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GEOGRAPHICAL PATTERNS OF BIOLOGICAL DIVERSITY IN THE PALAEARCTIC REGION AND THE CARPATHIAN BASIN

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Species diversity varies spatially. It can be characterised not only by some latitudinal and longitudinal gradients but also by numerous *core areas*, i.e. by restricted territories with cumulated presence of stenochorous ("*endemic*") species.

Patterns of diversity can be explained by the spatio-temporal dynamics of the processes which i. generate diversity by speciation, ii. reduce diversity by extinction.

A major part of the core areas served as *conservation centres of forested biomes* in their regressive phases during the younger Pleistocene. The periodical expansion of the "*non-forest*" biomes during the glaciations (e.g. periglacial tundra and loess steppe) has isolated the forest refugia. On the other hand, the extension of the grassland and desert biomes was restricted by the recurrent inter- and post-glacial spread of wooded biomes.

The Carpathian Basin with a mosaic pattern of forested and open landscapes displayed very intricate dynamics of faunal types during the Quaternary period. Its geographically transitional position resulted in a conspicuous mixture of faunal elements of diverse origin and geographical history. The compartment structure of the vegetation complexes, typical for the Pannonian forest-steppe, has promoted the survival of some strictly localised, relict-like faunal elements. Especially the hilly areas of transitional climatic conditions, surrounding the Pannonian lowland are populated by numerous, biogeographically significant species and communities.

Key words: area dynamics, speciation, core areas, glacial refuges, oreal fauna, faunal types, Carpathian Basin

GENERAL CONSIDERATIONS

Area Dynamics and Speciation

Species diversity is generated by branching processes called *speciation* which can be interpreted as a partition of the genetic variation into discrete units separated by reproductive isolation. The subdivision of the formerly – at least potentially – coherent gene-pool may arise under the constraints of the niche-structure of the ecosystem, i.e. *diversity generates diversity*. On the other hand, processes of speciation are subjected to the spatio-temporal changes of the habitats in which the populations are living. Hence, the patterns of species diversity can be described in terms of the community structure and by the regularities of the geographical distribution of species and natural, monophyletic higher taxa, as well.

A general strategy of searching for repetitive patterns studied by the geographical ecology, has been formulated by MACARTHUR (1972): "The imperfection of repetitions gives us the means of making comparisons". Some basic repetitions are given in the distribution patterns of flocks of species (i.e. *faunal types*) which have essentially similar ranges with only slightly modified geographical boundaries in the individual cases.

By the overlapping of similar areas of small or moderate size, some surfaces of congruence are to be outlined which can be characterised by a cumulated presence of stenochorous ("*endemic*") species (cf. DE LATTIN 1967, MÜLLER 1974, 1977, VARGA 1975, 1977). The presence and evolutionary significance of these core areas can be corroborated by the existence of homologous structures in the subspecific division of widely dispersed, often disjunct polytypic species and also by species abundance centres of monophyletic supraspecific units, i.e. genera, subfamilies or families.

The evolutionary explanation of these core areas is based on the principle that biotic diversity is a result of events of differentiation within spatially isolated populations, accumulated over time. According to the refuge modell (BROWN 1982, CRACRAFT 1982, 1983, CRACRAFT & PRUM 1988, Haffer 1976, 1977, MÜLLER 1974 ff.) *core areas arose as the results of cyclical expansion and contraction of forested versus nonforested biomes during the Quaternary climatic fluctuations.*

The "pacemaker" of these evolutionary events was the "*antagonistic dynamics*" (DE LATTIN 1967) of the macrohabitat types which are contrasting by the strikingly different level of their primary production (cf. Table 1, cf. VARGA 1975, 1977). The periodical subdivision of formerly continuous biomes into geographically isolated refuges has generated the evolution of vicariant taxa. This "*dichopatric*" type of subdivision has succeeded several times and the relative constancy of the refuge areas, determined by the major paleogeographical features, resulted in a high probability of species conservation, which have survived or/and evolved (as neo-endemics) in these core areas. The summation of these speciation and species conservation events which took place in the core areas, are responsible for the high level of species diversity of these territories.

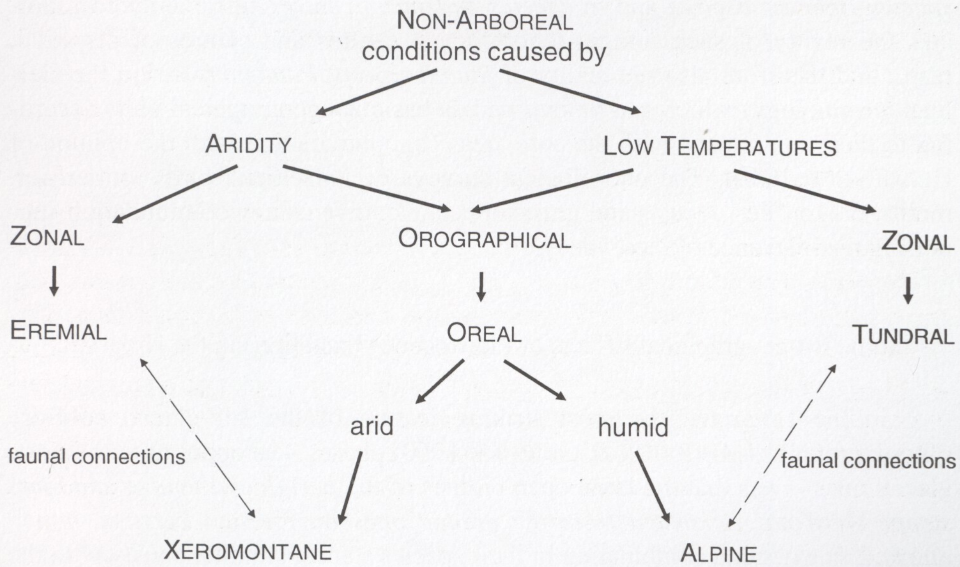
Review of the Quaternary Area Dynamics of Biomes

The general validity of these ideas on speciation and species diversity was supported by numerous surveys carried out on different continents. They have confirmed that a major part of the core areas (i.e. centres of endemism) served as conservation centres of forested biomes during their regressive phases in the course of the younger Pleistocene. Most studies, published during the last two

