balkan Peninsula during the Upper Pleistocene. These connections show a contrasting picture compared to the refugia of the Iberian and the Apennine peninsula which have been much more sheltered by the glaciated mountains of the Pyrenées and the Alps, respectively. At least two major arboreal refugia can be traced here: the Illyrian refugium related to the Dinarids and its foothills and the Carpatho-Dacian refugium related to the Carpathians and its foothills. Some areas attached to these refuges served as periodic habitats over climatically favourable periods. These are regarded as fluctuation zones (Varga 1995; Sümegi et al. 1998; Deli and Sümegi 1999).

Since the Carpathian Basin occupied a transitional position between the Balkanic refugia and the cold-continental tundra-steppe zone during the glacial periods, the post-glacial re-population of the Carpathian Basin proceeded (1) by long-distance dispersal from the more remote (atlanto- and ponto-) Mediterranean and Southern Continental refugia, and (2) also from some adjacent local survival areas, e.g. from North-Western Balkanic (“Illyrian”) versus South Transylvanian (“Dacian”) arboreal refugia. In such cases, the arrows of the Northwards dispersal of the South-Western and South-Eastern populations surround the arid central part of the basin. These components of the flora and fauna extend Northwards through the foothills of the Eastern Alps and Southwest-Pannonian hilly regions on the one hand, and through the hilly regions of the Banat area and the Western foothills of the Transylvanian “Island” mountains (Apuseni Mts.), on the other. In some cases, the populations of the South-Western and South-Eastern “strains” do not display any significant taxonomical differentiation, e.g. the silver lime (*Tilia tomentosa*) or



**Table 3** Endemic subspecies of *Erebia* (Nymphalidae, Satyrinae) and *Glacies* (Geometridae, Ennominae) in the Carpathians (maps of *Erebia* spp.: Varga 1975; Varga and Schmitt 2008)

Name	Typical locality	Range
<i>Erebia manto traianus</i> (Hormuzaki, 1895)	Rareu (NE Carpathians)	NE-SE-S Carpathians
<i>Erebia epiphron transsylvanica</i> (Rebel, 1908)	Bucegi (SE Carpathians)	the whole Carpathian arc
<i>Erebia pharte belaensis</i> v. Goltz, 1937 (= <i>E. pharte</i> <i>carpatina</i> A. Popescu-Gorj & A. Szabó, 1986)	“Belaer Kalkalpen” (= Belanské Tatry) Rodna Mts. (NE Carpathians)	N + E Carpathians, S Carpathians
<i>Erebia sudetica radnaensis</i> (Rebel, 1915)	Rodna Mts. (NE Carpathians)	NE Carpathians, S Carpathians
<i>Erebia gorge rudkowskii</i> (Bang-Haas, 1933)	Tatra Mts.	Tatra Mts., NE Carpathians
<i>Erebia gorge fridericikoenigi</i> (Varga 1998)	Piatra Craiului (SE Carpathians)	SE-S Carpathians
<i>Erebia cassioides neleus</i> (Freyer, 1833)	“Banater Gebirge”	S Carpathians
<i>Erebia melas melas</i> (Herbst, 1796)	“Transylvania” (Mți Cernei)	Mți Cernei (Domogled)
<i>Erebia melas carpathicola</i> (Alexinschi and Popescu- Gorj, 1959)	Haghmașul Mare (E Carpathians)	E-SE Carpathians
<i>Erebia melas runcensis</i> (König, 1965)	Cheile Runcului (Mți Apuseni)	Mți Apuseni
<i>Erebia pronoe regalis</i> (Hormuzaki, 1937)	Bucegi (SE Carpathians)	SE Carpathians
<i>Erebia pandrose roberti</i> (Peschke, 1920).	Tatra Mts.	Tatra Mts, NE Carpathians
<i>Erebia pandrose cibiniaca</i> (Dannehl, 1927)	“Cibinsgebirge”	SE-S Carpathians
<i>Glacies canaliculata</i> <i>schwingenschussi</i> (Wehrli, 1921)	Tatra Mts.	higher mountains of the whole Carpathian arc
<i>Glacies noricana carpathica</i> (Schwingenschuss, 1915)	“Belaer Kalkalpen” (= Belanské Tatry), Mt. Bujacie	Belanské Tatry, Bucegi, Retezat
<i>Glacies bentelii retyezatensis</i> (Bartha, 1933) – subspecific status dubious!	Retezat Mts. (Lac. Zenoaga)	Retezat, Bucegi (ssp.?)
<i>Glacies coracina dioszeghyi</i> (Schmidt, 1930)	Retezat Mts. (Lac. Zenoaga)	Retezat, Bucegi (ssp.?)

