A photograph of a grassy field with purple flowers and trees in the background. The text is overlaid on the image.

Biogeographical connections of Pannonian steppic woods

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Biogeographical connections of Pannonian steppic woods

Synopsis

- **Biogeographical setting of the Palaearctic forest-steppe zone:
The sub-Mediterranean and the continental type of the forest-steppe zone**
- **Case studies from Eastern Palaearctic semi-arid belts:
Turkmenistan, Kazakhstan and Mongolia**
- **Compositional traits of Pannonian forest-steppe: dynamics of faunal types**
- **Case studies: Habitat types of steppic forests and forest-steppe sigmeta: Insect flagship species and assemblages**
- **Recent dynamics of sigmeta: fringe structures (*"Versaumung"*)**
- **Vegetation and faunal history and phylogeography of the Pannonian region – examples and preliminary conclusions**

Biogeographical connections of Pannonian steppic woods

In the Pannonian region different **species compositions** and different **habitat structures** overlap. General ecological rule: **ecotones evolve along the environmental gradients**.

At the contact zones of extended zonobiomes **macro-ecotones** can be observed and also the **texture** of the vegetation is patchy in large-scale (e.g. in Eastern European table-land).

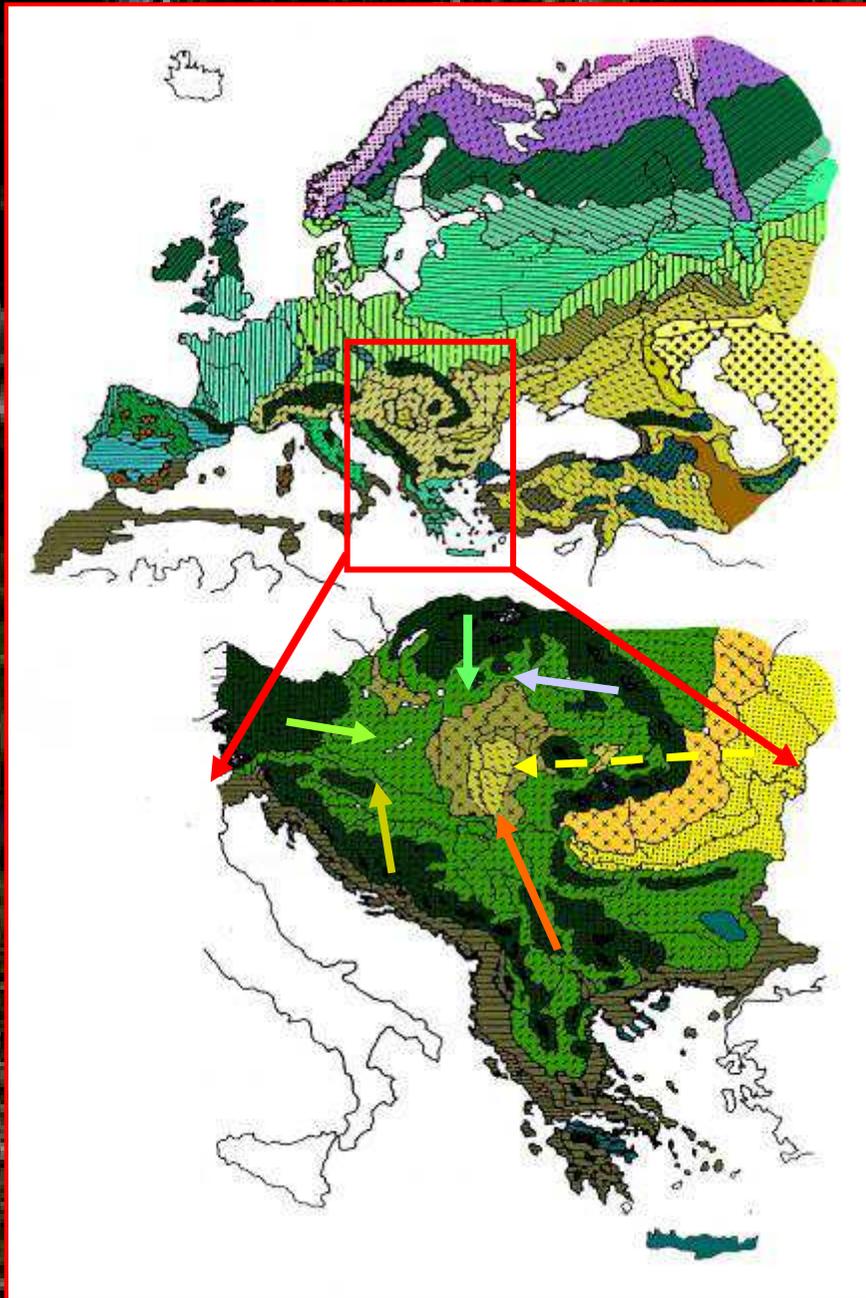
Oppositely, in the Pannonian region the **zonal setting is strongly modified according to the different landscapes**. Thus, diverse **micro-ecotones** emerge not only at the fringes of woody habitats but also **at the inner gaps of light-penetrated steppic forests**.

These habitat skirts are characterised by a **fine-scale** patchy dynamics of herbaceous and chamaephytic **polycormons**, **tall forbs** (mostly Apiaceae and Asteraceae) and **lower scrubs** (mostly Rosaceae), e.g. in sand steppic oak forests or in lanuginose oak scrub forests.

These fringe structures appear, however, also in formerly traditionally used but abandoned steppic and semi-dry grasslands ("Versaumung"), mimicking the physiognomical traits of the meadow steppes.

Fekete Gábor – Varga Zoltán (2003): Pannonian vegetation

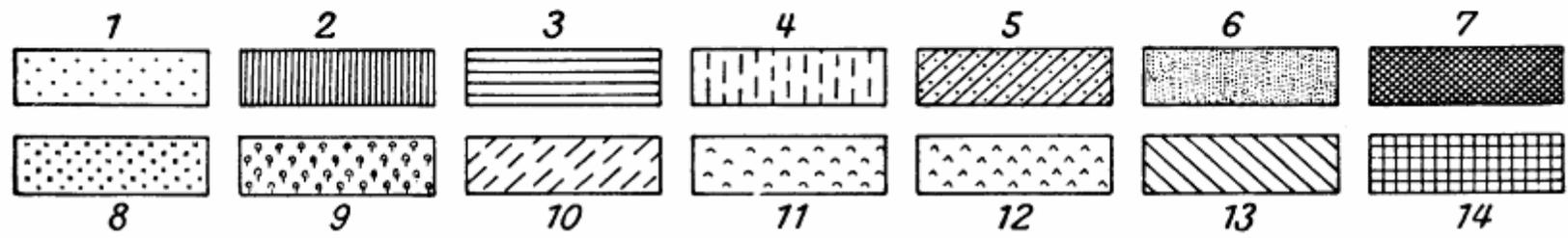
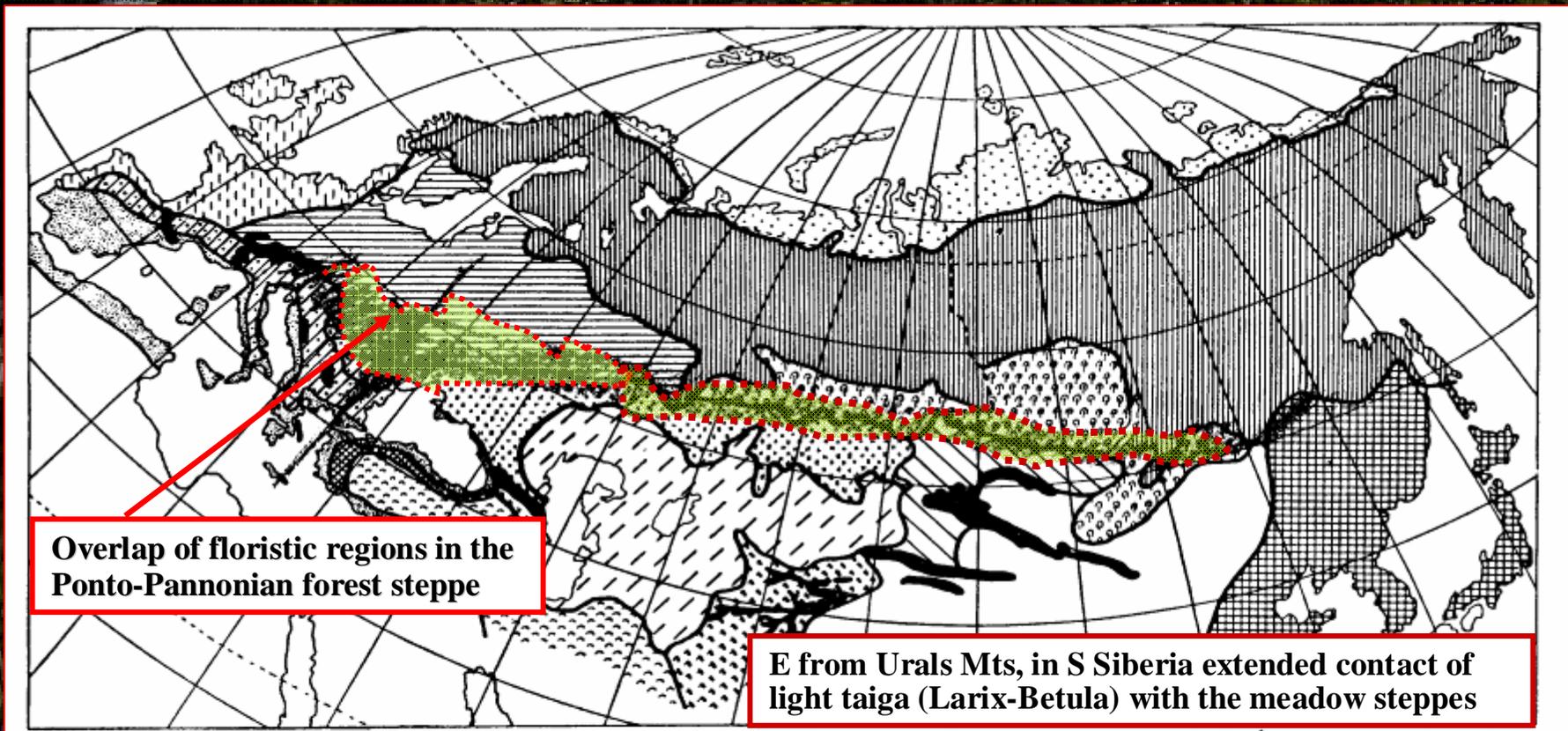
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The Pannonian region in Europe