Table 1. Comparison of arboreal vs. non-arboreal biomes

	Arboreal	Non-arboreal
Duration of water circulation	more than 3 months	less than 3 months
Primary production in one year	moderate – high: 25-500 q/hectar	low, less than 25 q/hectar
Structure of vegetation	several layers (synusia)	only one (or two) layers
Temperature budget of the surface	like water surface	like bare rocky surface
Soil, humification, nitrification	more layers, intensive humification, mycorrhiza, intensive nitrification	immature, skeletic soils, slow and local humification

Biogeographical Review of Non-Arboreal Biomes and Faunal Types



decennia, concentrated on the elucidation of the paleogeographic history of the tropical rain forest ("*Hylaea*") biome, undoubtedly one of the most fascinating treasuries of actual biodiversity (cf. BROWN 1982, 1987, CRACRAFT 1983, 1985, CRACRAFT & PRUM 1988, HAFFER 1974, 1976, 1977, 1987, MÜLLER 1974, 1977, PRANCE 1973, 1987, SIMPSON & HAFFER 1978 etc.). Centres of endemism in flowering plants, butterflies, reptiles and birds were outlined and compared in several studies. An essentially similar history of taxon pulse has been pointed out in the arboreal biomes of Australia, too (CRACRAFT 1982). The evolutionary significance of the – at least partial – concordance of core areas was improved also by cladistic analyses which have corroborated the general ideas on "*dichopatric*" events and explained their temporal sequence during speciation.

In the Holarctic the disjunct patterns of distribution of numerous arboreal genera are well known (cf. REINIG 1937, 1938, 1950, DE LATTIN 1953, 1956, 1967, MATJUSHKIN 1972, 1982, SCHINTLMEISTER 1989, etc.) and interpreted by the refugial model. A large number of vicariant taxa – species or subspecies depending on the rate of differentiation – demonstrates the evolutionary significance of the core areas which served as centres of dispersal ("*Ausbreitungszentren*", cf. DE LATTIN 1956, 1967) for the post-glacial re-forestation and re-population of Holarctic temperate biomes.

Although the distinction of the effects of the historical, evolutionary events from the consequences of the recent ecological factors is often difficult, if not impossible (cf. ENDLER 1982*a, b*), I think that the high level of *concordance in species richness centres* and in *species endemism centres* sufficiently corroborates the reality of such refugia (chorological centres and centres of dispersal, resp.) and therefore also the reality of *faunal types* ("*Faunenkreise*" in the German terminology) which can be outlined as basic zoogeographical units according to their consistence with the core areas (in contradiction with the opinion of HENGEVELD 1990). The chorological surveys of Palaearctic birds, butterflies, moths, dragonflies, locusts and grasshoppers etc. give us a wide foundation supporting the relevance of these ideas.

Some Biogeographical Effects of Pleistocene Glaciations in the Holarctic

In the Holarctic, the most striking feature of the late-glacial cold-dry ("kryoxerotic", cf. GRICHUK & GRICHUK 1960) phases – as opposed to the postglacial ones – was that the large open biomes of the *periglacial tundra and loess steppe were not separated from the eremic ones* by forested barriers, which allowed an extended combination in their species stands, simultaneously with the contraction of the forested biomes and refugial isolations in the distribution ranges of their inhabitants.

On the contrary, in the interglacial and postglacial phases, *the expanding forest biomes have disjointed the range of open macro-habitats* (cf. VARGA 1975, 1977, 1989). The orographically limited, azonal oreal biomes have been generally separated from the tundral zonobiomes which were forced to "creep" northwards. The steppe zonobiomes were also completely separated from the tundral ones, but only partially from the oreal habitats. In the less continental climatic belts, the forested zonobiomes have been inserted between the arctic tundral and semi-arid steppe biomes. Thus, they became completely divided by wide and manifold forested territories.

On the other hand, in the vast Central and Inner Asiatic regions the forested belts became scattered, fragmented into the regionally or locally more humid macro-slopes of the mountains. Thus, the mountain steppes and semi-deserts continuously intergrade into the xerophytic high-mountain vegetation (cf. the vegetation zonation of the ranges Pamir, some parts of Hindukush and Tienshan, Mongol and Gobi Altaj, see: AGAHANJANTS 1981, BRECKLE 1974, SIPOS and VARGA 1992, etc.). This gradient is a powerful potential of faunal mixing, too (VARGA *et al.* 1989).

Several *centres of endemism are lying in the arid-semiarid mountain belts* and the introgression of their expansive elements into the steppe zonobiome seems to be a general feature of distribution patterns in numerous genera, rich in species and typical for the arid-semiarid (*xeromontane*) mountaineous habitats of Central Asia (VARGA 1976, 1977, 1993, VARGA & RONKAY 1987, VARGA *et al.* 1989, VARGA *et al.* 1990, RONKAY 1988, RONKAY & VARGA 1990, HACKER 1992*a,b*, HACKER & RONKAY 1992, etc.).

Evolutionary Role of Aridisation in the Temperate Grassland Biomes

The faunal changes of the Palaearctic have been described up to the present mostly in terms of the fluctuation of cold, glacial and warm-temperate, interglacial or interstadial phases. Several conclusions, however, drawn from the very recent climatic changes, called the attention the processes of aridisation which can succeed in fairly different temporal dimensions. The economic and social effects of the actual aridisation of Central and Inner Asia, proceeding nowadays too, involve numerous consequences which are, unfortunately, only very incompletely realized by the "developed" countries. We know only some very rough outlines of the scenario of the general aridisation during the last thousand years which led to the complete desertification of Sahara and resulted in the decline of the famous civilisations of city-states (Samarkand, Bokhara) in Central Asia.

These processes have resulted in a decimation and marginal isolations of the Afro- (and Pan-) tropical elements in the Maghreb area and the relict-like isolations of Mediterranean elements in the old massifs of the Sahara, surrounded by deserts (pers. comm. BORHIDI 1993). These phenomena are, however, only the culmination of a long course of events, which began with the areal glaciation of the Antarctica during the Miocene and conduced to a radical decrease of the deep-sea temperature and to a global regression of the sea-level. As a consequence of the increasing continentality, extended open biomes emerged which resulted in a radical change in foraging strategy and life-history of numerous phytophagous groups, e.g. the emergence of grass-feeding Ungulates, the first large radiation of rodents, the arise of subterraneous way of life in convergent groups of rodents and *the emergence of the cutworm-type life-history of noctuid-moth caterpillars*, etc.