some butterflies and moths (*Pyronia tithonus*, *Aplasta ononaria*, *Idaea nitidata*, *Zanclognatha tenuialis*). Much more evidence is provided by the re-population of the Carpathian Basin from different directions in the cases of vicarious pairs of closely related species or in subspecies of polycentric species. Such cases can mostly be mentioned in land gastropods, e.g. *Pomatias elegans* – *P. rivulare*,

*Chilostoma illyricum* – *Ch. banaticum*, or in flightless insects, e.g. short-winged Orthoptera: *Odontopodisma schmidti* – *O. rubripes*, *Isophya modestior* – *I. stysi* (Orci et al. 2005).

The Western Balkanic (“Illyrean”) influences are most significant in the Southern and South-Western parts of Transdanubia. These areas are characterised by a humid sub-Mediterranean climate and do not have a significant rainfall deficit in the summer period. They belong to the belt of mesophilous zonal forests of *Fagion illyricum* and *Quercus-Carpinion illyricum* and the Illyrean-Pannonian hardwood gallery forests (*Fraxino pannonicae-Ulmetum*) characterised by a richness in tertiary/inter-glacial relict, often geophytic plant species (Horvat et al. 1974).

The Transylvanian (“Dacian”) influences are connected with the forested areas of the Eastern Carpathians and often transmitted by the Western Transylvanian mountains (Mahunka 1993, 2007; Varga 1989, 1995, 2003a,b). The occurrence of Dacian elements is typical of the Eastern part of the Hungarian Middle Range, especially in the higher parts of the volcanic Eperjes-Tokaj range and in the Karst areas of N Hungary and S Slovakia. Eastern Balkanic influences reach also the Hungarian Middle Range by relict-like occurrences of some Balkanic and Balkanic-Anatolian elements (e.g. *Noctuidae*: *A. syriacus* and *D. schmidti*), especially in the warm foothill zone where the sub-Mediterranean influences are also significant. Relict occurrences of Dacian elements (bush-crickets: *Isophya stysi*, *Leptophyes discoidalis*, *Pholidoptera transsylvanica*; ground-beetles: *Carabus hampei ormayi*) have been recently discovered on the small, island-like volcanic hills of the Bereg lowland.

The influences of the Northern Carpathians are also significant in the NE part of the Hungarian Middle Range. There is a characteristic difference between the Eperjes-Tokaj volcanic chain on the one hand, and the limestone plateau of the Bükk Mts. and the N Hungarian karst on the other. The biotic contact of the Eperjes-Tokaj range with the Carpathians is young, obviously post-glacial, and can be characterised mostly by the presence of species, which are either typical of the montane forest belts of the Carpathians (e.g. numerous land snails: *Bielzia coeruleans*, *Vestia gulo* and ground-beetles: *Carabus obsoletus*, *C. zawadzkyi*, *Abax schueppeli*) or widely dispersed in the Northern part of Central Europe, often having a Euro-Siberian distribution. The Bükk Mts., however, display an insular character. Its Carpathian and de-Alpine elements (e.g. land snails: *Spelaediscus triaria*, *Phenacolimax annularis*, the Geometrid moth *Entephria cyanata gerennae*) are isolated relicts. In the Aggtelek Karst area, the immediate contact with the higher limestone plateaus of Slovakia is combined with the occurrence of Carpathian (land snails: *B. coeruleans*, *Cochlodina cerata*, *Trichia unidentata*; ground-beetles: *C. obsoletus*, *C. zawadzkyi*, *A. schueppeli*, *Trichotichnus laevicollis carpathicus*), boreal and xeromontane species at surprisingly low altitudes, influenced by the conspicuous meso-climatic and geomorphological features of this area. Some influences of the Northern and the Eastern Carpathians are to be observed at the NE marginal areas of the Pannonian lowland, i.e. along the upper course of the river Tisza and its tributaries (e.g. occurrence of land gastropods *Vitrea diaphana*, *B. coeruleans*, *Balea stabilis*, *Perforatella dibothrion*, *P. vicina*).