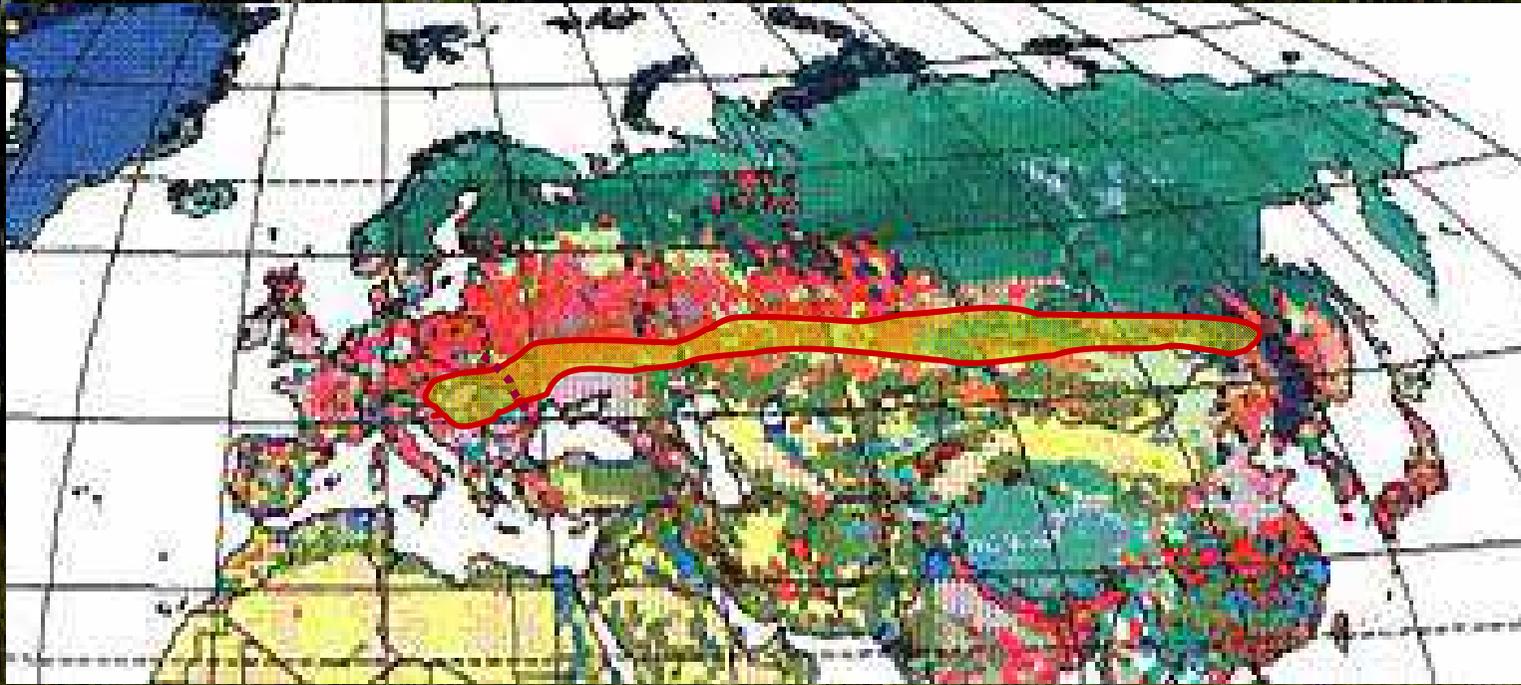
- The general zonal setting of Europe is transformed in SE Europe and Carpathian basin
- The Pannonian region occupies a Central position within the Carpathian basin
- It is nearly completely surrounded by high mountains
- The Alps and Carpathians filter but also transmit diverse floral and faunal elements
- In the Carpathian Basin the forest-steppe, typical in the central lowland and hilly parts of the basin, is represented by numerous regional variations with distinct geological, edaphic and climatic characters.

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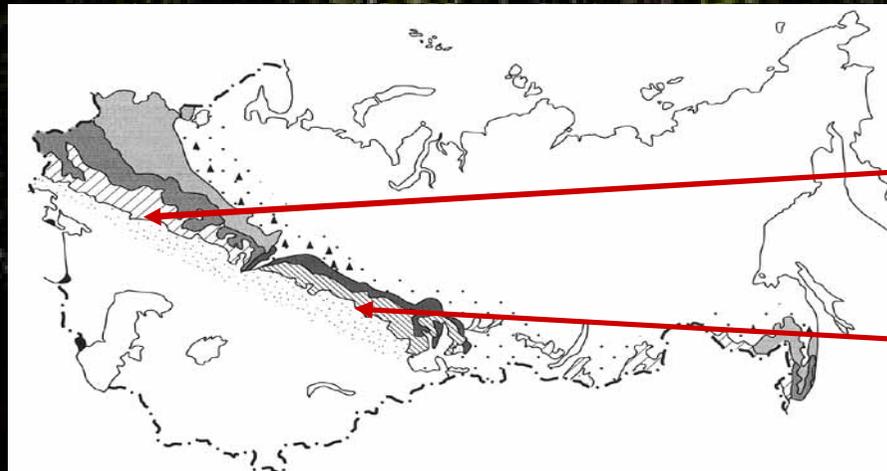
- (1) Arctic (2) Boreal (3) European nemoral (4) Atlantic (5) Sub-Mediterranean
- (6) Mediterranean (7) Euxinic (8) Ponto-Caspic (9) South-Siberian (10) Turanic
- (11) Anatolian-Iranian (12) Central-Asiatic (13) N-Mongolian (15) Pacific

Biogeographical connections of Pannonian steppic woods

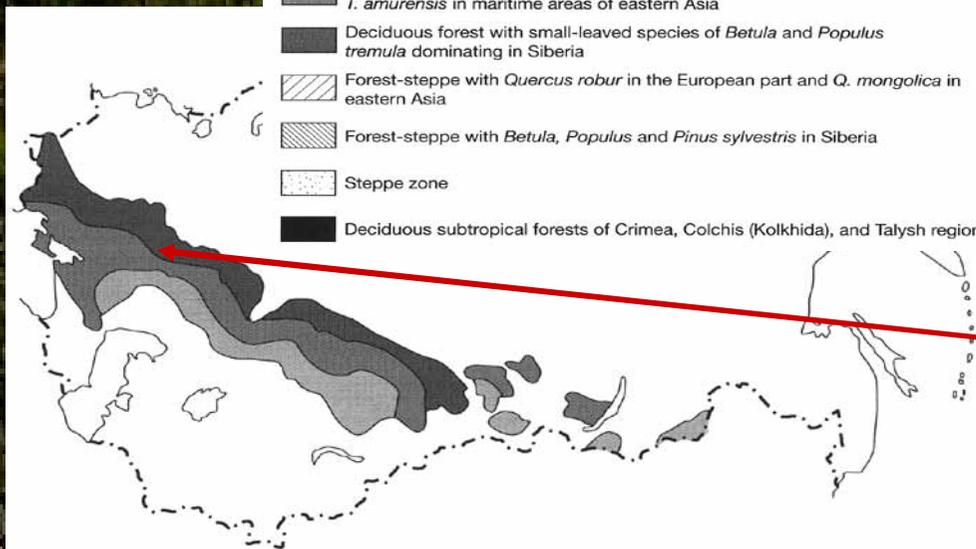


The western Palaeartic forest steppe belt is subdivided by the Carpathians into a Pannonian (sub-Mediterranean) and a Continental sub-zone, differentiated in biogeographical connections, vegetation structure and composition, and also in phylogeographic dynamics. In European part mixed (in Pannonian: light-penetrated) deciduous forests are contacting with meadow steppes. E from Urals the light-penetrated (svetlohvojnaya) taiga predominates with birch (kolyki) and larch stands, combined with the vertical zonation (Stufenfolge) in high mountains (examples below).

Biogeographical connections of Pannonian steppic woods



- Coniferous forest with sporadic occurrences of *Tilia*, predominately in subordinate layers
- Mixed (coniferous-deciduous) forest with *Tilia cordata* in the European part and *T. amurensis* in maritime areas of eastern Asia
- Deciduous forest with *Tilia cordata* dominating in the European part and *T. amurensis* in maritime areas of eastern Asia
- Deciduous forest with small-leaved species of *Betula* and *Populus tremula* dominating in Siberia
- Forest-steppe with *Quercus robur* in the European part and *Q. mongolica* in eastern Asia
- Forest-steppe with *Betula*, *Populus* and *Pinus sylvestris* in Siberia
- Steppe zone
- Deciduous subtropical forests of Crimea, Colchis (Kolkhida), and Talysh regions



- Polydominant herb-grass communities on leached and thick chernozems
- Feather grass (*Stipa-Festuca*) communities on typical and southern chernozems
- Artemisia*-feather grass communities and depleted *Artemisia*-dwarf shrub communities

The belt of deciduous forests is distinctly marked in the middle part of the E European plain where deciduous species (*Q. robur*, *Tilia cordata*, *Acer campestre*) are dominants and edificators. The small-leaved forests of Western Siberia are original forests which form an ecotone between taiga and forest-steppe. The forest-steppe extends as uninterrupted zone from Carpathians to the Altay and becomes fragmented further east.

Forest-steppes represent a *mosaic* of meadow steppe and woodlands. Steppes and forest-steppes have been transformed by human activities. In European part the biogeography of the European steppes and forest-steppes is now cultural rather than natural.

