Post-glacial dispersal strategies of Orthoptera and Lepidoptera in Europe and in the Carpathian basin

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Abstract

Ecologically transitional regions are characterised by high species diversity due to the overlap of species with different geographical origins caused by dispersal processes along gradients, e.g. the overlap of species belonging to different zonobiomes. The overlap of azonal communities along short-distance gradients results in the organisation of community-complexes and landscape mosaics connected by habitat ecotones characterised by overlap of several faunal types, like Mediterranean, Balkanic, Siberian, Ponto-Caspian, Ponto-Pannonian, Turano-Eremic and Xeromontane elements in the Pannonian forest-steppe complexes.

For some invertebrate groups, such as the land gastropods or some soil arthropods, the Carpathian basin contains a considerable proportion of endemic species. The eastern and southern Carpathians, together with the mountains of western Transsylvania, can be considered as core areas of survival and autochtonous evolution in some invertebrate groups with limited mobility. In mobile insect groups only peripherically isolated sibling (sub)species have evolved, which display manifold biogeographic connections, for instance to the Balkan peninsula, Asia minor or southern Russia. The distribution of Mediterranean-Manchurian bicentric faunal elements, connected to the Ponto-Caspian waterway-system, shows long-distance disjunctions from the eastern Asiatic taxa. Gallery forests of the Illyrian and Pannonian types and wetlands accompanying the large rivers of the Pannonian lowland have served as corridors of the northward expansion of these species.

The post-glacial repopulation of the Carpathian basin from different directions has been supported by Illyrian versus Dacian vicarious pairs of sister (sub)species. Cases of vicarious 'Siberian'-Mediterranean sibling taxa have also been established. Recent results confirm that the montane part of the range of several 'Siberian' boreo-montane species does not have its origin in post-glacial 'Siberian' invasion.

Populations of some butterfly species have been studied in different geographical scales. Patterns of metapopulation structure and of genetic differentiation have been established.

Key words: biogeography, Lepidoptera, Orthoptera, dispersal, Carpathian basin.

Introduction: biodiversity and phylogeography

The continuity of life is maintained by distinct biological individuals of limited life-span. Similarly, the continuity of changing genetic information, called evolution, is carried by species of limited life-span. Species diversity is generated by *branching processes* called *speciation*: by partition of the genetic variation into distinct breeding systems with specific mate recognition signals (SMRS) and separated by reproductive isolation. The subdivision of the formerly at least potentially coherent gene-pool results in the genealogical diversity (Eldredge 1985, Eldredge & Salthe 1984). *Genealogical diversity* is usually connected with some *core areas* which can be outlined by areographical methods and tested by tools of the phylogenetic analysis (Cracraft 1983, Cracraft & Prum 1988). The other aspect of the biological diversity is the *compositional* one. Due to dispersal, overlap and survival of species belonging to different biogeographical types some regions can be characterised by the accumulated presence of floristic and faunistic elements of diverse age and different geographical origin.

The study of the structure and dynamics of ranges by genetic markers, called 'phylogeography' (Avise 1989, 1994, 1999, Avise & Hamrick 1996, Roderick 1996) has become to one of the most rapidly evolving fields of population biology. Phylogeny means the topology of the process of evolution at different hierarchical levels of organisation (Avise 1994): the level of genetic identity versus non-identity, the level of kinship in sexually reproducing organisms, the level of differentiation into ecotypes, geographical races and species (the level of emerging reproductive barriers) and the level of phylogenetic lineages separated by reproductive isolation (monophyletic supraspecific units). The study of genetic differentiation of genealogical lineages and the analysis of the processes governing their geographical distribution (phylogeography) has demonstrated that the cladograms of groups of related species (supraspecific taxa) should match the historical 'area-cladograms' of the geographical ranges occupied by them (Enghoff 1993, 1995, Oosterbroek & Arntzen 1992). The processes which generate spatial patterns of diversity, exhibit some basic features:

- The genetic differentiation of populations results in 'elementary' branching processes which form a reticulating network of populations connected by more or less regular, or restricted gene-flow, as a consequence of full or limited exchangeability of individuals.
- There are 'hot spots' (core areas of diversity), characterised by the occurrence of numerous strictly endemic species. These areas appear to be repeated more or less regularly in the different taxonomical groups. The 'hot spots' are considered to have a long-term ecological stability (Fjeldså & Lovett 1997, Fjeldså et al. 1997), which cause the accumulation of the genetic information ('gene-centres'). The genealogical connections of endemic taxa, belonging to well-defined core areas, can be analysed by phylogenetic methods ('areas of endemism', Harold & Mooi 1994).
- There are ecologically transitional regions with high numbers of species, but without high proportions of endemism (Williams et al. 1999, 2000). They are characterised by the overlap of ranges of species of different geographical origins caused by dispersal processes along gradients. An example is the overlap of species belonging to different zonobiomes and azonal communities in forest-steppe areas of the Carpathian basin (Varga 1995).