### 4.3 *The Forest: Steppe Dynamics in the Carpathian Basin*

The Carpathian Basin belongs to the regions of Europe with the highest biodiversity (Williams et al. 1999). Due to its transitional position during the Quaternary climatic fluctuations, the overlap and accumulation of floristic and faunistic elements of contrasting habitats occurred here. This overlapping of different climatic provinces, enhanced by the varied relief, edaphic and hydrographic conditions, has resulted in suitable conditions for the survival of a large number of species belonging to different core areas and displaying various patterns of long-distance and short-distance re-populations.

It is typical for South-Eastern Central Europe that the large-scaled zonal settling of vegetation, characteristically developed in the East-European table-land, breaks down. In the Carpathian Basin, the concentric arrangement of vegetation belts is influenced by numerous climatic, orographic, hydrographic and edaphic factors (Varga 1995, 2003b). The forest-steppe, which is typical in the major, central lowland and hilly parts of the basin, is represented by a number of regional variants showing distinct geological, edaphic and meso-climatic characters. The forest, skirt and grassland compartments of each regional variant of the forest-steppe are highly intercorrelated. The Carpathians transmit (e.g. boreal) also filter certain different (e.g. steppic) biogeographical influences. Populations passing through the Carpathians will often be isolated and differentiated from the populations inhabiting other parts of their range of distribution.

The geographically transitional position of the Carpathian Basin resulted in a conspicuous mixture of faunal elements of diverse origins and geographical histories. The compartment structure of the vegetation complexes, typical for the Pannonian forest-steppe, has promoted the survival of very different faunal elements. Especially, the hilly areas of transitional climatic conditions surrounding the Pannonian lowland are populated by numerous, biogeographically important species and communities. The Southern, xerothermic slopes and foothills of the Hungarian Middle Range served both as refuges for thermo-xerophilous elements during several cold and cool-humid climatic phases of the Quaternary and as centres of their dispersal (Soó 1940, 1959; Wendelberger 1954, 1959; Zólyomi 1949, 1953, 1964). Thus, many thermophilous elements probably populated the Carpathian Basin not only by long-distance colonisation from remote, large glacial refuges, but also from numerous meso- or microclimatically favourable sites lying at the fluctuating borderlines of the Mediterranean refugial and periglacial belts. The varied and fine biostratigraphical structure of the Hungarian young Pleistocene, often characterised by a coexistence of forest and non-forest faunal elements (e.g. Jánossy 1979; Kordos 1977; Kretzoi 1969, 1977), provides evidences to support this view and demonstrates the transitional biogeographical character of this region during the whole time-span of the Quaternary period. New palynological data from the Eastern part of the Pannonian lowland (Bátorliget) also suggest the presence of forest refuges during the last glacial period (see also: 3.2.).

#### 4.4 *Relict Species with Long-Distance Disjunctions in the Carpathian Basin*

There are several Mediterranean-Manchurian bicentric faunal elements with disjunct range occurring in the Carpathian Basin. The distribution of this species group is connected with the Ponto-Caspian waterway-system, and displays long-distance disjunctions from the vicarious Eastern Asiatic taxa, which often are only subspecifically differentiated (Lepidoptera: *Apatura metis metis* – *Apatura m. substituta*, *Chariaspilates formosarius hungaricus* – *Chariaspilates f. formosarius*, *Rhyparioides m. metelkanus* – *Rhyparioides metelkanus flavidus*, *Arytrura musculus* ssp. – *Arytrura m. musculus*). These and also some other species of this group (*Polygogon gryphalis*, *Herminia tenuialis*, *Diachrysia nadeja*) occur at the lower course of the Danube and the Drava as well as in swampy-boggy areas of the lowlands in Transdanubia, in the Banat and Eastern Hungary. The refugia of these faunal elements were probably along the lower courses of the Danube and its tributaries. Gallery forests of the Illyrian and the Pannonian type and alluvial wetlands accompanying the large rivers of the Pannonian lowland served as corridors for the Northwards expansion of these species.

Different types of long-distance disjunctions have been observed in the relict-like steppe and semi-desert species. The polytypic butterfly *Melanargia russiae*, which is widespread in West and Central Asia, South Siberia and in the mountains of Italy and the Balkan Peninsula, occurred locally – as *M. russiae clotho* – on tall-grass clearings of birch gallery forests of the sandy lowland in Kiskunság. Its extinction was partly due to the consequence of overcollecting, and mostly because of destroying the habitats (re-forestation with *Robinia pseudoacacia*). The habitats of *Chondrosoma fiduciarium* (Kasy 1965) are also tall-grass lowland and hilly steppes often mixed with slightly saline patches. Other species are confined to open dolomitic rocky swards (e.g. *Phyllometra culminaria*, *Lignyoptera fumidaria*, *C. mixta lorica*) or open sandy and rupicolous grasslands (*Oxytripia orbiculosa*, vanishing).