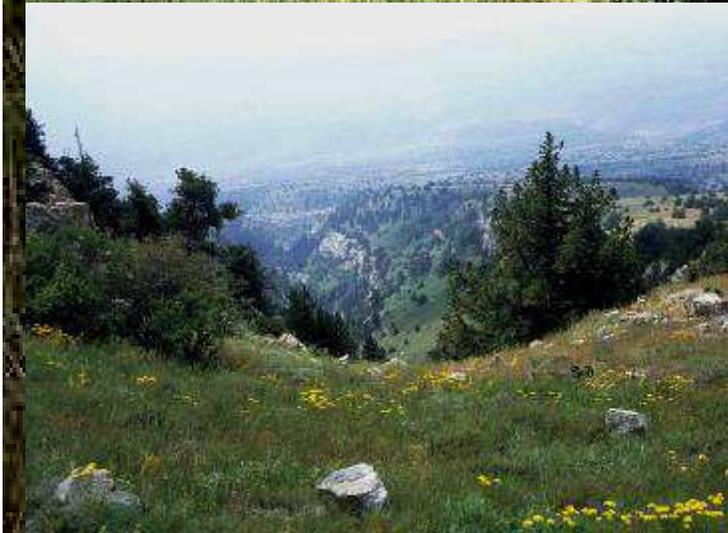
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The E Palearctic forest-steppe: the forest – meadow steppe contact:

Examples from Turkmenistan to Mongolia

Turkmenistan: Kopet Dagh

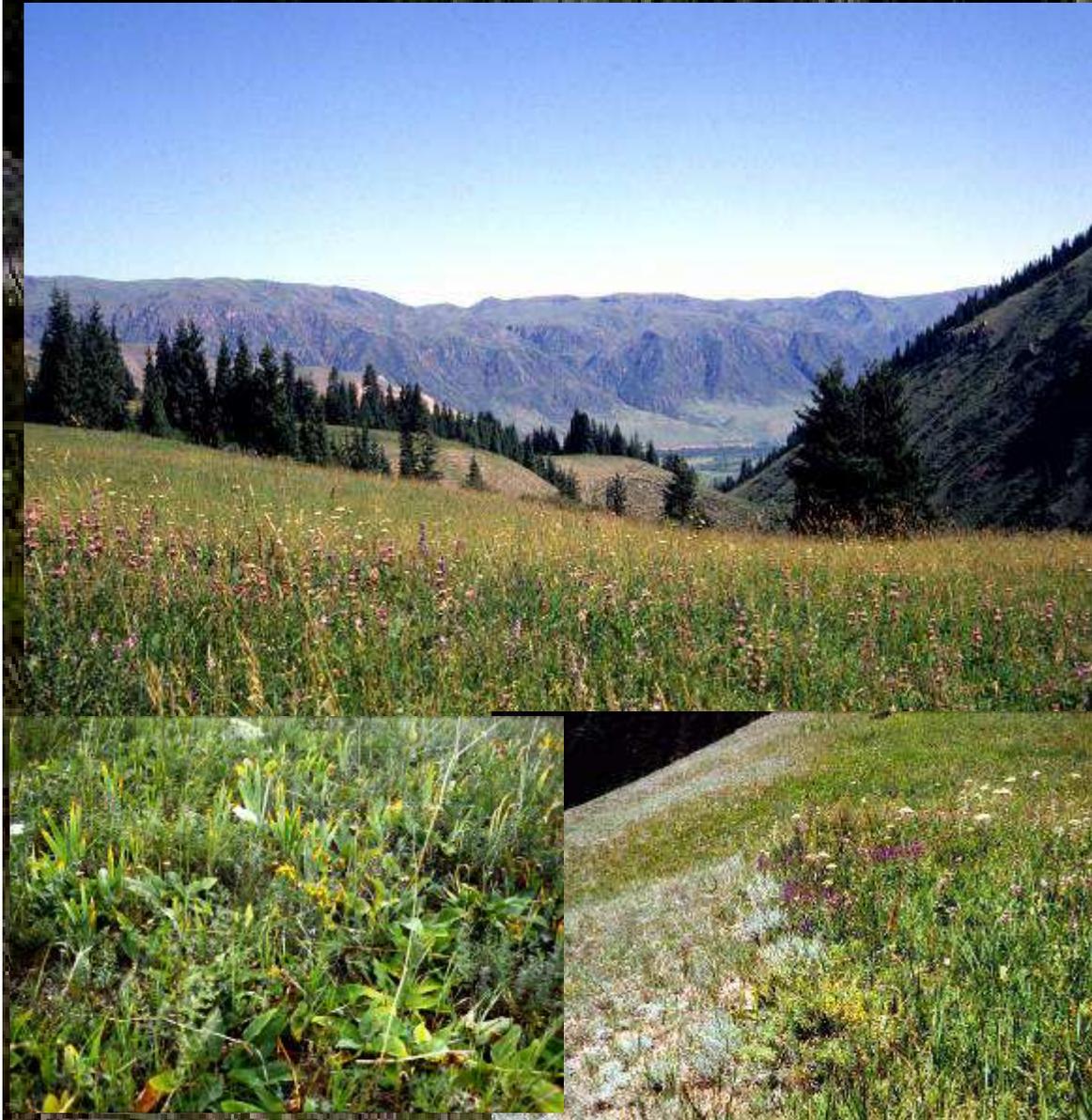
Important genetic core area of wild and cultivated spp.: Rosaceae (*Prunus*, *Cerasus*, *Amygdalus*), *Vitis*, *Acer*, *Ulmus*, wild *Triticum* and related gen. Tall grass – tall forb (*Ferula*!) meadow steppes on plateaus, forests in protected (humid!) ravines. Strong influence of (over)grazing. Rich in endemic genera and spp. (e.g. flightless Orthoptera, Noctuidae).



Biogeographical connections of Pannonian steppic woods

The E Palearctic forest-steppe: the forest – meadow steppe contact

Examples from Turkmenistan to Mongolia



Kazakhstan

Transili-Alatoo: tall-grass meadow steppes within and above the *Picea schrenckiana*-zone. Dominant species are partly S Siberian, partly trans-Palaeartic spp. as *Brachypodium pinnatum*, *Festuca rupicola*, *Koeleria cristata*, *Iris ruthenica*, *Campanula glomerata*, *Galium verum*, *Filipendula vulgaris*, *Phlomis tuberosa*, *Pulsatilla patens*, *Prunella grandiflora*, *Salvia nemorosa*, *Trifolium montanum*, *Veronica spicata*, in xeric slopes: *Artemisia* spp., *Stipa lessingiana*, *Poa bulbosa*, *Caragana* spp., ephemeroide: *Eremurus* spp., *Tulipa* spp.

Biogeographical connections of Pannonian steppic woods

The E Palearctic forest-steppe: the boreal forest – meadow steppe contact
Examples from Turkmenistan to Mongolia

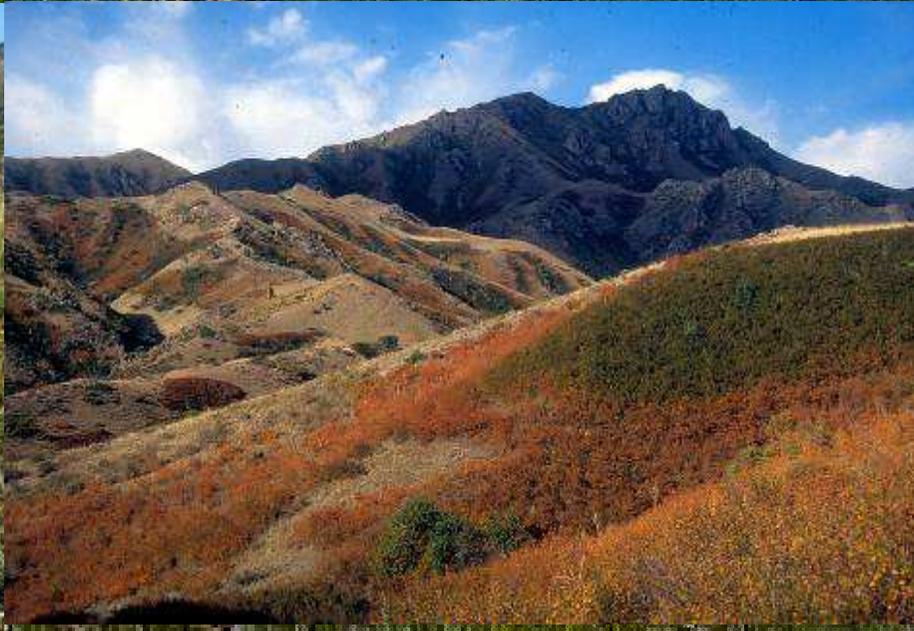
Kazakhstan: Dzhungarian Ala-too

Two typical semi-arid habitat types:

(i) Tall forb meadow steppe with *Peucedanum*, *Libanotis*, *Prangos* spp. (Apiaceae) and *Aster* (sect. *Galatella*) spp., composition and structure like Pannonian *Peucedano-Asteretum* (similar associations also in European S Russia and S Siberia).

(ii) Rosaria: dwarf scrubby vegetation with

Rosa, *Spiraea*,
Cotoneaster,
Amygdalus spp.,
Rosa sect.
spinosissima.
with included dry
grassy patches +
chamaephyta
(*Dracocephalum*,
Zizyphora spp.)