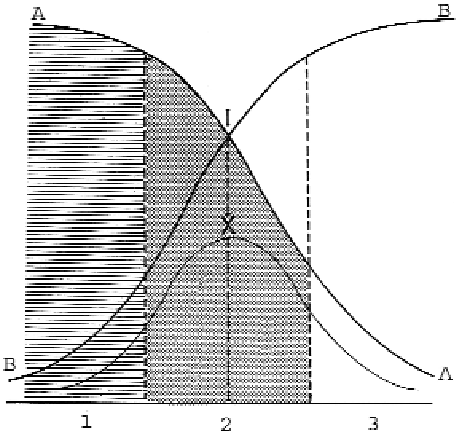

Figure 1
The graph and sectors of the 'centrifugally' decreasing species number of a faunal type under ideal conditions. A. centrifugal decrease of the species number, B. cumulative curve of the normal type of distribution, X. arithmetic mean of the normal distribution (Gauss curve), I. point of inflexion, 1. section of the zonal distribution of the faunal type, 2. section of the disaggregation (fluctuation) of the faunal type (with peripheric subspeciation), 3. section of the biogeographical extinction of the faunal type.

In this paper, the biogeographical terminology is adopted from Natura 2000 (Council of Europe 1998).

Overlaps by dispersal along gradients

In the Palaearctic region, the most important possibility of long-distance extension is the east-west dispersal along geographical latitudes, north to the chains of the Eurasiatic mountain system. A large number of 'trans-Palaearctic', Euro-Siberian areas has been established by this mechanism, which resulted in the formation of several peripherically isolated and often taxonomically differentiated populations at the zone of 'disaggregation' of the distribution at the mountain regions of Central and South Europe (Varga 1977). Supposed the normal distribution of area sizes belonging to the same core area (to the same faunal type), the graph of the centrifugally decreasing species number represents the inverse of the cumulative graph of the normal distribution, which can be subdivided into three sectors by tangents of maximal convexity and concavity of the graph (fig. 1): the sector of 1. zonal distribution, 2. disaggregation and 3. the extinction of the faunal type in question. The normal distribution of the area sizes will be performed only under ideal conditions. Under real circumstances it is strongly influenced by climatic, orographical and other conditions. For instance, the Pyrenees and the Carpathians have served as effective barriers of dispersal in numerous atlanto-mediterranean (including Lusitanian) and ponto-mediterranean (including Balkanic) species, respectively. Thus, in these faunal types the number of species with restricted areas is relatively high, as illustrated by the numerous Iberian and Balkanic endemics.

In the Palaearctic region there are two main consequences of dispersal along gradients:

1. The overlap of zonobiomes along long-distance gradients: formation of transitions with overlaps of 'zonal' sectors of several faunal types, e.g. the overlap of Mediterranean (s.l.), Ponto-Caspian and Siberian (West-Siberian, Mandzhurian, East-Siberian) faunal types in the East European forest-steppe, with gradual decrease of the Mediterranean component and increase of the Siberian component along a west-eastern gradient (De Lattin 1957, 1967). This appears to be typical for the orographically less varied eastern European (Boreal, Continental and Steppic) regions.
2. The overlap of azonal communities along short-distance gradients resulting in the organisation of community-complexes ('sigmeta' of German phytosociological tradition) and landscape mosaics connected by habitat ecotones. These community-complexes are characterised by the overlap of several faunal types, both in zonal sectors and in sectors of disaggregation, e.g. the overlap of Mediterranean, Balkanic, Siberian, Ponto-Caspian, Ponto-Pannonian, Turano-Eremic and Xeromontane faunal elements in the Pannonian forest-steppe complexes (Varga 1989a, 1992, 1995, 1996, 1997). They have been proved to be rather dynamic overlaps, often with short-term fluctuation dynamics, especially in the boundary regions of lowland and hilly areas, with a variety of relatively stable versus mobile ecotones.

The orographically varied landscapes of Central Europe and the Carpathian basin display several different cases of short-distance overlaps. Southern parts of Central Europe, North of the Alps and Balkans (like southern France, southern Germany, hilly parts of the Carpathian basin, Williams et al. 1999, 2000) belong to the regions of Europe having the highest number of species in vascular plants, in some groups of insects and vertebrates, without a significant fraction of point-endemics. This clearly demonstrates the importance of the overlap of different floral and faunal elements populated this region post-glacially from different core areas.

The mosaic-like structure of the traditional Central European cultural landscape with a variety of managed open habitats and their ecotones (hedges, ridges, lines of trees, forest fringes etc.) in a forested matrix proved to be rather suitable to preserve the connectivity of habitats and also a high level of *compositional* diversity. A large number of species has been successfully adapted to moderate perturbations (extensive grazing, mowing by hand, coppicing), typical for traditional land use (fig. 2).

Endemism and autochtonous evolution in the Carpathian basin

Core areas are characterised by numerous endemic taxa. The level of endemism is generally correlated with the geological age of the refugia where relict-like taxa have been evolved and/or could survive (Fjeldså & Lovett 1997). From a geological point of view, the Carpathian basin belongs to the youngest areas of Europe. Its relief has developed under the influence of the Alpine orogenesis and by retreat of the Pannonian inland sea. There are, however, some taxonomical groups which show considerable proportion of endemic species, such as the land gastropods (Soós 1943), or some soil arthropods, like Opiliones and Diplopoda (Korsós 1994).