Eremic species are restricted to semi-desert-like habitats of the lowland with extreme edaphic conditions. This faunal type is represented by very few vertebrates: only the small rodent *Sicista subtilis* and the short-toed lark *Calandrella brachydactyla* belong to this group. Abundant examples can be found in strictly localised phytophagous insects, which are often connected with special halophytic plant communities. They are often represented by endemic Pannonian subspecies or allopatric sibling species of Turanian origin, e.g. the Noctuid moths *Saragossa porosa kenderesiensis* and *H. dianthi hungarica* or the Microlepidoptera: *Coleophora hungariae*, *C. klimeschiella*, *C. magyarica*, *C. peisoniella*, *Holcophora statices*, *Stenodes coenosana*, *Agriphila tersella hungarica*, etc. The dispersal of this species group could have taken place in the late glacial phases on the Pannonian lowland, with a subsequent isolation as a result of the post-glacial expansion of the forested belts.

Last but not the least, *xeromontane* elements are present also in the Carpathian Basin. Their two main groups are: the Mediterranean-xeromontane species,

represented by a few vertebrates (e.g. *Monticola saxatilis* or the secondarily more expanded *Phoenicurus ochrurus*). A larger number of species, however, belongs to some insect groups, e.g. Noctuidae (*E. vitta*, *E. decora*, *E. birivia*, *Dichagyris candelisequa*, *Yigoga nigrescens*, *Chersotis margaritacea*, *Ch. fimbriola*, *Apamea platinea*, etc.) and Orthoptera (e.g. *Paracaloptenus caloptenoides*). The continental-xeromontane type is represented by some members of widely distributed Asiatic mountain steppe species as *Euxoa recussa*, *Dichagyris musiva* (Noctuidae) and by some relict-like inhabitants of the rocky dolomitic grasslands as *P. culminaria*, *L. fumidaria* (Geometridae). It seems to be very probable that numerous genera, typical for the steppe biome, might have a xeromontane origin (especially Lycaenidae: e.g. the subgenus *Agrodiaetus* and other species groups of *Polyommatus* and *Plebeius*; Satyridae: *Chazara*, *Pseudochazara*, *Hyponephele*; Noctuidae: *Euxoa*, *Agrotis*, *Dichagyris*, *Yigoga*, *Rhyacia*, *Chersotis*, *Eugnorisma*, etc.). The same has to be supposed in the case of some endemic elements of the Pannonian flora (*Linum dolomiticum*, *Seseli leucospermum*, *Ferula sadleriana*, *Onosma tornense*, etc.).

## 5 Summary and Conclusions

The European fauna has traditionally been subdivided into a “*holothermic*” refugial and a “*holopsychric*” invasion type. The former type was differentiated according to the secondary subdivision of the Mediterranean refugial area. This view was confirmed and modulated by molecular results. A general conclusion was that temperate species mainly derive from Mediterranean refugial populations that underwent range expansion in the late glacial and early post-glacial periods. The other main group has been considered for a long time as a result of the “Siberian” invasion despite the evidences, which have revealed the taxonomical differentiation of North-Eastern “boreal” and Southern European montane populations. Several authors have suggested an additional mode of colonisation of Central and Northern Europe by *non-Mediterranean* populations, coming from one or more “continental” refugia. Fossil pollen data and macrofossil remains from the time of the Last Glacial Maximum indicate that several tree species remained in small favourable spots at the Southern edge of the steppe-tundra area. Research on small mammals has also questioned the universality of Mediterranean refugia. It was suggested that the Mediterranean “sanctuaria” in general were *not* also core areas of post-glacial expansion into deglaciated areas.