Biogeographical connections of Pannonian steppic woods

The E Palearctic forest-steppe: the boreal forest – meadow steppe contact

Examples from Turkmenistan to Mongolia Mongolia – northern light taiga



Light-penetrated *Larix sibirica* with included tall grass – tall forb meadow steppes: extremely high species diversity in plants

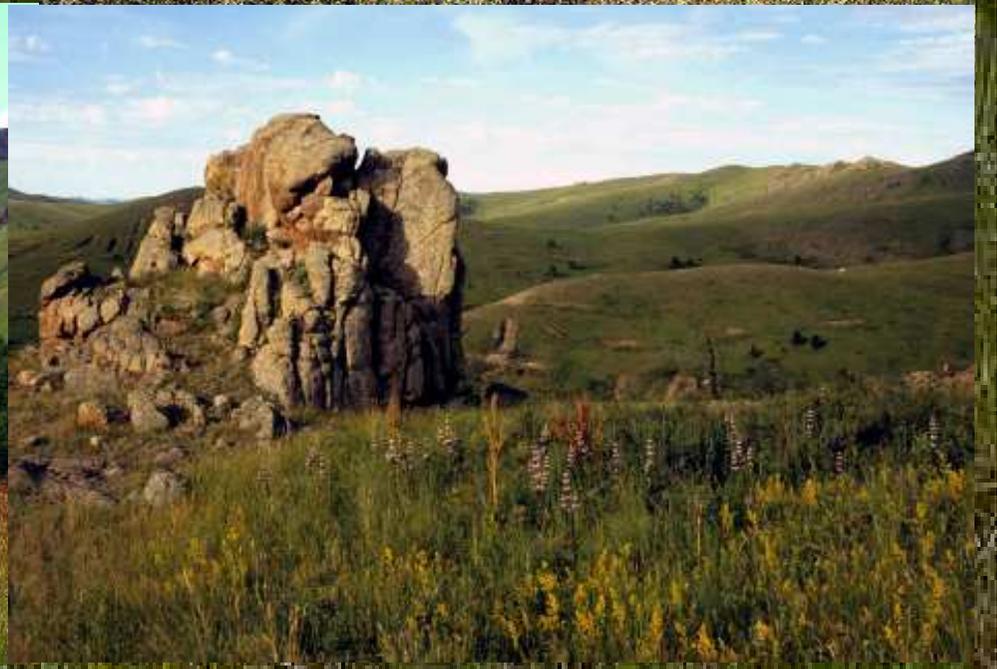
(*Aconitum barbatum*, *Artemisia laciniata*, *Campanula glomerata*, *Delphinium elatum*, *Dianthus superbis*, *Lathyrus versicolor*, *Schizonepeta multifida*, *Trifolium lupinaster*) but also in insects, e.g. butterflies and noctuid moths (*Parnassius nomion*, *Brenthis ino*, *Neptis rivularis*, *Erebia neriene*, *Aricia eumedon*, *A. artaxerxes*, *Pseudohermonassa cicatricosa*, *P. melancholica*, *Noctua chardinyi*, *Prognorisma albifurca*, *Ledereragrotis difficilis*, *Panchrysia dives*, *P. ornata*, *Polychrysia esmeralda*, etc.)

Biogeographical connections of Pannonian steppic woods

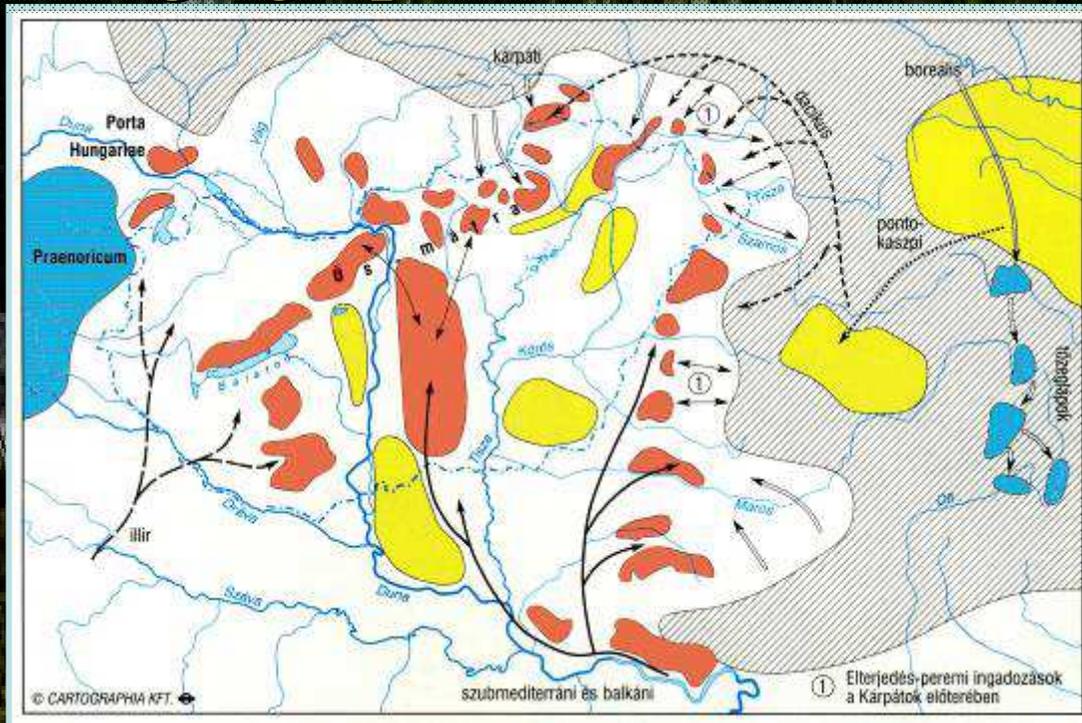
The E Palearctic forest-steppe: the boreal forest – meadow steppe contact
Examples from Turkmenistan to Mongolia

Mongolia

Diverse types of mountain steppes from N (Chentej Mts.) to W (Chasagt Chajrchan), substrate-dependent (granitic vs. calcareous rocks) with large elevational gradients – many W Palearctic connections (*Echinops ruthenicus*, *Galium verum*, *Phlomis tuberosa*, *Pulsatilla patens*, *Pseudolysimachion incanum*, *Dracocephalum ruyschiana*).



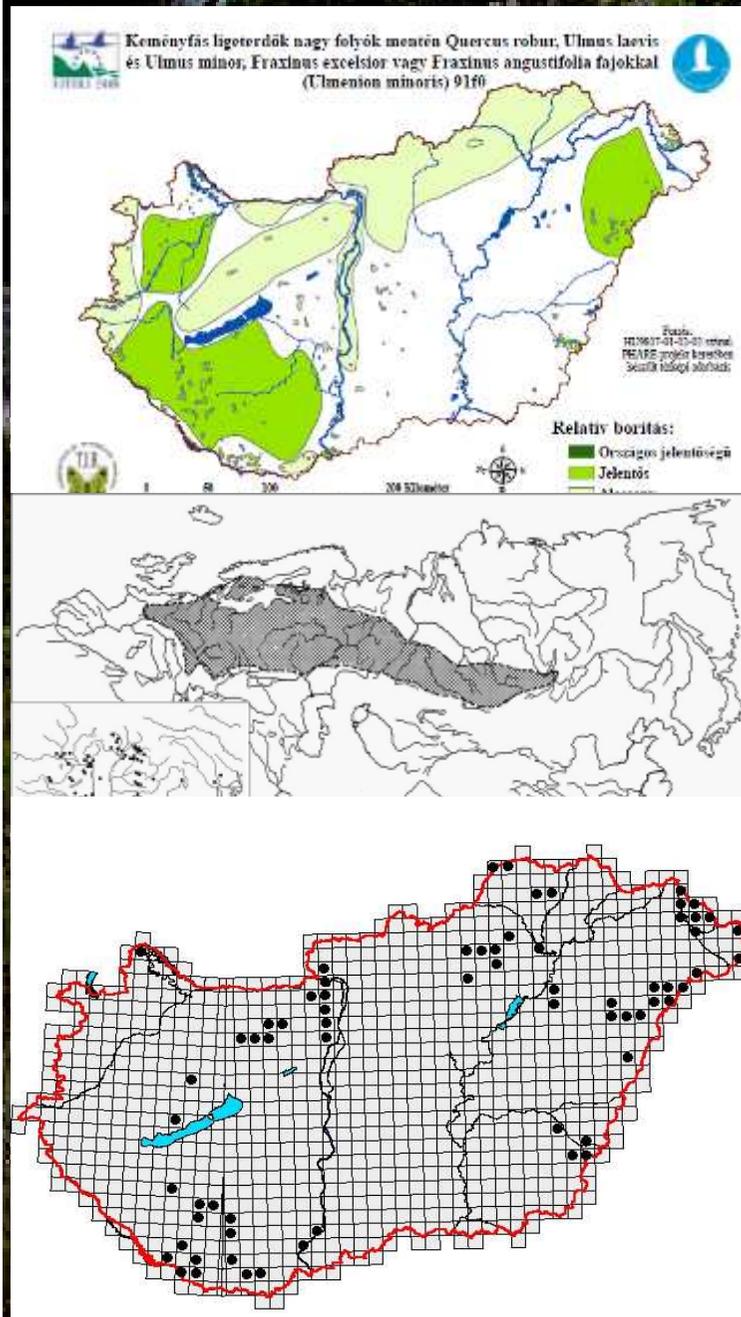
Biogeographical connections of Pannonian steppic woods



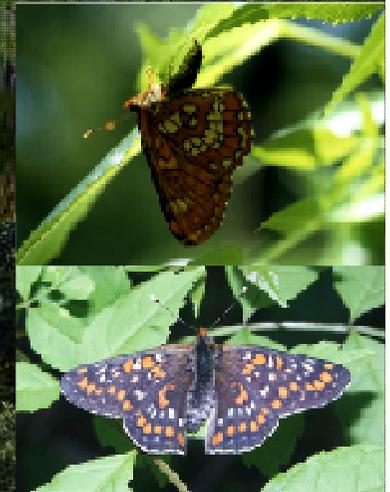
High diversity of faunal types. The East Alpine, Illyrian, Dacian, Carpathian, Holo- and Ponto-Mediterranean and Ponto-Pannonian influences mostly overlap at the edges of the lowland and hilly areas in SW and NE parts of the Carpathian basin.

The organisation of **community-complexes** of the Pannonian forest-steppe connected by **habitat ecotones** resulted in the overlap of several different faunal types, e.g. Mediterranean, Balkanic, Siberian, Ponto-Caspian, Ponto-Pannonian, Turano-Eremic and Xeromontane elements. Especially the hilly areas of transitional climatic conditions, surrounding the Pannonian lowland are populated by numerous, biogeographically important species and communities, e.g. the **lanuginose and Turkey oak forests**, and also the **steppic oak forests of sandy ridges**.