Most endemics are narrow specialists, inhabiting extreme habitats: thermal springs (Gastropoda: *Melanopsis parreysi* Philippi, *Theodoxus prevostianus* C. Pfeiffer), karstic caves (Gastropoda: Paladilhia hungarica Soós, *Paladilhiopsis* spe-

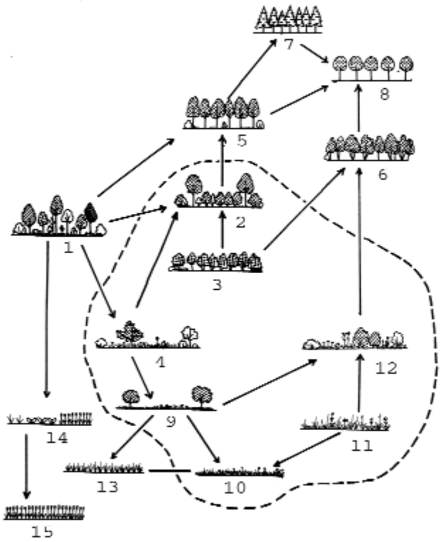

Figure 2
Habitat types and species diversity in the European cultural landscape. 1. virgin forest, 2. nature-like mixed forest after logging and abandoning, 3. young forest after coppicing ('Niederwald'), 4. grazed steppe forest ('Hudewald'), 5. homogenous managed forest ('Hochwald'), 6. dense medium-aged forest after repeated coppicing, 7. coniferous plantation, 8. deciduous, intensively used plantation, 9. wooded pasture, 10. extensively managed greenland (hayfield), 11. abandoned, semi-natural grassland with tall-forbs ('Versaumung'), 12. abandoned, semi-natural grassland with tall-forbs and scrubs, 13. intensive greenland, 14. traditional agricultural land, 15. intensively used, monoculture-like agricultural land. Area surrounded with broken line: habitat types with high species diversity.

cies; Palpigradi: *Eukoenenia vagvoelgyii* Szalay; Amphipoda: *Niphargus* species; Isopoda: *Mesoniscus graniger* I. Frivaldszky; Diplopoda: *Brachydesmus troglobius* Daday, *Haasea hungarica* Verhoeff, *Hungarosoma bokori* Verhoeff; Carabidae: *Anophthalmus*, *Duvalius*, *Typhlotrechus* species) and karst springs (Gastropoda: *Sadleriana pannonica* Frauenfeld; Trichoptera: *Drusus*, *Rhyacophila* species, mostly in the Apuşeni mountains and the eastern and southern Carpathians).

The endemic insects of the Carpathians are, as a rule, short-winged, flightless forms which have been isolated in 'massifs de refuge' (Orthoptera: *Isophya*, *Odontopodisma*, *Poecilimon* species; the relict-like species: *Capraiuscola ebneri* Galvagni, *Podismopsis transsylvanica* Ramme, *Uvarovitettix transsylvanica* Bazyluk & Kis, *Zubovskia banatica* Kis; Kis 1962a,b, 1965, 1980; Coleoptera, Carabidae: *Duvalius*, *Morphocarabus*, *Patrobus*, *Trechus* species; Curculionidae: *Otiorrhynchus* species) (some of these species have been suggested for inclusion into the Annex II-IV of the Natura 2000). The bulk of these endemic taxa is confined to the Eastern and Southern Carpathians, to the Apuseni mountains and to the mountains of Banat, which could preserve relict species (such as the Tertiary relict gastropods *Chilostoma banaticum* Rossmaessler, *Pomatias rivulare* Eichwald) or point-endemics (Orthoptera: *Capraiuscola ebneri* Galvagni, *Podismopsis transsylvanica* Ramme, *Uvarovitettix transsylvanica* Bazyluk & Kis, *Zubovskia banatica* Kis; Isopoda: *Hyloniscus transsylvanicus* Verhoeff, *Protracheoniscus politus* C.L. Koch; Diplopoda: *Entomobielzia gaetica* Verhoeff, *Karpathophilon dacicus* Verhoeff) in refugia of deciduous forests, in areas with not frozen soil during the younger glaciations (Bennett et al. 1991, Krolopp & Sümegi 1995, Willis et al. 1995).

In the more mobile insect groups, the proportion of endemism lies rather low. For instance, in Odonata no endemic taxa occur in the Carpathian basin. Most endemic Lepidoptera of the Carpathian basin belong to Microlepidoptera, which are strictly specialised to some food-plants and the females are flightless, for instance species of Coleophoridae: *Coleophora hungariae* Gozmány (*Camphorosma annua*), *C. peisoniella* Kasy (*Artemisia santonicum*), Gelechiidae: *Ilseopsis hungariae* Staudinger, *I. salinella salicorniae* E. Hering (*Salicornia prostrata*), living on halophytic plants in the saline grasslands of the Fertő-Neusiedlersee area and of the Great Hungarian plain (Kasy 1965, 1981). Endemic subspecies of Geometridae and Noctuidae have evolved in the same habitats, as peripheric isolates of turano-eremic species from the late-glacial, kryoxerotic periods, like *Narraga tessularia kasyi* Moucha & Povolny, *Saragossa porosa kenderesensis* Kovács (*Artemisia santonicum*, *A. pontica*) and *Discestra dianthi hungarica*

Wagner (*Gypsophila muralis*). Some endemic taxa of the sandy areas of the Pannonian lowland are specialised predators or parasitoids, such as the spider *Dictyna szaboi* Chyzer and the pompilid wasp *Cryptocheilus szabopatayi* Móczár. Further species described as endemics later proved to be widespread steppicolous species.