Some Trends of Evolution in the Oreal Biomes in the Palaearctic

By the evolution of all these non-arboreal zonobiomes and orobiomes, together with their typical *faunations*, the biogeographical counterpart of the arboreal ones has been established and the northward spread of the "*Kathaysian*" arboreal elements was forced to pass through some *filter-corridors.* Numerous elements of the monsoonic mountain forests could penetrate to the South-Siberian high-mountains (STEGMANN 1937, VARGA 1977, VARGA *et al.* 1990). Two-

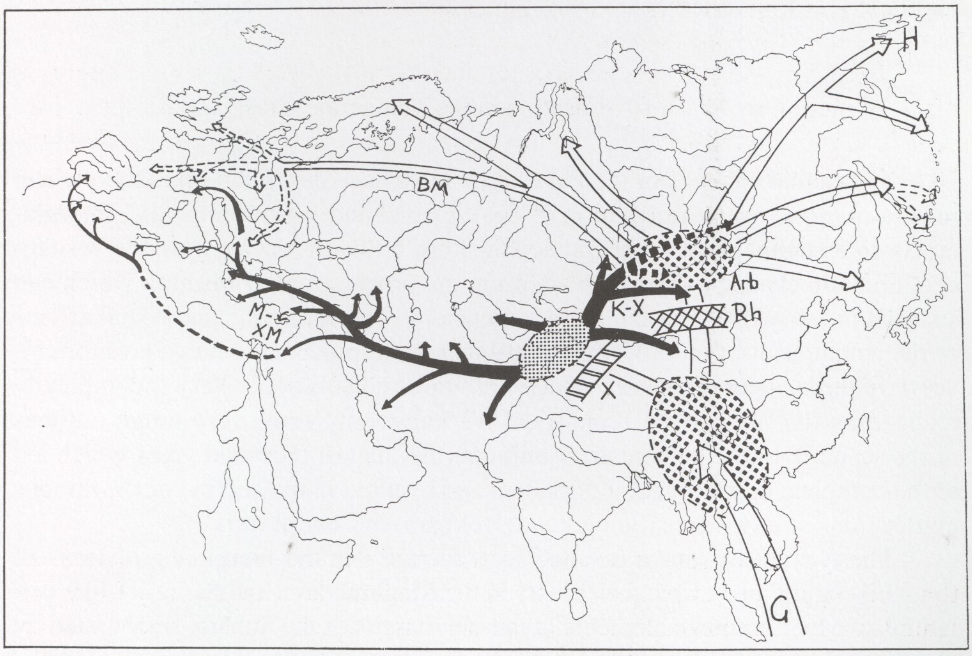


Fig. 1. General features of faunal migrations in the Palaearctic. G = Gondwanian connections, X = Xeromontane filter and main bifurcation in the Xeromontane fauna, M–XM = Mediterrane–xeromontane faunal types, K–X = Continental xeromontane faunal types, Rh = "*Rhododendron*"-filter in the Monsoonic arboreal fauna with secondary centre of diversity in Southern Siberian mountains, B–M = Boreo-montane connections, H = Holarctic connections

fold consequences of this process have been derived: the origin of Holarctic-circumboreal distribution of cold-adapted elements of the temperate forest-belts (mainly: coniferous, taiga) on the one hand, and the formation of disjunct SE-Asiatic – South-Siberian ranges after the breakdown of this corridor by aridisation of Central Asia, on the other. The importance of the Southern Siberian mountain taiga as possible *primary core area* of boreal-Holarctic Noctuidae species agrees well with new data on a *Beringian refuge*, as the most recent centre of survival and dispersal of these elements during the late-glacial and postglacial phases (MIKKOLA *et al.* 1991).

An other part of the biota of the monsoonic orobiomes has been constrained to penetrate across the so-called "*xeromontane*" filter, because at the end of the Tertiary a progressive glaciation of the perpetually emerging Himalaya-Transhimalaya chains and Tibet plateau took place which resulted in a general climatic re-arrangement of the whole Central Asiatic region (HSÜ JEN 1981, 1984, LI JI-JUN *et al.* 1981). The Transhimalaya–Karakoram–Ladakh area and the Tienshan system became main centres of differentiation of the continental xeromontane fauna in the Palearctic. By the phylogenetic–systematic analysis of some xeromontane groups of Noctuidae it was pointed out that the *diversification of numerous genera was subdivided into two main lineages* (VARGA 1989).

Secondary centres of diversification arose in the Mediterranean semi-arid high-mountains from Atlas range to Asia Minor and also in the West-Central-Asiatic territory from the Armenian plateau through Iran and Turkmenistan to the Hindukush and Pamir ranges, where an overlap of both types of xeromontane fauna can be observed (VARGA 1976, 1977, 1989, 1992, VARGA & RONKAY 1987, 1989, VARGA *et al.* 1989, VARGA *et al.* 1990, HACKER & VARGA 1989, RONKAY & VARGA 1990, etc., Fig. 1).

AREA DYNAMICS, EVOLUTION AND DIVERSITY PATTERNS IN THE CARPATHIAN BASIN

Zones and Landscapes

It is typical for southeastern Central Europe that the large-scaled zonal settling of vegetation, characteristically developed in the vast Eastern European table-land, breaks down. In the Carpathian Basin a more or less concentric arrangement of vegetation belts is to be observed, modified by numerous climatic, orographic, hydrographic and edaphic factors. The "overall zonality" is replaced by a mosaic-like interlocking of individual landscapes. The forest-steppe, typical for the major, central lowland and hilly part of the basin, is represented here by a number of its regional variants, showing distinct geological features, edaphic properties and meso-climatic characters (cf. VARGA 1989). The forest, skirt and grassland "compartments" of each regional variant of the forest-steppe are highly interdependent and correlated. The forested belts of this district display also their local or regional features, determined by the prevailing climatic influences and also by the peculiar character of the neighbouring mountain system (Alps and Carpathians, resp., but in some cases, the mountains of the Balkan Peninsula, too). The orobiomes of the Carpathians are "archipelago"-like, regionally well-differentiated, which depends on the varied contribution of alpine, continental and balcanic influences.