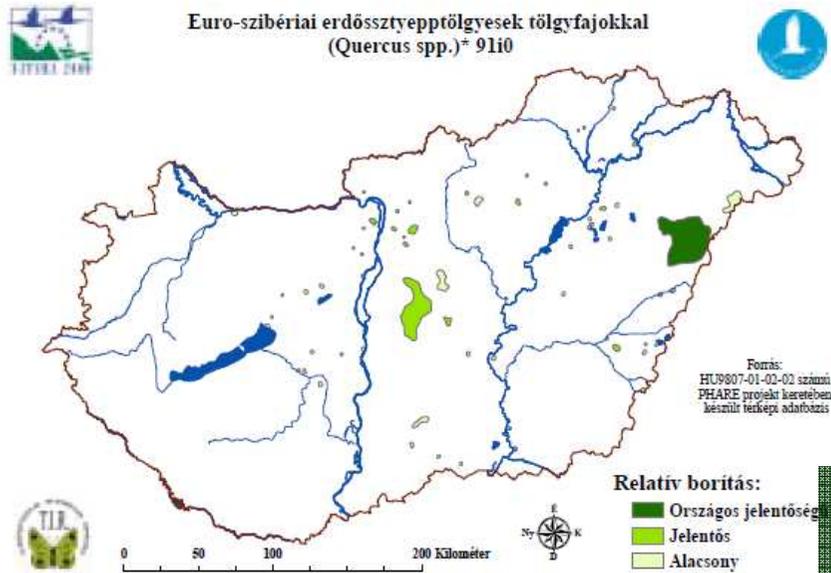
Biogeographical connections of Pannonian steppic woods



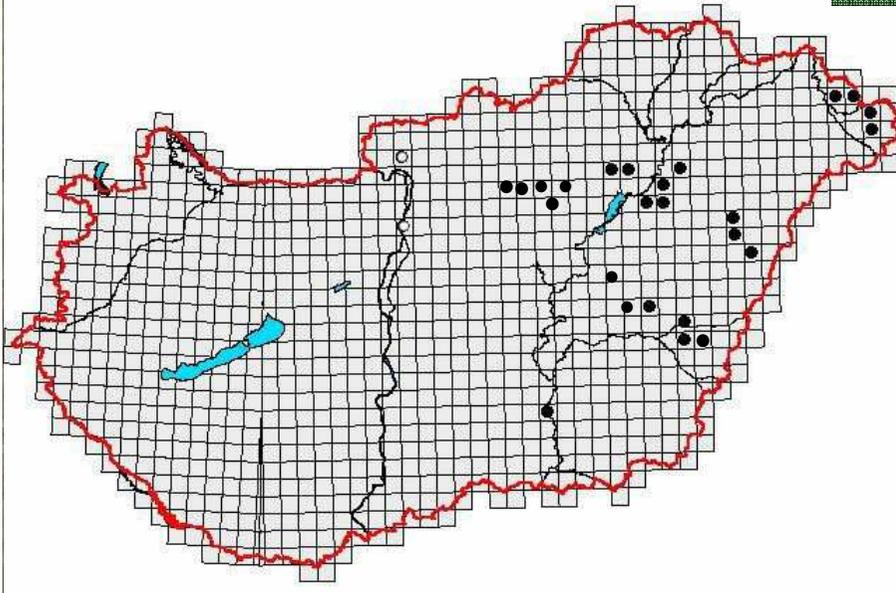
Southern continental species in hardwood gallery forests: example – *Euphydryas maturna* VU - Connected with fringe structures with young *Fraxinus angustifolia*, with scrubs of *Ligustrum* (larval food plants), *Cornus sanguinea*, *Acer tataricum* (nectar sources). The populations need complex habitat structures, thus **its occurrence signals a high species diversity (umbrella sp.)!**



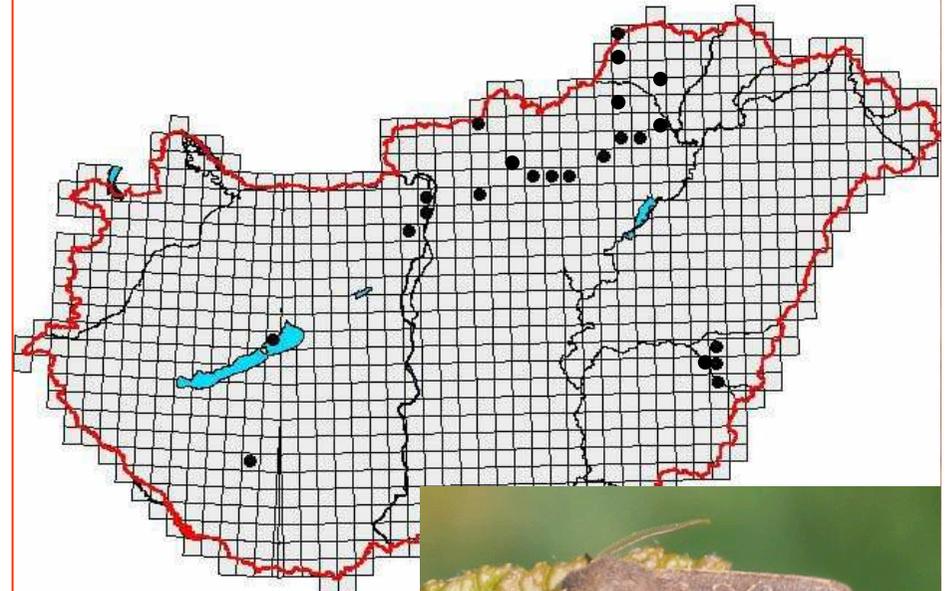
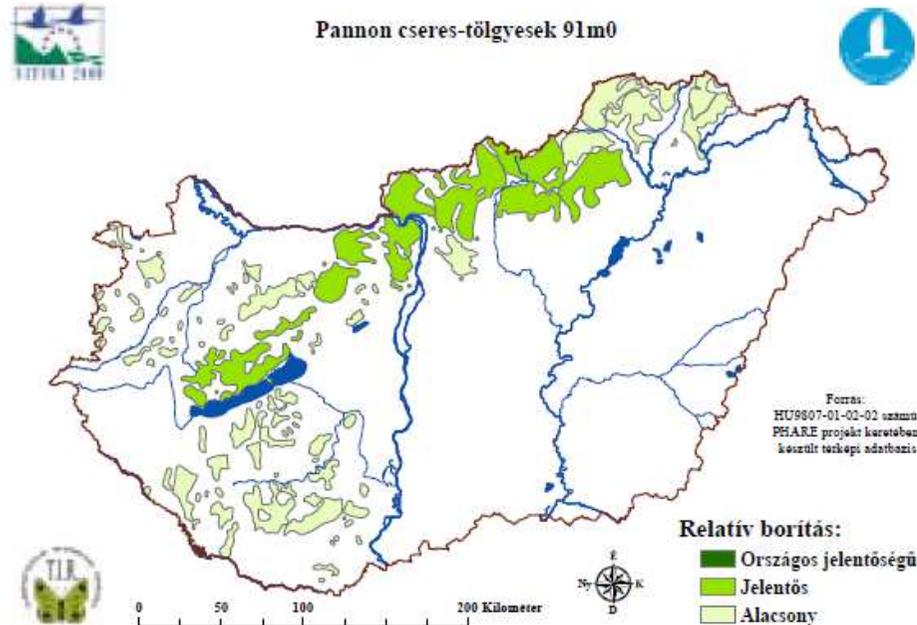
Biogeographical connections of Pannonian steppic woods



The Pannonian lowland steppic forests usually are light-penetrated stands with included edaphic (alkali, sandy, loess) grasslands.



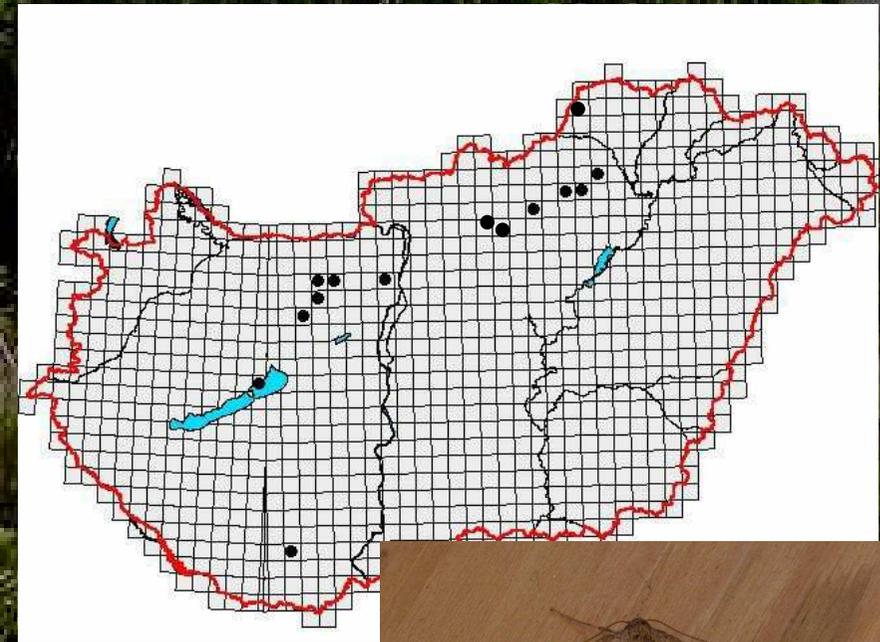
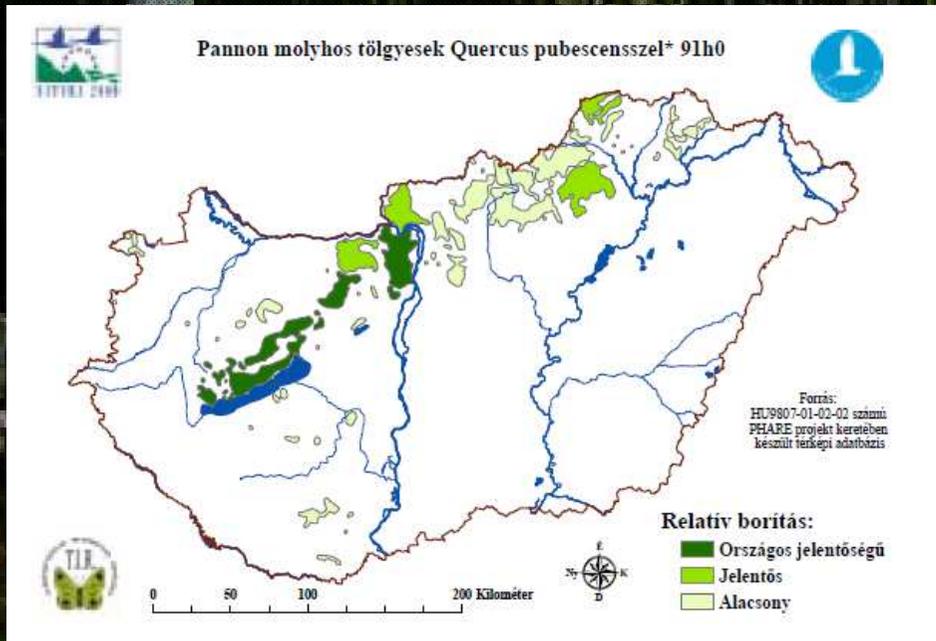
Biogeographical connections of Pannonian steppic woods