In 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 (for instance, in warm-humid alluvial areas: *Apamea sicula tallosi* Kovács & Varga, in Pannonian xerothermic oak forests: *Dioszeghyana s. schmidtii* Diószeghy, *Asteroscopus syriacus decipulae* Kovács, in the Villány mountains: *Polymixis rufocincta isolata* Ronkay & Uherkovich; in the dolomitic areas of the Transdanubian Middle Range: *Chersotis f. fimbriola* Esper, *Euxoa v. vitta* Esper, *E. hastifera pomazensis* Kovács, *Cucullia mixta lorica* Ronkay & Ronkay; in the Aggtelek Karst: *Chersotis fimbriola baloghi* Hacker & Varga). Similar connections can be observed in butterfly species, restricted to special, Pontic-Pannonian food plants, like *Plebeius sephirus* I. Frivaldszky (*Astragalus dasyanthus*, *A. exscapus*), *Melitaea telona kovacsi* Varga (*Cirsium pannonicum*).

Some endemic Macrolepidoptera subspecies of the Carpathians belong to the genera *Erebia* (*E. epiphron transsylvanica* Rebel, *E. pharte belaensis* Goltz, *E. manto traianus* Hormuzachi, *E. gorge fridericikoenigi* Varga, *E. pandrose roberti* Peschke, *E. pronoe regalis* Hormuzachi) and Glacies (*G. coracina dioszeghyi* Schmidt, *G. noricana carpathica* Schwingenschuss, *G. canaliculata schwingenschussi* Wehrli). Some endemic taxa are widespread in the Carpathians and in the neighbouring mountainous areas, like *Aricia artaxerxes issekutzi* I. Balogh and *Photedes captiuncula delattini* Varga, others are confined to the southern Carpathians, often with balkanic connections: *Erebia cassioides neleus* Freyer, *Coenonympha rhodopensis schmidtii* Diószeghy. The subspecies of *Erebia melas* inhabit island-like, calcareous mountain stocks, *Erebia m. melas* Herbst in Cernei mountain, *E. melas carpathicola* P. Gorj & Alexinschi in the eastern Carpathians and *E. melas runcensis* König in Apuşeni mountain). All these data clearly demonstrate that the Carpathians, especially the eastern and southern parts, together with the mountains of western Transsylvania (Apuºeni and Banat mountains) can be considered as core areas of survival and autochtonous evolution in many invertebrate groups of limited mobility. On the other hand, in the mobile insect groups, only peripherically isolated subspecies have been evolved, which display manifold biogeographic connections.

Relict species with long-distance disjunctions in the Carpathian basin

Several Mediterranean-Manchurian bicentric faunal elements with disjunct ranges occur in the Carpathian basin. The distribution of this species group is connected to the Ponto-Caspian waterway-system, and displays long-distance disjunctions from the eastern Asiatic vicariant taxa, which are often only subspecifically differentiated (Lepidoptera: *Apatura m. metis* Freyer – *Apatura metis substituta* Butler, *Chariaspilates formosarius hungaricus* Vojnits – *Chariaspilates f. formosarius* Eversmann, *Rhyparioides m. metelkanus* Lederer – *Rhyparioides metelkanus flavidus* Bremer, *Arytrura musculus* subspecies – *Arytrura m. musculus* Ménétries). Some species of this group occur at the lower course of the Danube and Drava and also in swampy-boggy areas of the lowlands in Transdanubia, in the Banat and eastern Hungary (*Polypogon gryphalis* Herrich-Schaeffer, *Herminia tenuialis* Rebel, *Diachrysia nadeja* Oberthur and also the species mentioned above). The refugia of these faunal elements had probably been at the lower course of the Danube and its tributaries. Gallery forests of the Illyrian and Pannonian type and alluvial wetlands accompanying the large rivers of the Pannonian lowland have served as corridors of the northward 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* Esper, widespread in West and Central Asia, South Siberia and in mountains of Italy and Balkan peninsula, had locally occurred – as *M. russiae clotho* Herbst – on tall-grass clearings of birch gallery forests of the sandy lowland in Kiskunság. Its extinction was partly the consequence of overcollecting, but mostly of destroying of the habitats (re-forestation with black locust *Robinia pseudoacacia*). The habitats of *Chondrosoma fiduciarium* Anker (Kasy 1965, 1981) are also tall-grass lowland and hilly steppes, often mixed with slightly saline patches. Other species are confined to open dolomitic rocky swards (*Phyllometra culminaria* Eversmann, *Lignyoptera fumidaria* Hübner, *Cucullia mixta lorica* Ronkay & Ronkay) or to open sandy and rupicolous grasslands (*Oxytripia orbiculosa* Esper, also vanishing). The rapidly growing garden suburbs of the Buda hills and the metastasis-like expansion of 'green-field' investments around the capital are the most recent threatening factors, often with considerable political and economical interests in the 'background'.

There are numerous halophytic food-plant specialists of the alkaline habitats, mentioned above, which are specifically or subspecifically differentiated. They represent marginal isolates of turano-eremic species, widespread in Transcaspia and Central Asia. The common characteristic feature of the area structure of these species is the large-scale disjunction between the Carpathian basin and the Eastern Ucranian-South Russian steppes.

Polycentric postglacial repopulation patterns in the Carpathian basin: areography and phylogeography

The Carpathian basin belongs to the regions of Europe, which have the highest biodiversity (Williams et al. 1999, 2000). Due to its transitional position during the Quaternary climatic fluctuations, the overlap and accumulation of the floristic and faunistic elements of contrasting habitats took place here. The overlapping of different climatic provinces, enhanced by the varied relief, edaphic and hydrographic conditions, has resulted in suitable conditions to survive for a large number of species, belonging to different core areas and displaying various patterns of long-distance and short-distance re-populations.