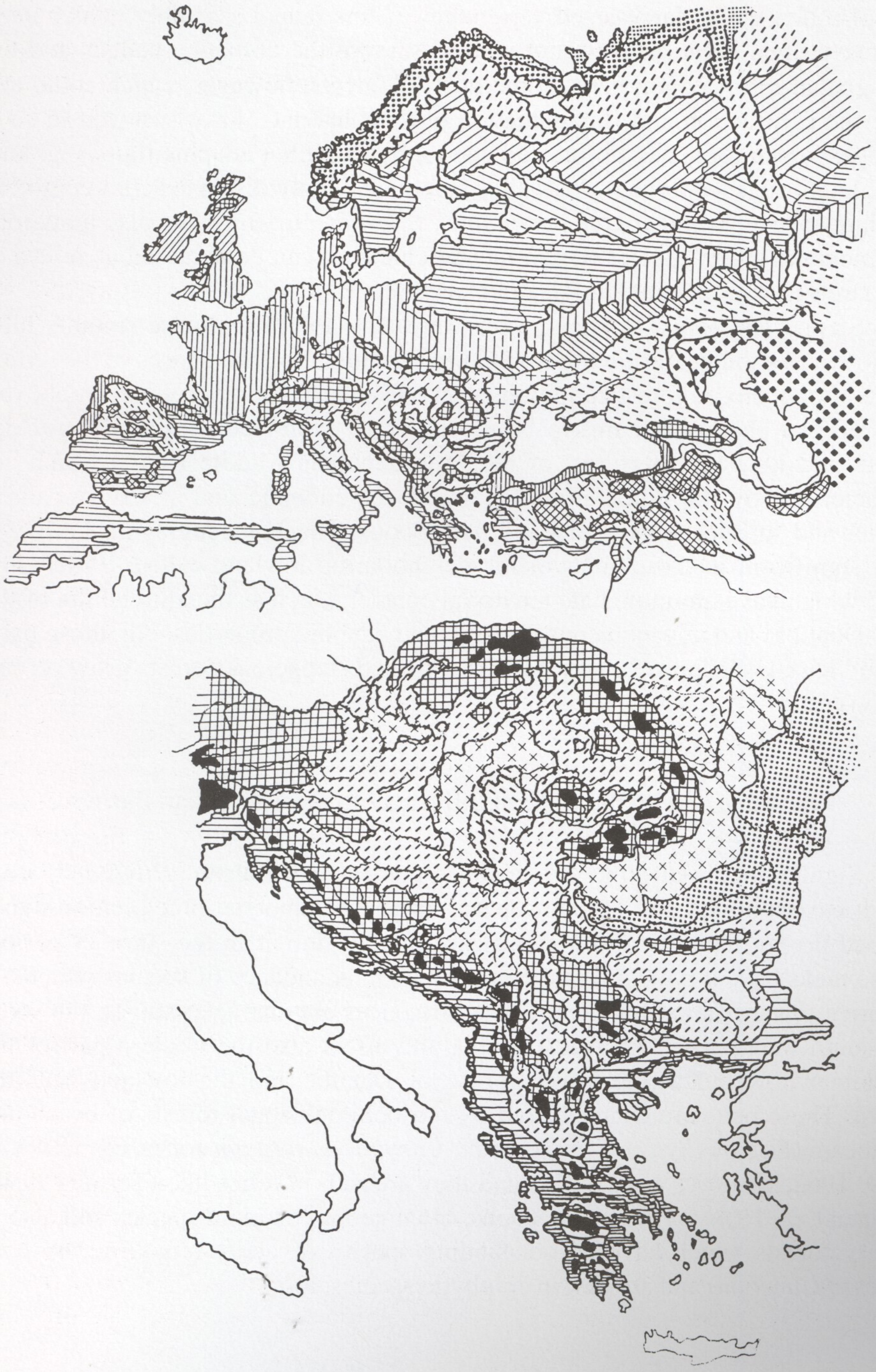
The biogeographical features of a given territory are determined by their own natural endowments and by the various influences, coming from neighbouring territories, as well. The most significant regional biogeographic influences in the Carpathian Basin are as follows.

Dispersal History of the Steppe Elements: The Forest – Steppe Dynamics

The Hungarian Middle Range occupies a central position in the Carpathian Basin not only in topographical sense. Their southern, xerothermic slopes and foothills (called "Ősmátra", cf. BORBÁS 1908, *cit.* SOÓ 1959, SOÓ 1929, 1940, 1959, ZÓLYOMI 1949, 1953, 1957, 1964, WENDELBERGER 1954, 1973, etc.) 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, as well. Thus, the thermophilous elements probably populated the Carpathian Basin not only by long-distance colonisation from remote, large glacial refuges, but also – especially after the last, late glacial and early post-glacial cold phases – from numerous meso- or microclimatically favourable sites, lying at the continuously fluctuating borderline of the Mediterranean refugial and periglacial belts. The varied and fine biostratigraphical structure of the Hungarian young Pleistocene, which is often characterised by a coexistence of forest and non-forest faunal elements (JÁNOSSY 1979, KORDOS 1977, KRETZOI 1953, 1967, 1977, etc.), provides evidences to support this view and demonstrate 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.

The cold phases of the Würm glaciation can be characterised by a simultaneous presence of tundral (*Lemmus, Dicrostonyx, Microtus gregalis, Gulo, Rangifer*), tundro-alpine (*Lagopus*), oreal (*Rupicapra, Ibex*), cold-steppe (*Lagurus, Allactaga, Cricetulus, Ochotona, Marmota*) and cold-adapted forest (*Lyrurus, Castor, Alces, Mustela erminea, Talpa*, etc.) elements. This faunal mixture sug-

Fig. 2. Breakdown of general in SE Central Europe – geographical background of faunal diversity



gests the presence of a varied vegetation of fairly high productivity which provided for large flocks of grazing Ungulates, Proboscidea and also for a great variety of rodents. The large-sized vertebrates of this faunal assembly, which need extensive open habitats, were not able to survive the climatic changes and the post-glacial reforestation here. Some of its elements, however, which could tolerate the contraction and fragmentation of their habitats, have survived in such biotopes which remained unforested due to their peculiar edaphic traits, e.g. kurgans, loess ridges, dolomite grasslands etc. Such widely dispersed cold-continental plant species as *Agropyron pectinatum, Eurotia ceratoides* and also numerous xeromontane insect species of continental character can be regarded as relicts of the extremely continental late-glacial phases (cf. VARGA 1989).