The lowland steppic forests have a broad contact zone with the sub-Mediterranean-Balkan Turkey-sessile oak woods. Thus, they have similar species composition. Flagship sp.: *Dioszeghyana sch. schmidtii* (Diószeghy, 1935)
Habitats: Pannonian-Balkan Turkey-sessile oak forests.
Range: Marginal areas of Pannonian lowland, zonal Turkey oak forests of sub-Mediterranean hilly regions at the N Middle range, S Slovakia, Romania (Banat), Balkans, Asia Minor. Umbrella sp.: co-occurs with numerous sub-Mediterranean species: *Paraboarmia viertlii*, *Marumba quercus*, *Asphalia ruficollis*, *Catocala nymphagoga*, etc.



Biogeographical connections of Pannonian steppic woods



Pannonian lanuginose oak forests are the northernmost „foreposts” of a Balkanic light penetrated formation. Numerous species reach in this region a N-most boundary! A flagship species: *Erannis a. ankeraria* Staudinger, 1861 Habitat: Lanuginose oak scrub forests. Life cycle: early spring flying period, ♀♀ flightless. Range: S slopes of Middle Range with sub-Mediterranean climatic influences; S Slovakia, Balkans, S Italy. Taxonomically isolated relict sp. of the Mediterranean ”winter fauna”. Umbrella spp.: co-occur with numerous sub-Mediterranean spp.: *Phalera bucephaloides*, *Rileyana fovea*, *Asteroscopus syriacus decipulae*, etc.



Biogeographical connections of Pannonian steppic woods

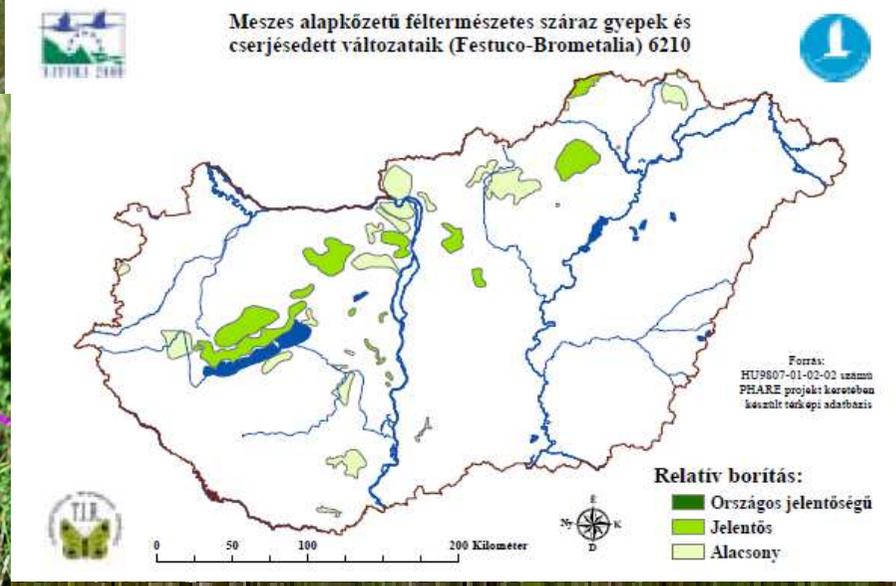
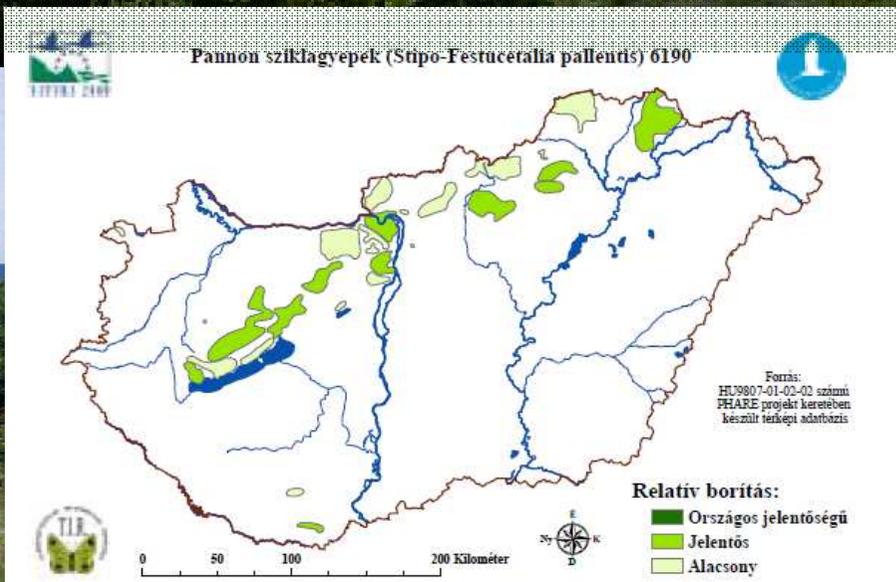


The lanuginose oak steppic forests belong to the sub-Mediterranean colline-submontane level of the Middle Range. Usually, they are forming typical mosaic complexes with the Pannonian rupicolous and steppic grasslands or even with Pannonian semi-dry swards. Thus, they belong to the habitats with the highest species diversity.



Biogeographical connections of Pannonian steppic woods

The Pannonian steppic oak forests are forming habitat mosaics with Pannonian grasslands: Pannonian rupicolous grasslands, sub-Pannonian steppic grasslands and Pannonian semi-dry grasslands.



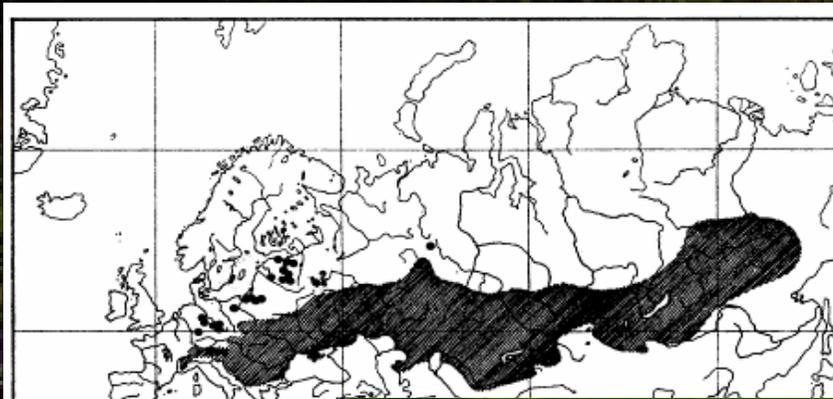
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Endemic subspecies of a Ponto-Mediterranean-Turkestanic sp.: *Melitaea ornata kovacsi* Varga 1967, specialised on *Cirsium pannonicum*. This endemic subsp. needs mosaic habitats with semi-shadowed patches for aestivation of larvae in hot summer period. The habitat is also an endemic Pannonian habitat type: *Cirsio-Brachypodium* alliance, with structural similarity to continental meadow steppes.



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The steppic- and semi-dry sward mosaic habitats with abundant fringe structures usually have an extreme high biodiversity with co-occurrence of several Ponto-Pannonian spp., incl. also some endemic subspecies or "micro"-species. Some of these steppic spp. are important tools of biodiversity as food-plants of special herbivorous insects, as: *Astragalus exscapus*, *A. dasyanthus*, *Cirsium pannonicum*, *Onobrychis arenaria*. The food plant specialists often have narrower range than their food plants, e.g. *Cupido osiris*, *Polyommatus admetus*, *Zygaena brizae*.