The 'molecular toolbox' of phylogeography (Roderick 1996) have facilitated the recent revisitation of many taxonomical and biogeographical problems. 'Hard' evidences gained by molecular studies could support, complete or correct some of the previous biogeographical hypotheses. For instance, numerous genetic analyses could verify the existence of different glacial refugia within the Mediterranean region (Assmann et al. 1994; Cooper et al. 1995, Demesure et al. 1996, Dumoulin-Lapègue et al. 1997, Hewitt 1996, 2000, Lagercrantz & Ryman 1990, Schmitt & Seitz 2001a, Schmitt et al. 2001, Taberlet & Bouvet 1994, Taberlet et al. 1994, 1998, Wallis & Arntzen 1989) and demonstrated, that several species have repopulated Central Europe in the post-glacial period from different refugia in more waves. The 'secondary subdivision' (De Lattin 1957, 1967, Reinig 1950) of the Mediterranean refugium has also been repeatedly demonstrated, for instance in *Chorthippus parallelus* Zetterstedt, in the European hedgehog (Santucci et al. 1998) or by the comparative area analysis of several plant and mammalian species (Cooper et al. 1995, Hewitt 1996, Taberlet et al. 1998). The importance of the Siberian refugium (s.l.) has been pointed out (Nève 1996, Taberlet & Bouvet 1994, 1998) and evidence has been found supporting some kinds of the Mediterranean-Siberian polycentry in several cases (Nève 1996, Schmitt 1999, Schmitt et al. 2000, Schmitt & Seitz 2001b). In contrast with the opinion of De Lattin (1957, 1967), these results confirm the statement of the author (Varga 1975, 1977, 1989b) that the montane part of the ranges of several boreo-montane species has not been established by post-glacial 'Siberian' invasion, but has been formed by South European montane refugia. Results of selected lepidopterological studies are summarized here.

The Illyrian-Dacian vicariant taxa: the importance of the southwest-southeast 'pincer'

Because the Carpathian basin had occupied a transitional position between the Balkanic refugia and the cold-continental periglacial loess steppe zone during the glacial periods, the postglacial repopulation of the Carpathian basin has proceded both 1. by long-distance dispersal from the more remote (atlanto- and ponto-) Mediterranean and southern continental refugia, and 2. from some adjacent local survival areas, for instance from Northwest Balkanic ('Illyrian') versus South Transylvanian ('Dacian') Arboreal refugia. In such cases the 'arrows' of the northward dispersal of the southwestern and southeastern populations surround the mostly arid central part of the basin. These components of the flora and fauna extend northwards on the one hand through the foothills of the eastern Alps and Southwest-Pannonian hilly regions, and through the hilly regions of the Banat area and the western foothill of the Transylvanian 'Island' mountains (Apuşeni mountain), on the other. These areas are also characterised by some secondary precipitation maxima of sub-Mediterranean type during the 'aequinoctial' periods of the year.

In some cases the populations of the southwestern and southeastern 'strains' do not display any significant taxonomical differentiation, for instance in the silver lime (*Tilia tomentosa*) or some butterflies and moths (*Pyronia tithonus* Linnaeus, *Maculinea arion ligurica* Wagner, *Aplasta ononaria* Fuessly, *Idaea nitidata* Herrich-Schaeffer, *Zanclognatha tenuialis* Rebel). Much more evident is the repopulation 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 be mentioned mostly for land gastropods, like *Pomatias elegans* O.F. Müller – *P. rivulare* Eichwald, *Chilostoma illyricum* – *C. banaticum* Rossmaessler, or in flighless insect groups, like short-winged Orthoptera: *Odontopodisma schmidti* Fieber – *O. rubripes* Ramme, *Isophya modestior* Brunner von Wattenwyl – *I. stysi* Cejchan. In the latter pair of species, a clear differentiation in the stridulation and in allozyme pattern has been observed (Orci et al. 2001, Pecsenye et al. in prep.). In addition, some vicariant atlanto- versus ponto-Mediterranean sibling pairs can also be observed in the more mobile insect groups, as in the butterflies *Spialia sertorius* Hoffmannsegg and *S. orbifer* Hübner.

The Mediterranean-Siberian polycentricity in the Carpathian basin

There are numerous cases of vicarious 'Siberian' (s.l.) – Mediterranean/arboreal and 'Siberian' (s.l.) – Mediterranean/oreal sibling taxa. By 'Siberian' we understand all continental arboreal species dispersed north of the steppe zone and which did not pass into the Mediterranean region. They have formed the ultimate peripheric isolates in the high mountains of this area, which represent a 'fluctuation belt' of Siberian faunal type (Varga 1977). The 'Siberian' species are widespread in temperate Eurasia ('Euro-Siberian' or trans-palaearctic type of area), and usually exhibit a wide range of morphological variation and ecological valence (e.g. the butterfly species *Maculinea arion* Linnaeus, *Melitaea phoebe* Denis & Schiffermüller, *Mellicta athalia* Rottemburg, *Euphydryas aurinia* Rottemburg). Their Mediterranean vicarious taxa (sibling species or semispecies) are usually confined to one of the Mediterranean 'secondary refugia' (De Lattin 1957, 1967): *M. a. ligurica* Wagner to the Adriato-Mediterranean, *M. ph. telona* Fruhstorfer to the ponto-Mediterranean, *P. m. malvoides* Elwes & Edwards, *M. a. celadussa* Fruhstorfer and *E. a. desfontainei* Boisduval to the atlanto-Mediterranean refugia.