Steppe and forest-steppe species were also able to colonise suitable hilly and lowland habitats during the Boreal period and during the phases of the retreat of the humid, closed forest zonobiomes (cf. "Ősmátra"-theory, references above). The refugial character seems to be most clearly expressed in a number of dolomite and limestone territory of the Transdanubian Middle Range which are characterised by the cumulative occurrence of endemic and strictly localised species and subspecies of plants and Arthropods. Their biogeographical effect is most significant in those areas of the neighbouring lowland called "*Praematricum*" which have an immediate territorial contact, (such as the alluvial fan of the river Danube) and advantageous climatic and edaphic properties, e.g. those parts of the "Kiskunság" area in which grasslands and steppe oak forests grow on calcareous sand.

Balcanic and Mediterranean Influences in the Carpathian Basin

Significant are also the influences of the Western Balcan ("*Illyrean*") areas which have a humid sub-Mediterranean climate, equinoctial precipitation maxima and do not have usually a significant rainfall deficit in the summer period. These areas have a typical forest climate and an abundance of species which are sensitive towards a hard winter. These influences are characteristic on the south and south-western part of Transdanubia and affect also the western part of the Pannonian lowland at the lower course of Danube and the lowland near the Drava. These belts are characterised by mesophilous zonal forests of beach and hornbeam (*Fagion illyricum* and *Querco-Carpinion illyricum* zones, cf. HORVAT 1959, 1962, HORVAT *et al.* 1974) and they are rich in relict-like (Tertiary or interglacial, cf. HORVAT *l.c.*) herbaceous, often geophytic plant species and also in gallery forests which have an outstanding species diversity (e.g. *Fraxino pannonicae-Ulmetum*) and are rich in epiphytic species, too.

The influence of the Eastern Balcan territories has a double character, because these areas are transitional between a continentally influenced sub-Mediterranean and the steppe climate. These influences are present along the western border of the W Transylvanian Mountains (Bihar Mts, Mts Apuseni) and along the great rivers of the eastern part of the Pannonian lowland. The surprising occurrence of some southern elements in the NE part of the Pannonian plain (e.g. Nyírség) and in the sub-Carpathian lowland and hilly regions (MAHUNKA 1993, VARGA 1989, VARGA in FÉSÜS *et al.* 1991) can be explained by this dispersal route. Some eastern Balcanic influences reach also the Hungarian Middle Range where the relict-like occurrences of some Balcanic and Balcanic-Anatolian elements (e.g. the Noctuid moths *Asteroscopus syriacus* WARREN and *Dioszeghyana schmidtii* DIÓSZEGHY) are present, especially in the warm foothill zone where also significant sub-Mediterranean influences prevail.

The Mediterranean – mostly sub-Mediterranean and ponto-Mediterranean – influences are also significant. Some representatives of these faunal types occur as northernmost marginal isolates in different parts of the Carpathian Basin. Especially rich in such, relict-like elements are e.g. the surrounding of the "*Iron Gate*" at the lower course of Danube, the island-like hilly parts of Southern Transdanubia (Villány Hills and Mecsek Mts) and the xerothermic oak forest and scrub-forest belt of the Hungarian Middle Range with its very diverse and valuable forest-steppe communities, mostly on dolomite and limestone. The relative richness of the calcareous sandy area of Kiskunság region in Mediterranean elements can be explained by its meso-climatic character and by its territorial connection with the former area ("Praematricum"), as well. The taxonomical isolation of populations of some Mediterranean, Balkanic and Balkanic-Anatolian elements demonstrates the possibility of the existence of some local refugia in climatically favourable parts of the Carpathian Basin during the last glaciations.

Carpathic and Alpine Influences in the Carpathian Basin

The Transylvanian ("Dacian") influences occur in relation to the forested areas of the Eastern Carpathians and often transmitted by the western Transylvanian mountains. The occurrence of some Dacian elements is typical for the eastern part of the Hungarian Middle Range, especially in the higher parts of the volcanic Eperjes-Tokaj range (=Zemplén range) and in the Karst areas of Northern Hungary and Southern Slovakia. Isolated, relict-like occurrences of Dacian elements (Tettigonoidea: *Isophya modestior stysi* CEJCHAN, *Pholidoptera transsylvanica* FISCHER-WALDHEIM; Carabidae: *Carabus hampei ormayi* REITTER) have been recently discovered on the small, island-like volcanic hills of the NE (Bereg) Plain.

The influences of the Northern Carpathians are in our territory the most significant in the NE part of the Hungarian Middle Range. There is, however, a characteristic difference between the Eperjes-Tokaj volcanic chain, on the one hand and the limestone plateau of the Bükk Mts and N Hungarian Karst area, on the other. The biotic contact of the Eperjes-Tokaj range with the Carpathians is a young, obviously postglacial one and can be characterised mostly by the presence of species which are either typical for the montane forest belt of the Carpathians (e.g. numerous Gastropoda: *Bielzia coerulans* BIELZ, *Vestia gulo* BIELZ and Carabidae: *Carabus obsoletus* STURM, *C. zawadszkyi* KRAATZ, *Abax schueppeli* LETZN.) or widely dispersed in the northern part of Central Europe, having often a wide Euro-Siberian distribution. The Bükk Mts, however, displays a very interesting insular character and its Carpathian and de-Alpine elements (e.g. Gastro-