Biogeographical connections of Pannonian steppic woods

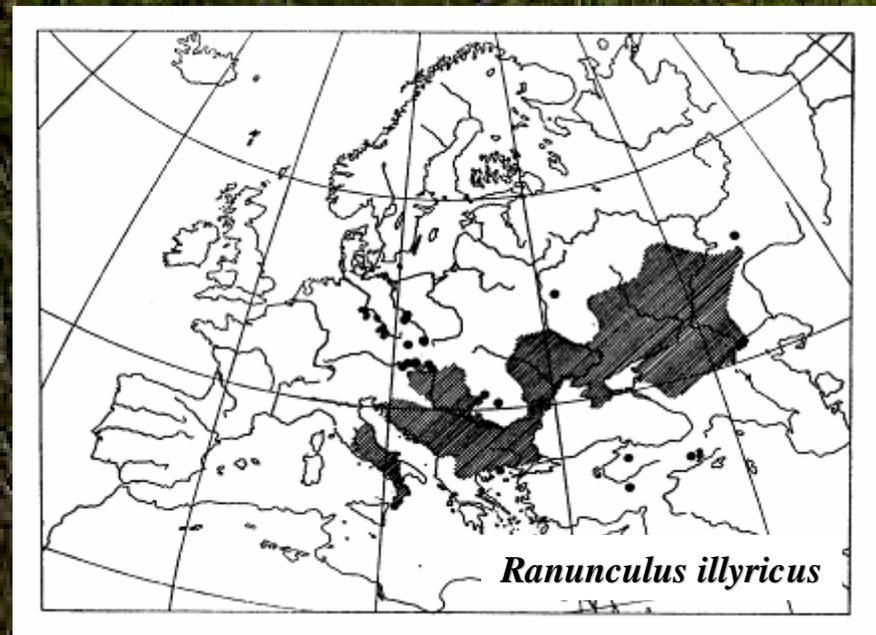
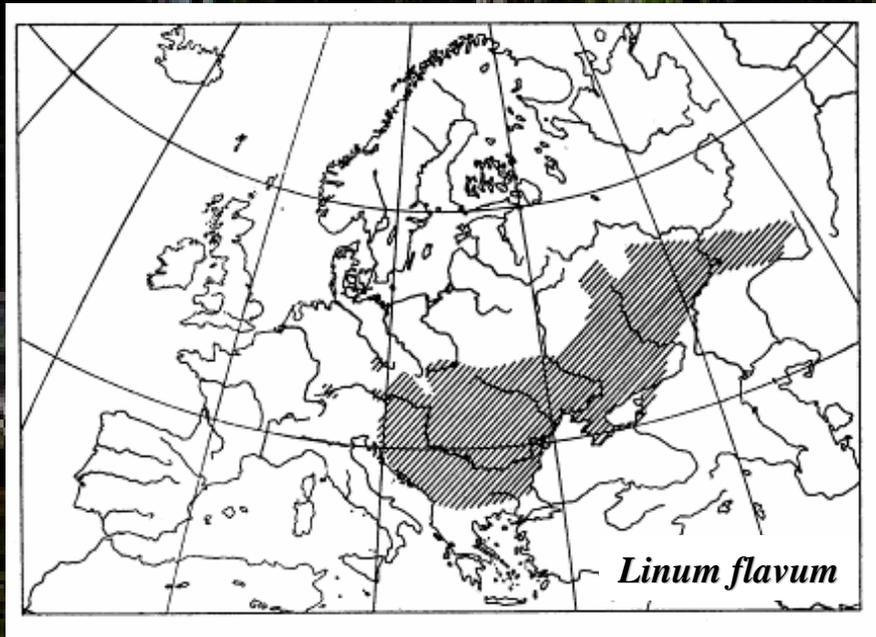
Some of these food plant specialists have a high biogeographical importance as the allopatric siblings of *Plebejus pylaon* (Fischer-Waldheim, 1832) superspecies with the Pannonian-Balkan *P. sephirus* (Frivaldszky, 1835) and further spp. in Iberia, SW Alps, Asia Minor and Levant.



Biogeographical connections of Pannonian steppic woods

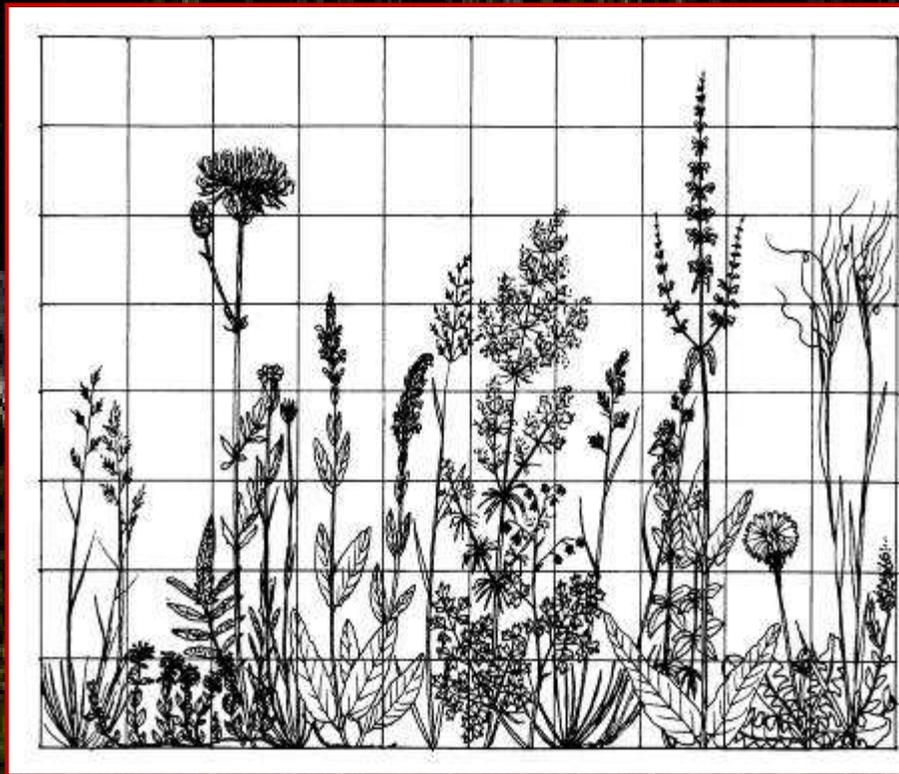
Ponto-Pannonian biogeographical connections

The ranges of several steppic species extend to the S Ural Mts., but they do not reach to Kazakhstan, S Siberia and N Mongolia. These species can be characterised as *Ponto-Pannonian* spp., richly represented in the steppic habitats of the Pannonian region.

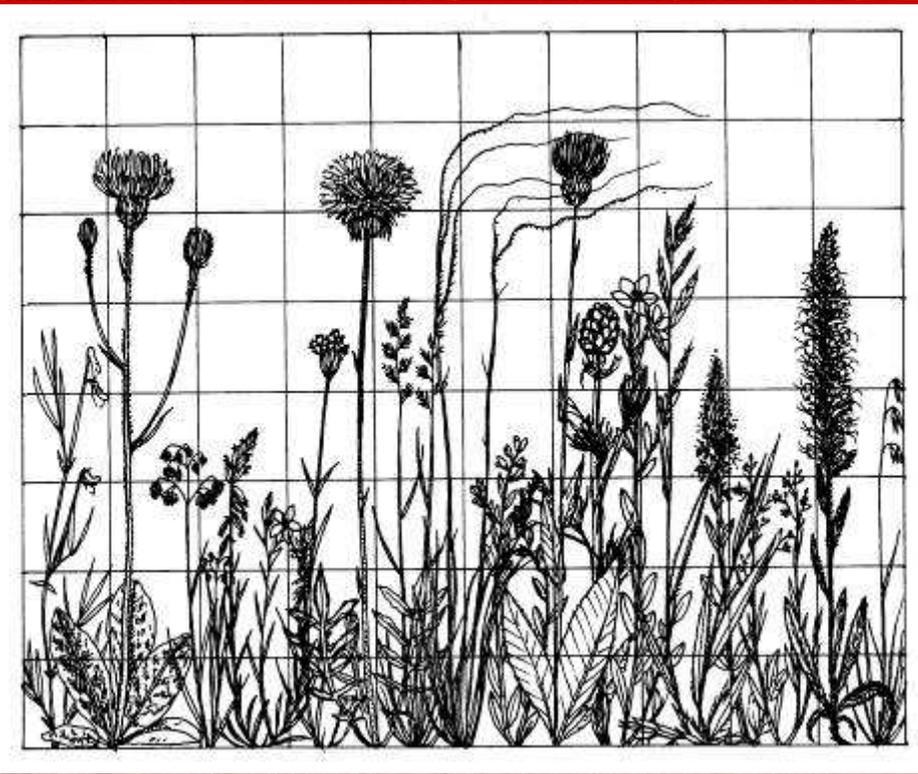


Typical representants of this type are e.g. *Iris aphylla*, *Pulsatilla grandis*, *Linum flavum*, *Ranunculus illyricus*, *Thymus kosteleckianus*, etc.

Biogeographical connections of Pannonian steppic woods



Idealised section of a loess meadow steppe from SE part of Pannonian lowland (Kistompapuszta). Vertical scale: about 10 cm. species from L to R: *Festuca rupicola*, *Thymus marschallianus*, *Centaurea spinulosa*, *Dianthus pontederae*, *Salvia nemorosa*, *Koeleria cristata*, *Galium verum*, *Thalictrum minus*, *Festuca rupicola*, *Cruciata glabra*, *Phlomis tuberosa*, *Taraxacum serotinum*, *Stipa capillata*, *Pseudolysimachion spicatum*.



Idealised section of a semi-dry sward of Aggtelek karst (Jósvafő). Vertical scale about 10 cm. Species from L to R: *Lathyrus pannonicus*, *Hypochoeris maculata*, *Briza media*, *Polygala maior*, *Dianthus pontederae*, *Jurinea mollis*, *Festuca rupicola*, *Stipa joannis*, *Polygala maior*, *Cirsium pannonicum*, *Adonis vernalis*, *Linum flavum*, *Brachypodium pinnatum*, *Pseudolysimachion spicatum*, *Thesium linophyllum*, *Echium maculatum*, *Danthonia alpina*.