They also often have a considerable range of variation, in some cases due to the incomplete reproductive isolation and hybridisation with the 'Siberian' taxa. Habitats, food-plants and phenological traits of the Siberian-Mediterranean vicarious pairs are often different. *Maculinea a. arion*, for instance, is connected to short-grass swards with cushions of *Thymus* species (Thomas 1995), which is the initial larval foodplant (exceptionally also *Origanum vulgare*). On the contrary, the initial foodplant of *Maculinea a. ligurica* is exclusively *Origanum vulgare*. The imaginal period is synchronised with the flowering period of *Thymus* and *Origanum*, respectively, because the females usually deposit the eggs on flower capitula of the initial food-plant. Thus, sympatric populations of both are ecologically and seasonally isolated. The Siberian species, *Melitaea phoebe* is euryoecious, polyphagous (with food-plants: *Centaurea*, *Carduus*, *Cirsium* species etc.) and widespread in the Carpathian basin. In contrast, the Ponto-Mediterranean sister (semi-) species *M. telona* is restricted to forest-steppe mosaics with semi-dry swards, where its larval food-plant, *Cirsium pannonicum* is abundant. *Melitaea phoebe* is regularly bivoltinous, while *M. telona* only exceptionally produces a very scarce second brood in the Carpathian basin.

In the case of the Siberian – Ponto-Mediterranean oreal pair of heath butterflies *Coenonympha tullia* Müller and *C. rhodopensis* Elwes the isolation is complete, as the vicarious taxa occupy only topographically, but not ecologically overlapping

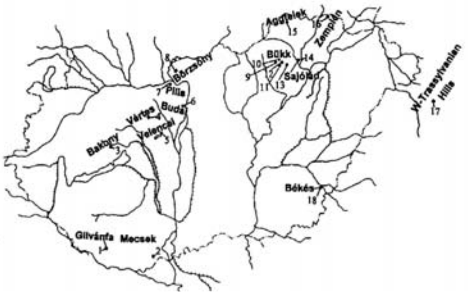

Figure 3
Sampling localities of *Parnassius mnemosyne* populations. 1. Gilvánfa, 2. Misina (Mecsek mountains), 3. Hárskút (Bakony mountains), 4. Vérteskozma (Vértes mountains), 5. Nadap (Velencei mountains), Nagyszénás (Budai mountains), 7. Pilisszentkereszt (Pilis mountains), 8. Magas-Tax (Börzsöny mountains), 9. Bányahegy (Bükk mountains), 10. Lusta valley (Bükk mountains), 11. Gyertyán valley (Bükk mountains), 12. Hollóstetö (Bükk mountains), 13. Kékmezö (Bükk mountains), 14. Sajólád, 15. Nagyoldal (Aggtelek karst), 16. Nagy-Milic (Zemplén mountains), 17. Szokácsi forest (West-Transsylvanian hills), 18. Békés.

areas in the Dinaric karst area. Similar trends have also been observed in the polymorphic lycaenid *Aricia artaxerxes* Fabricius – *inhonora* Jachontov – *allous* Geyer – *montensis* Verity superspecies, consisting of Siberian, European (sub-)alpine and Mediterranean-oreal taxa. The phylogeographical analysis of such supraspecific groups can explain some basic trends of the Quaternary faunal history in the Palaearctic.

In this context, the results of Schmitt (Schmitt 1999; Schmitt & Seitz 2001b) proved to be especially relevant. He subdivided the European populations of *Erebia medusa* Denis & Schiffermüller into five main groups, based on the study of 19 enzyme loci in 53 samples. The ‘West-Central European’ group (*E. medusa brigobanna* Fruhstorfer) consists of populations from France and Germany and one single sample from the Czech Erz mountains. The large ‘East-Central European’ group (*E. m. medusa* Denis & Schiffermüller) includes all populations from Czechia, Slovakia and North Hungary. The third group of populations is formed by those of West Hungary (and probably also West Balkans; *E. medusa narona* Fruhstorfer), while the isolated deme from Monte Baldo (southern Alps; *E. medusa hippomedusa* Ochsenheimer) shows the most extreme differences. *Erebia medusa psodea* Hübner, which is externally the most different subspecies, occurring in the South Carpathians and East Balkans, was not studied electrophoretically. The highest level of genetic variation has been found in the East-Central European group, which can probably be derived from a large, extended East European (and Siberian?) refugial population of the last glacial period. The observed genetic differences strongly support the hypothesis, that all subspecies have survived at least the last glaciation in different refugia.

Genetic differentiation and metapopulation structures in some butterflies in the Carpathian basin

Populations of some butterfly species have been studied in the Carpathian basin at different geographical scales. Populations of *Parnassius mnemosyne* Linnaeus and *Euphydryas maturna* Linnaeus have been compared both in larger and smaller regional scales, while populations of *Aricia artaxerxes* Fabricius and *Maculinea alcon* Denis & Schiffermüller – *M. rebeli* Hirschke have only been studied in a smaller region.

Parnassius mnemosyne: Populations from 11 geographical regions (Transdanubian Middle Range: Bakony, Vértes, Velencei, Budai and Pilis mountains; Mecsek mountains; Northern Middle

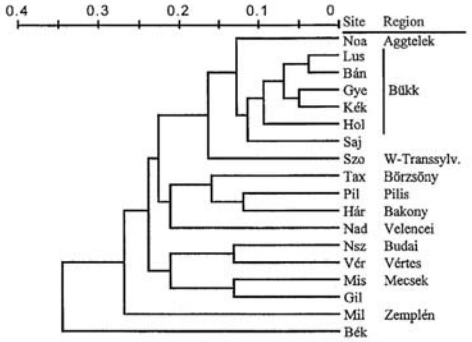

Figure 4
UPGMA dendrogram of *Parnassius mnemosyne* in Hungary, constructed on the basis of Cavalli-Sforza and Edwards chord genetic distances.