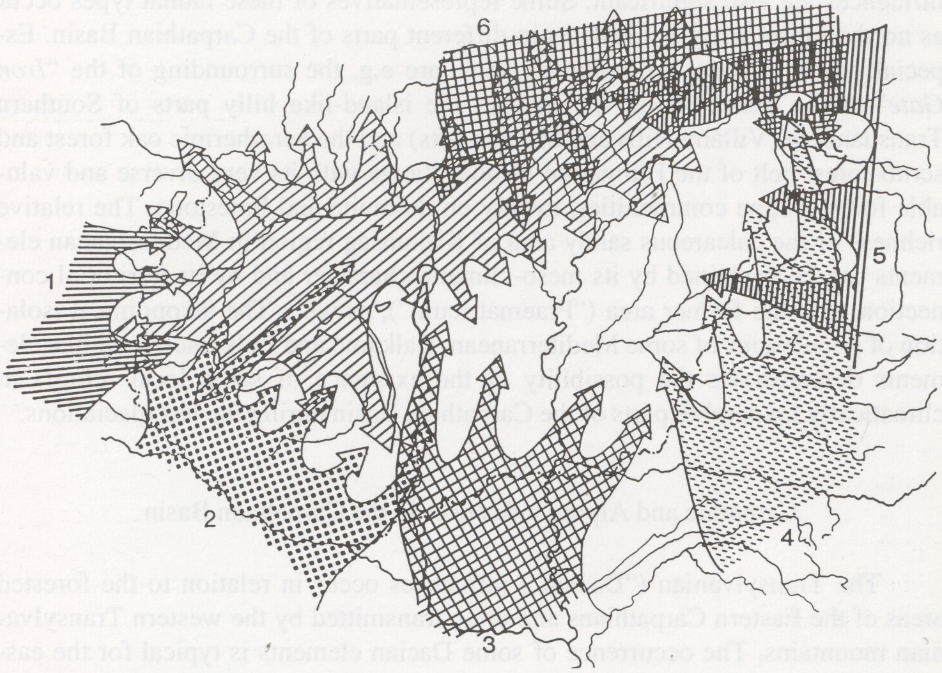


Fig. 3. Biogeographically relevant sources of faunal diversity in central part of the Carpathian Basin. 1 = Alpine–de-alpine faunal elements, 2 = Illyrian (W Balcanic) faunal elements, 3 = expansion route of some Mediterranean species along the Danube valley, 4 = Moesian (E Balcanic) faunal elements, 5 = Dacian (Transylvanian) faunal elements, 7 = Submediterranean elements expanding along the Middle Range ("Ősmátra"), NB = Xeromontane elements have only isolated relict sites

poda: *Spelaeodiscus triaria* ROSSMAESSLER, *Phenacolimax annularis* STUDER, Lepidoptera, Geometridae: *Entephria cyanata gerennae* GYULAI) are often relict-like which have no actual contacts with the populations living in the Carpathians. In the N-Hungarian Karst area the immediate area contact with the higher limestone plateaus of Slovakia is combined with the occurrence of Carpathian (Gastropoda: *Bielzia coerulans* BIELZ, *Cochlodina cerata* ROSSMAESSLER, *Trichia unidentata* DRAPARNAUD; Carabidae: *Carabus obsoletus* STURM, *C. zawadszkyi* KRAATZ, *Abax schueppeli* LETZN., *Trichotichnus laevicollis carpathicus* SCHAUBG.), boreal (Gastropoda: *Vertigo substriata* JEFFREY) and xeromontane species at surprisingly low altitudes, influenced by the special meso-climatic and geomorphological features of this area. It is also worth to mention that some influences of the Northern and Eastern Carpathians are to observed at the NE marginal areas of the Pannonian lowland, too, i.e. at the upper reaches of the river Tisza and its tributaries (e.g. the occurrence of Gastropoda: *Vitrea diaphana* STUDER, *Bielzia coerulans* BIELZ, *Balea stabilis* L. PFEIFFER, *Perforatella dibothrion* KIMAKOWICZ, *P. vicina* ROSSMAESSLER etc.).

The Alpine (mostly: eastern Alpine, "Noric") influences are typical for the mountainous areas of Western Transdanubia (Kőszeg and Sopron Mts and the N-NW part of the Bakony Mts). They are, however, not high enough and originally nearly completely forested, thus, they could not preserve a greater number of dealpine species.

Distribution of Continental Species in the Carpathian Basin

The boreal and boreo-continental influences are often combined with Carpathian and Alpine ones. The explanation of this situation is quite simple: the Carpathians have a screening effect from northern and eastern directions. Thus, the boreal elements could penetrate into the Carpathian Basin either mediated by the Carpathians or – passed round – at the eastern border of the Alps and through the "*Porta Hungarica*". As a consequence of this situation, we can observe the highest number of boreal elements in the northeastern part of the Hungarian Middle Range, on the one hand, and in the hilly-mountainous part of western Transdanubia on the other. Relict-like occurrences of boreal and boreo-continental (Siberian) species are present also in some parts of the Pannonian lowland, too, especially in the swampy-boggy areas of the northeastern part of the plain. Some small, isolated peat-bogs have preserved the relict-like ecosystems of the cool-continental early post-glacial periods.

Representatives of Mediterranean-Manchurian faunal elements with disjunct area also occur in some parts of the Carpathian Basin. The distribution of this species group is often connected with the Ponto-Caspian waterway-system and displays actually interrupted connections with eastern Asiatic vicariant, often only subspecifically differentiated taxa (e.g. *Apatura metis* FREYER, *Arytrura musculus* MÉNÉTRIES, *Rhyparioides metelkanus* LEDERER). The refuges of such faunal elements were mostly at the lower course of Danube and its tributaries. Some species of this group occur also at the lower course of Dráva and in some swampy-boggy areas of the lowland in western Transylvania and eastern Hungary.

The influences of the Ponto-Caspian steppe belts are characteristic for the Carpathian Basin. Some of their elements are recent invaders, e.g. the butterfly *Colias erate* ESPER, dispersed during the last 10-15 years in great part of the Carpathian Basin, reaching E Austria and SW Slovakia. Other members of this group need large open habitats. Hence, they are threatened by retreat and fragmentation of great, open grasslands, e.g. the great bustard, *Otis tarda* L. Numerous steppe species fluctuate at the western limit of distribution, e.g. *Glareola nordmanni* FISCHER, *Pastor roseus* L. Typical inhabitants of the grasslands of lower altitudes are: *Mustela eversmanni* LESSON, the grasshoppers *Dociostaurus brevicollis* EVERSMANN and *Gampsocleis glabra* HERBST, etc. Others are restricted to isolated sites of edaphic grasslands, e.g. *Stenobothrus eurasius* ZUBOWSKI, *Arcyptera microptera* FISCHER-WALDHEIM, *Isophya costata* BRUNNER v. W. They can be regarded as relicts from the post-glacial steppe period, corroborated in some cases also by geographical isolation and taxonomical differentiation, as well, e.g. *Vipera berus rakosiensis* MÉHELY or the Zephyr blue (*Plebejus sephirus* FRIVALDSZKY) with four isolated colonies in the Carpathian Basin: sandy grasslands near Budapest, the Tokaj Hills, the Deliblát sandy area and steppe-like habitats of the Transylvanian "Mezőség").