The Pleistocene glacial-interglacial cycles have resulted in the “*antagonistic dynamics*” of biota pertaining to contrasting macrohabitats. Principally, two basic types of zonal setting can be distinguished. The glacial periods have been characterised by a regressive fragmentation of wooded habitats and, consequently, by a broad contact of the tundra and the steppe zoniomes with some forested “pockets” North of the refugial belt of the Mediterranean area. Transitional *zono-ecotones* developed at the forest-belt fringes: tundra-taiga and boreal forest-steppe. Pollen-based



“tree-less tundra” models for Europe, North of the transverse mountain ranges, have repeatedly been questioned by researchers of the late Pleistocene mammalian fauna because the carrying capacity sufficient to feed numerous large herbivores demands a very productive environment (“mammoth steppe”). Thus, non-analogue communities were composed by mixing tundra, steppic and eremic-oreal elements. This boreal forest-steppe habitat type appears to have included also cold-tolerant species of temperate habitats.

The species of the boreal zone show a significant diversity of extension and of taxonomical structure of ranges. Comparison of phylogeographic structures in several Eurasiatic boreal species has shown that species associated with the taiga forest revealed essentially similar patterns. The number of exclusively European boreal and boreo-montane species is relatively low. However, a molecular biogeographical analysis of such species can unravel the European coniferous forest refugia. The existence of European coniferous forest refugia is also supported by the East–West subdivision of several boreal species. Temperate refugia in Europe during cold periods might not have been restricted to the three Southern peninsulas. These refugia were most likely to be located near the Alps or in the Carpathians and, possibly, at the network of streams in the marginal areas of the Carpathian Basin.

The level of endemism generally correlates with the geological age of the refugia where relict-like taxa have been evolved and/or could survive. The Carpathian Basin belongs to the geologically youngest areas of Europe. Its relief developed under the influence of the Alpine orogenesis and by retreat of the Paratethys and the Pannonian inland sea. There are, however, some taxonomical groups which show considerable proportion of endemic species (land gastropods, earthworms or some soil arthropods). Most endemic species are narrow specialists inhabiting extreme habitats, e.g. thermal springs, karstic caves and karstic springs. A bulk of these endemic taxa is confined to the Eastern and Southern Carpathians, to the Apuseni Mts. and to the mountains of Banat, which could preserve relict species or some narrow endemics in refugia without permafrost phenomena during the last glaciations. Since the Carpathian Basin occupied a transitional position between the Balkanic refugia and the cold-continental tundra-steppe zone during the glacial periods, the post-glacial re-population of the Carpathian Basin was preceded (1) by long-distance dispersal from the more remote (atlanto- and ponto-) Mediterranean and Southern continental refugia, and (2) also from some adjacent local survival areas, e.g. from North-Western Balkanic (“Illyrian”) versus South Transylvanian (“Dacian”) arboreal refugia. In such cases, the arrows of the Northwards dispersal of the South-Western and South-Eastern populations surround the arid central part of the basin.

In the Carpathian Basin, the concentric arrangement of vegetation belts is influenced by numerous climatic, orographic, hydrographic and edaphic factors. The geographically transitional position of the Carpathian Basin resulted in a conspicuous mixture of faunal elements of diverse origins and geographical histories. The compartment structure of the vegetation complexes, typical of the Pannonian forest-steppe, has promoted the survival of very different faunal elements. Thus,

many thermophilic elements probably populated the Carpathian Basin not only by long-distance colonisation from remote, large glacial refuges, but also from numerous meso- or microclimatically favourable sites lying at the fluctuating borderlines of the Mediterranean refugial and periglacial belts. Eremic species are restricted to semi-desert-like habitats of the lowland with extreme edaphic conditions. Abundant examples can be found in strictly localised phytophagous insects, which are often connected with special halophytic plant communities. They are often represented by endemic Pannonian subspecies or allopatric sibling species of Turanian origin. The dispersal of this species group could have taken place in the late glacial phases on the Pannonian lowland with a subsequent isolation as a result of the post-glacial expansion of the forested belts. Two main groups of *xeromontane* elements are present in the Carpathian Basin. A larger number of species of the Mediterranean-xeromontane species belongs to some insect groups, e.g. Noctuidae and Orthoptera. The continental-xeromontane type is represented by some members of widely distributed Asiatic mountain steppe species and by some relict-like inhabitants of the rocky dolomit grasslands. It seems to be very probable that numerous genera, typical of the steppe biome, might have a xeromontane origin.

**Acknowledgements** I am deeply indebted to the precursors of modern phylogeographic thoughts: to the late Gustaf de Lattin and Willy Reinig who inseminated the biogeography by genetic insights and shaped my ideas. The Alexander von Humboldt Foundation repeatedly supported my research fellowships in Germany. The survey of the faunal history of Hungary was partly supported by the grant NKFP-3 B/023/2004.

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