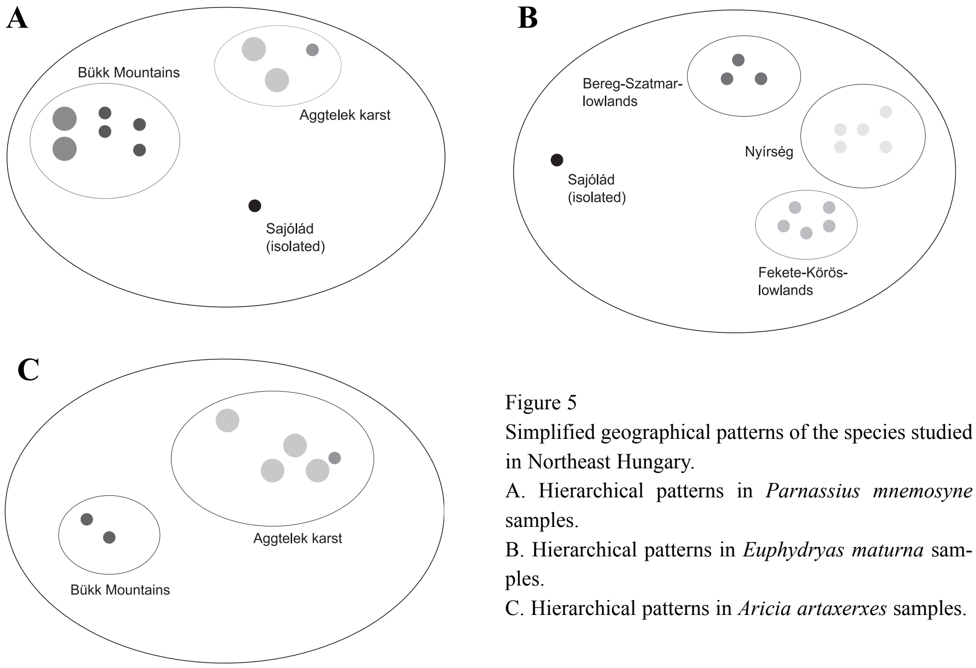

Figure 5
Simplified geographical patterns of the species studied in Northeast Hungary.
A. Hierarchical patterns in *Parnassius mnemosyne* samples.
B. Hierarchical patterns in *Euphydryas maturna* samples.
C. Hierarchical patterns in *Aricia artaxerxes* samples.

Range: Börzsöny, Bükk, Aggtelek karst, Zemplén mountains; lower foothills of the West-Transylvanian mountains) and three lowland isolates (Sajolád, Dráva valley, Black Körös valley) were sampled in Hungary and the neighbouring part of Rumania (fig. 3). The UPGMA dendrogram constructed on the basis of Cavalli-Sforza and Edwards genetic distances did not indicate a clear geographic pattern (fig. 3, 4, 5). The branching pattern among the populations from the Börzsöny mountains and Transdanubia did not correlate with the geographical distances between sampling localities. Populations of the Bükk mountains were clustered together, and they also showed genetic similarity to the Sajolád isolate, which is only separated by 15 km of unsuitable habitat from the Bükk mountains. These results support Eisner's statement (1954) who grouped most of the Transdanubian populations into one subspecies (*P. m. litavia*). When populations from Northeast Hungary (except for the Zemplen population) were also added to the Transdanubian data set, the F_{st} value hardly increased. If we accept that the populations of the Vértes, Budai, Bakony and Velencei mountains are all members of one subspecies, almost all the other investigated populations (except for Zemplén mountains and the Körös valley) should be also grouped to the same subspecies. The Zemplén and Körös valley populations proved to be genetically distinct. Meglécz et al. (1997) demonstrated that the Bükk populations exhibit metapopulation structure. Only occasional differentiation was observed between Bükk populations, while significant genetic differentiation was found between almost all pairs of populations from different regions. Even the small, recently isolated Sajolad population was found to be genetically different from the Bükk region.

Euphydryas maturna: Most of our samples originated from three regions of the eastern part of the Pannonian lowland (Bereg-Szatmár lowland, Nyírség and Black Körös valley), but also from some populations in southern Transdanubia and the North Hungarian middle range. The isolated population of the Sajólád forest was considered as a distinct region in this case as well. The UPGMA dendrogram constructed on the basis of Cavalli-Sforza and Edwards genetic distances shows that – as opposed to *P. mnemosyne* – most of the genetic variation could be observed among the populations within the regions, while the differentiation according to regions merely shows a lower level. Within all regions, all populations showed significantly different F_{st} values. Thus, no evident geographical differentiation has been established (fig. 5).

Aricia artaxerxes: Two larger isolates of this species, described as *A. artaxerxes issekutzi* I. Balogh occur in the North Hungarian-Slovakian karst region and in the Bükk mountains. The number of alleles pro loci was higher in the Karst region than in the Bükk mountains. Some rare alleles (e.g. *Est*, *Got*, *Mdh*, *Pgi*, *Pgm*) observed in the 'Karst' populations were lacking from the samples of the Bükk mountains. On the other hand, the frequency of the heterozygotes was not significantly lower in the Bükk mountains. In addition, the genetic differentiation of all samples proved to be significant. It means that the level of genetic differentiation shows a stronger correlation with the frequency distribution of the more frequent alleles than with the presence/absence of rare alleles.