Patterns of Distribution in Eremic and Xeromontane Species

Eremic, mostly turano-eremic species are restricted to some semi-desert-like habitats of the lowland with extreme edaphic conditions. There are very few vertebrate representatives of this faunal type: perhaps *Sicista subtilis* PALLAS and the "Hungarian" short-toed lark, *Calandrella brachydactyla hungarica* HORVÁTH belong to this group. More abundant examples can be found in some strictly localised phytophagous insects which are often connected with special halophytic plant communities of the lowland. They are often represented by endemic Pannonian subspecies or allopatric sibling species of Turanian origin, e.g. the Noctuid moths *Saragossa porosa kenderesiensis* KOVÁCS and *Discestra dianthi hungarica* WAGNER or the Microlepidoptera: *Coleophora hungariae* GOZMÁNY, *C. klimeschiella* TOLL, *C. magyarica* BALDIZZONE, *C. peisoniella* KASY, *Holcophora statices* STAUDINGER, *Stenodes coenosana* MANN, *Scrobipalpa semadensis plantaginella* STAINTON, *Agriphila tersella hungarica* SCHMIDT, etc.

The dispersal of this species group could have originally taken place in the late glacial (*kryoxerotic*) phases on the Pannonian Lowland, with a subsequent complete isolation as a result of the post-glacial expansion of the forested belts.

Last but not least, xeromontane elements are also present in the Carpathian Basin. Their two main groups are: the *Mediterranean-xeromontane* species, represented by very few vertebrates (e.g. *Monticola saxatilis* L. or the secondarily more expanded *Phoenicurus ochrurus* GMELIN), but a larger number of species in some insect groups, e.g. Noctuidae (*Euxoa vitta* ESPER, *E. decora* DENIS & SCHIFFERMÜLLER, *E. birivia* DENIS & SCHIFFERMÜLLER, *Dichagyris candelisequa* DENIS & SCHIFFERMÜLLER, *Yigoga nigrescens* HÖFNER, *Chersotis margaritacea* VILLIERS, *Ch. fimbriola* ESPER, *Apamea platinea* TREITSCHKE, etc.) and Orthoptera (e.g. *Paracaloptenus caloptenoides* BRUNNER v. W.). The *continental xeromontane* type is represented by some members of widely distributed Asiatic mountain steppe species as *Euxoa recussa* HÜBNER, *Dichagyris musiva* HÜBNER, *Heliophobus kitti* SCHAWERDA (Noctuidae) and by some relict-like inhabitants of the rocky dolomit grasslands as *Phyllometra culminaria* EVERSMANN, *Lignyoptera fumidaria* HÜBNER (Geometridae), etc.

It seems to be very probable that numerous genera, typical for the steppe biome have a xeromontainous origin (especially *Lycaenidae: Agrodiaetus*, species groups of *Polyommatus* and *Plebeius*; Satyridae: *Chazara, Pseudochazara, Hyponephele*; Noctuidae: *Euxoa, Agrotis, Dichagyris, Yigoga, Rhyacia, Chersotis, Eugnorisma*, etc.). The same is to be supposed in the case of numerous endemic elements of the Pannonian flora (*Linum dolomiticum, Seseli leucospermum, Ferula sadleriana, Onosma tornense*, etc.). These connections give us the valuable possibility of a large, continental-scale generalisation of the "Ősmátra"-theory.

Endemic Taxa and Autochthonous Evolution in the Carpathian Basin

Core areas are usually to be characterised by several endemic taxa. The level of endemism is, as a rule, highly correlated with the geological age of the refuges in which the relict-like taxa could survive and have been evolved. The Carpathian Basin belongs, however, to the geologically youngest areas of Europe with a rather eventful paleogeographical history during the Tertiary and Quaternary periods, thus, a very high level of endemism cannot be expected here. This statement is, however, at least in this generalised form, surely misleading. For instance, in the terrestrial Gastropoda of the Carpathian Basin the contribution of the endemic species reaches more than 30%. L. SOÓS (1943) in his great monograph on the Mollusca of the Carpathian Basin wrote (p. 453): "The level of endemism in our fauna (i.e. Carpathian Basin) is so high, as it used to be only in in-

Table 2. Distribution of the endemic species and subspecies in the Carpathian Basin

	Gastropoda (Carpathian basin; Soós 1943)	Orthoptera (Carpathian basin; Kis 1980)	Diurna (only ssp.)	Noctuidae (only ssp.)
Carpathians (incl. Carpathian-Sudetian)	10			2
Northern Carpathians		0/1	9	
Eastern Carpathians	7	7/0	1	
Southern Carpathians	17	6/0	8	2
Northern + Eastern Carpathians	1			1
Eastern + Southern Carpathians	2		5	
Villány Mts				1
Mecsek Mts	1			
Pannonian Lowland	3	0/4	9	10
N Hungarian Karst	1			1
Bihar Mts	1			
Bánát Mts	15	3/0		2
Transylvanian Basin			4	1

sular faunas". Similar situation can be observed in several groups of soil arthropods, too.

On the other hand, endemic species and subspecies represent only some few (mostly less than 5) percent of the fauna in most insect groups. Their regional distribution displays some typical patterns. The bulk of endemic taxa is confined to the Eastern and Southern Carpathians and in the mountains of Bánát, e.g. in Orthoptera. The majority of their endemic species are flightless mountain-inhabiting insects, belonging to genera *Isophya, Poecilimon* and *Odontopodisma*, furthermore the relict-like species: *Zubovskia banatica* KIS, *Miramella ebneri* GALVAGNI, *Podismopsis transsylvanica* RAMME, *Mischtschenkotetrix transylvanicus* BAZYLUK & KIS (KIS 1962*a,b,* 1965, 1980). Similarly, most endemic Coleoptera belong also to flightless genera (e.g. some Carabidae and Tenebrionidae). A high proportion of the endemic Coleoptera leads a cavernicolous way of life (e.g. many species of the genera *Duvalius, Neotrechus, Typhlotrechus, Anophthalmus, Patrobus*, etc.). They are, as a rule, closely related with congeneric, high-mountain-inhabiting petrophilous species which are also often confined to some strictly defined parts of the Carpathians (e.g. bulk of *Duvalius* species).

In the more mobile insect groups, the proportion of endemism lies rather low, e.g. in Odonata no endemic species or subspecies occur in the Carpathian Basin. Most endemic species of Lepidoptera in the Carpathian Basin belong to those

Endemic subspecies of Noctuidae in the Carpathian Basin

Pannonicum
- *Chersotis fimbriola fimbriola* ESP.
- *Euxoa vitta vitta* HBN.
- *Dioszeghyana schmidtii schmidtii* DIÓSZ.
- *Saragossa porosa kenderesensis* KOV.
- *Discestra dianthi hungarica* WAGN.
- *Asteroscopus syriacus decipulae* KOV.
- *Apamea sicula tallosi* KOV. & VARGA
- *Cucullia mixta lorica* RONKAY & RONKAY

N Hungarian Karst
- *Chersotis fimbriola baloghi* HACKER & VARGA

Villány Mts
- *Polymixis rufocincta isolata* RONKAY & UHERKOVICH

S Carpathians
- *Apamea zeta sandorkovacsi* VARGA & PEREGOVITS
- *Hadena caesia* ssp.