Significant deviations from the Hardy-Weinberg equilibrium were found at several loci (*Adh-1*, *Adh-2*, *Aldox*, *Est*, *Idh*). The Fisher's exact test has shown a significant heterozygote deficiency in both regions, which was mostly expressed in the *Aldox*, *Est* and *Me* loci. These results are confirmed also by the F-statistics. The populations showed a considerable level of genetic variance (F_{it}), in which the 'within populations' fraction proved to be larger than the 'between populations' fraction ($F_{is}>F_{st}$). The F_{is} values were significant at the *LDH*, *EST*, *ME* loci, while the F_{st} values at the *PGM*, *GOT*, *EST*, *ME*, *ADH*, *ACON*, *GDH* loci, and the F_{it} values at the *GOT*, *LDH*, *EST*, *ME*, *ADH*, *GDH* loci.

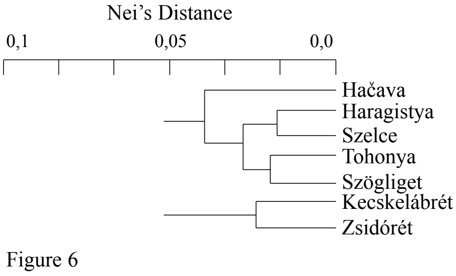

Figure 6

UPGMA dendrogram of the North Hungarian / South Slovakian populations of *Aricia artaxerxes*.

The UPGMA dendrogram constructed on the basis of Nei genetic distances, for both years 1999 and 2000, showed a peculiar geographical pattern also within the Karst region populations. The sample from the higher Zadielska planina (Hačava) was clearly separated from the other ones, and the pattern of differentiation of populations essentially reflected the vertical subdivision (higher versus lower karst plateaux) of the region (fig. 5, 6).

Summarizing conclusions: biodiversity and conservation priorities in the Carpathian basin

The Carpathian basin, and within it Hungary, shows a high level of biodiversity, despite the fact that in Hungary there are no high mountains nor any littoral habitats. As an explanation of this richness, the transitional biogeographical position of the Carpathian basin can be mentioned (see paragraph 2). The highest level of biodiversity has been observed in some marginal areas where the overlapping of several different faunal components has taken place, like the western and southwestern parts of Transdanubia with the overlap of Pannonian, Illyrean and Alpine influences and also the northeastern edges of the country with the overlap of Pannonian, Carpathian and Dacian influences. Accumulation of diverse faunal elements also took place at the colline altitudes of the Hungarian middle range, where the overlapping of Mediterranean (Holo- and Ponto-Mediterranean, Balkanic and Anatolian) elements has succeeded. Conservation centres of relict species – often as endemic species/subspecies – are typical for the edaphically extreme habitats which could resist against the postglacial re-forestation and could preserve the elements of earlier climatic periods under special ecological constraints. These patterns of species diversity are well demonstrated by the manifold composition of insect assemblages of vegetation complexes consisting of mosaic-like patterns of forest, skirt and grassland compartments. A nested hierarchy of diversity is present at levels of populations, communities, community-complexes (sigmata) and landscapes.

Recently, the biogeographical division of Europe has been completed by the addition of five further biogeographical regions: Arctic, Pannonian, Steppic, Black Sea and Anatolian (Natura 2000, directive 92/43/CEE, 1997). It means, that due to its peculiar biogeographical character, the Pannonian region has been recognized as equivalent to the further 11 large regions of Europe. The 'Areas of Special Conservation Interests' was completed with the list of threatened types of natural habitats which require special conservation measures (1998). In the Pannonian region at least 36 of these habitat types occur, and some of the most significant European stands of them can be preserved in this region. Studies on the biogeographical composition of the flora and fauna of the Carpathian basin exhibit also some important applied aspects.

The indicative value of species largely depends on their biogeographical character. Thus, the habitat lists and the species lists of the European nature conservation information systems and conventions (like the CORINE-system, the Habitat Directive and Natura 2000) must be revised, according to biogeographical points of view. Threatened species with scattered occurrence in Central Europe are often widely distributed in Eastern Europe. We have numerous species, vanishing or being in decline in Central and western Europe, which are represented in our region at least partly by strong populations. Strong, viable populations of such species can be successfully protected mostly in these regions, inter alia, in the Carpathian basin (*Euphydryas maturna*, *Lycaena dispar rutila*, *Maculinea teleius* etc.). In addition, the typical ecosystems of the Pannonian region (loess, sandy and alkali grasslands, rupicolous swards, white oak scrub forests etc.) exhibit numerous characteristic invertebrate species which do not occur more westwards than the Hungarian middle range, or in some cases the foothills of the Vienna Basin, South Slovakia and Moravia. Numerous characteristic species of the Pannonian region are connected with special habitat structures, like traditionally managed ecosystems, structured grasslands or forest-skirt/grassland complexes of the Pannonian forest-steppe (like many grasshopper and butterfly species). Effective conservation of them is possible only by preserving of the connectivity of their populations and metapopulation structures at the landscape level. The solution of these problems has outstanding importance for the protection of the natural heritage of the Carpathian basin, but also for Europe.

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