Bánát
- *Copiphana olivana deliblatica* RONKAY

Transylvanian Basin
- *Conisania poelli ostrogovichi* DRAUDT

Carpathians
- *Photedes captiuncula delattini* VARGA
- *Apamea rubrirena rubrirena* TR.

families of "Microlepidoptera" which are, as a rule, strictly specialised to some special food-plants and – in addition – often with secondarily flightless females, e.g. some Coleophoridae, living on halophytic species in saline grasslands of the Fertő-Neusiedlersee area and of the Great Hungarian Plain, e.g. Kiskunság and Hortobágy (KASY 1965, 1981). In "Macrolepidoptera" practically all endemic taxa belong to the subspecific level. Endemic subspecies of butterflies occur mostly in the Carpathians (see: *Erebia: E. epiphron transsylvanica* REBEL, *E. pharte rodnaensis* P. GORJ et SZABÓ, *E. pandrose roberti* PESCHKE, *E. manto traianus* HORMUZAKI, *E. pronoe regalis* P. GORJ) and in some island-like, mostly calcareous mountain stocks, often obviously with Balcanic areal connections (e.g. *Erebia melas melas* HERBST, *E. melas carpathicola* P. GORJ, *E. melas runcensis* KÖNIG, *E. cassioides neleus* FREYER, *Aricia artaxerxes issekutzi* BALOGH).

Endemic subspecies of Noctuidae have evolved partly as peripheric isolates of turano-eremic species from the late-glacial, *kryoxerotic* periods, e.g. *Saragossa porosa kenderesensis* KOVÁCS and *Discestra dianthi hungarica* WAGNER, in majority, however, as thermophilous post-(inter?)glacial relicts with connections to the Balcan peninsula, Asia Minor or Southern Russia (e.g. *Chersotis fimbriola fimbriola* ESPER, *Ch. fimbriola baloghi* HACKER et VARGA, *Euxoa vitta vitta* ESPER, *E. hastifera pomazensis* KOVÁCS, *Dioszeghyana schmidtii schmidtii* DIÓSZEGHY, *Cucullia mixta lorica* RONKAY & RONKAY, *Asteroscopus syriacus decipulae* KOVÁCS, *Apamea sicula tallosi* KOVÁCS & VARGA, *Polymixis rufocincta isolata* RONKAY & UHERKOVICH). Similar connections are present also in some butterflies, e.g. *Plebeius sephirus* FRIVALDSZKY, *Melitaea telona kovacsi* VARGA.

All these data clearly demonstrate that the Carpathians, especially the Eastern and Southern ones, together with the mountains of western Transsylvania

(Mts Apuseni and Bánát) can be evaluated as *core areas of survival and autochthonous evolution* in many invertebrate groups of *limited mobility*. On the other hand, in the *mobile insect groups*, only *peripherically isolated subspecific taxa* have been evolved which display manifold biogeographic connections.

CONCLUDING REMARKS

The results of this brief survey can be summarized from several aspects. It is a conspicuous fact that the very – and artificially – limited area of Hungary could preserve a relatively high level of biodiversity. It is very remarkable, especially if we take into consideration that there are no high-mountains and littoral habitats within this area.

To offer a possible explanation of this situation we can mention the transitional state of the Carpathian Basin with the overlap of several vegetation, floristic and faunal types, the mosaic-like arrangements of "individualistic" landscapes within the basin with their peculiar features of biotic composition, the compartment-structure of the Pannonian forest-steppe communities and – last but not least – the historical backgrounds of this recent situation.

The highest level of biotic diversity is observed, on the one hand, in some marginal areas where the overlapping of different elements is the most evident, e.g. the western and southwestern parts of Transdanubia with the overlap of Pannonian, Illyrean and Alpine influences and the northeastern edges of the country with the overlap of Pannonian, Carpathian and Dacian influences. The Mediterranean influence is practically significant on the major part of the country, the boreal one, however, only at the pre-Alpine and pre-Carpathian belts. Conservation centres of relict-like species (often as endemic species or subspecies) are typical for the edaphically extreme habitats which could resist the post-glacial reforestation and could preserve – under special ecological constraints – the relict-like elements from earlier climatic periods.

An other cumulation of faunal elements took place at the lower altitudes of the Hungarian Middle Range, where the overlapping of diverse Mediterranean, e.g. holo- and ponto-Mediterranean, Balcanic and Anatolian elements has succeeded. These patterns of species diversity is well demonstrated by the composition of insect assemblies living in xerothermic oak forests.

These patterns of species diversity prescribe to us several tasks of nature conservation. We have to continue our national programme of MAB Biosphere Reserves, we have to begin our forest-reserve programme and we have to outline a "*green network*" of nature-like and semi-natural habitats which counterbalance the splitting and fragmentation of nature-like habitats and connect the isolated nature conservation areas.

In order to fulfil these tasks, we need a new approach to biology education, too. Different branches of the organismic and supra-organismic biology were often depreciated as "descriptive", old-fashioned, etc. These views are especially deteriorative for the young generation which more and more lose immediate contact with nature. Systematic biology has nearly disappeared from the university curricula in several countries and the importance of evolutionary biology is often underestimated, too.

As a consequence of this situation, some deformations are evident in the development of the ecology, too. The neglecting of the necessity of a precise identification of the material, the one-sided "only-modelling" without a solid basis of facts, the underestimation of field studies on natural populations and communities, etc. are the typical symptoms. Unfortunately, the mentioned trends are not "Hungarian specialities". Nearly the same experiences were communicated during a "Biodiversity" symposium of the Swiss Academy of Sciences, Basel 1992, by scientists and university lecturers coming from several countries.

A Hungarian entomologist, J. MAJER put the question: "Are the taxonomists threatened species?" It would be quite tragic if only by the "Disappearing Biodiversity" (JUHÁSZ-NAGY 1993) could we suddenly realise the vital importance of systematic and evolutionary studies.

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