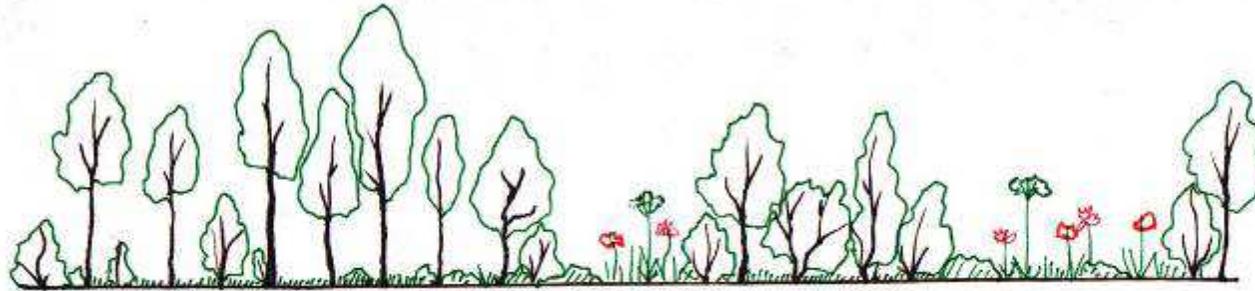
Biogeographical connections of Pannonian steppic woods



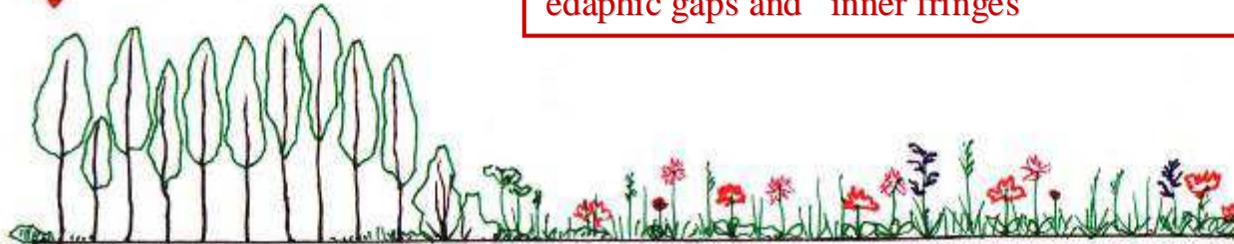
Fringe structures often appear in formerly mowed, abandoned orchards (*Streuobstwiesen*, s. L pictures) or on abandoned hayfields (R). The light relations are often similar to the nature-like forest-steppe (semi-shadow).

Biogeographical connections of Pannonian steppic woods

Change of vegetation in a colline forest steppe sigma-community due to traditional use and after abandoning



Natural, light penetrated steppic forest with edaphic gaps and "inner fringes"

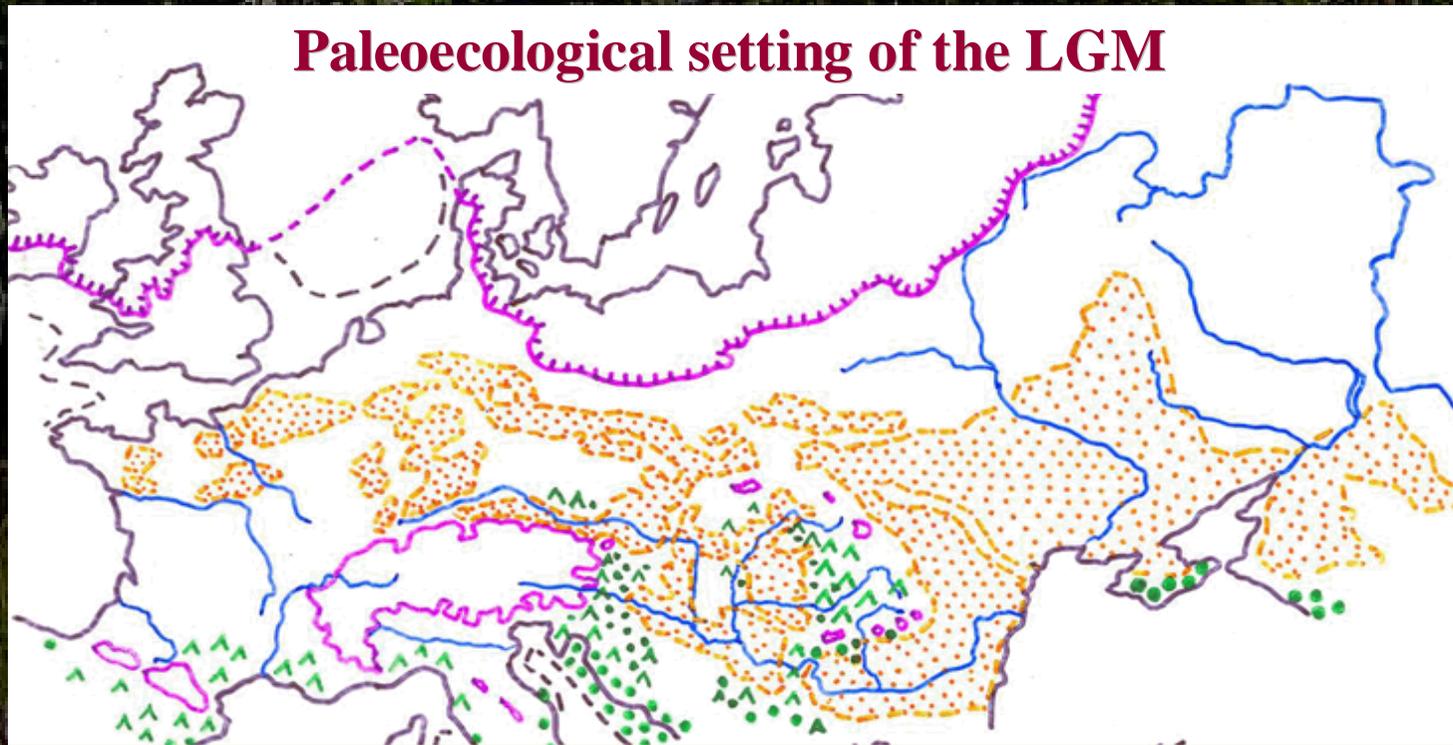


Closed, semi-cultural forest with narrow fringe contacted with traditionally used grassland



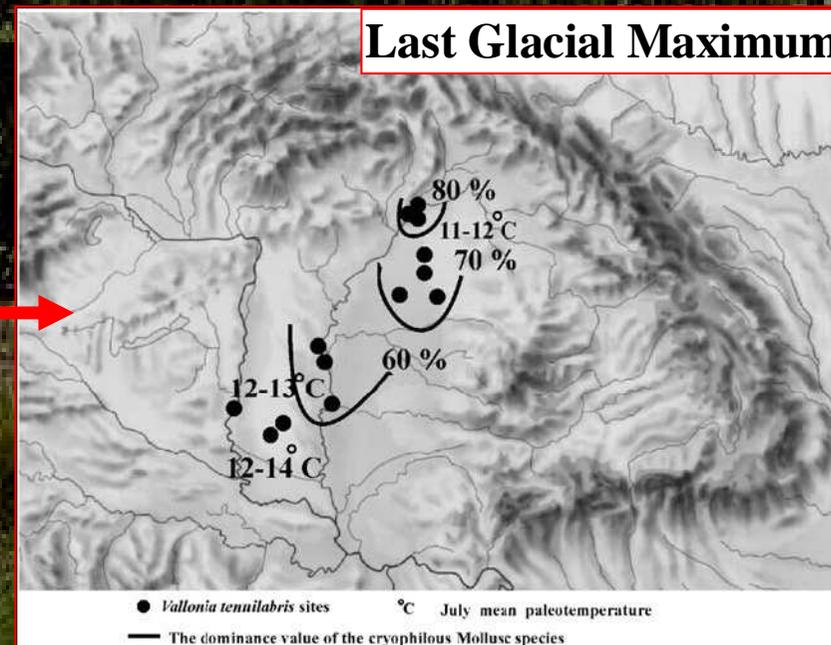
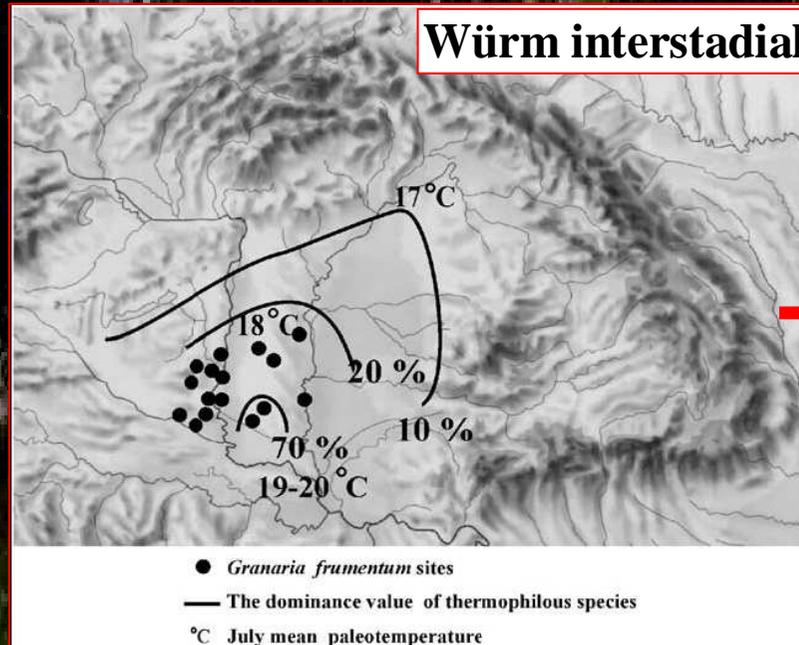
After abandoning extension of fringe-like structures („Versaumung”) patchy dynamics of tall forbs and polycormons (examples below)

Biogeographical connections of Pannonian steppic woods



The earlier ‘tree-less tundra’ models for Europe north of the transverse mountain ranges of the Pyrenees, Alps and Carpathians have been questioned by surveys of the Late Pleistocene Mammalian fauna. The *carrying capacity* adequate to feed the herds of large herbivores demands a rather productive environment, like the cold-continental meadow steppes in southern Siberia and northern Mongolia. The tundra-steppic areas of E Europe and the mountain belts of Central Asia were connected and *nonanalogue communities* have established by mixing of tundra, steppic and eremic-oreal elements (e.g. *Lemmus* and *Dicrostonyx* spp. together with *Citellus*, *Allactaga*, *Sicista*, *Lagurus*, *Marmota* and *Ochotona*). This habitat type appears to have included also species from deciduous woodland, e.g. *Clethrionomys glareolus* and *Apodemus sylvaticus*.

Biogeographical connections of Pannonian steppic woods



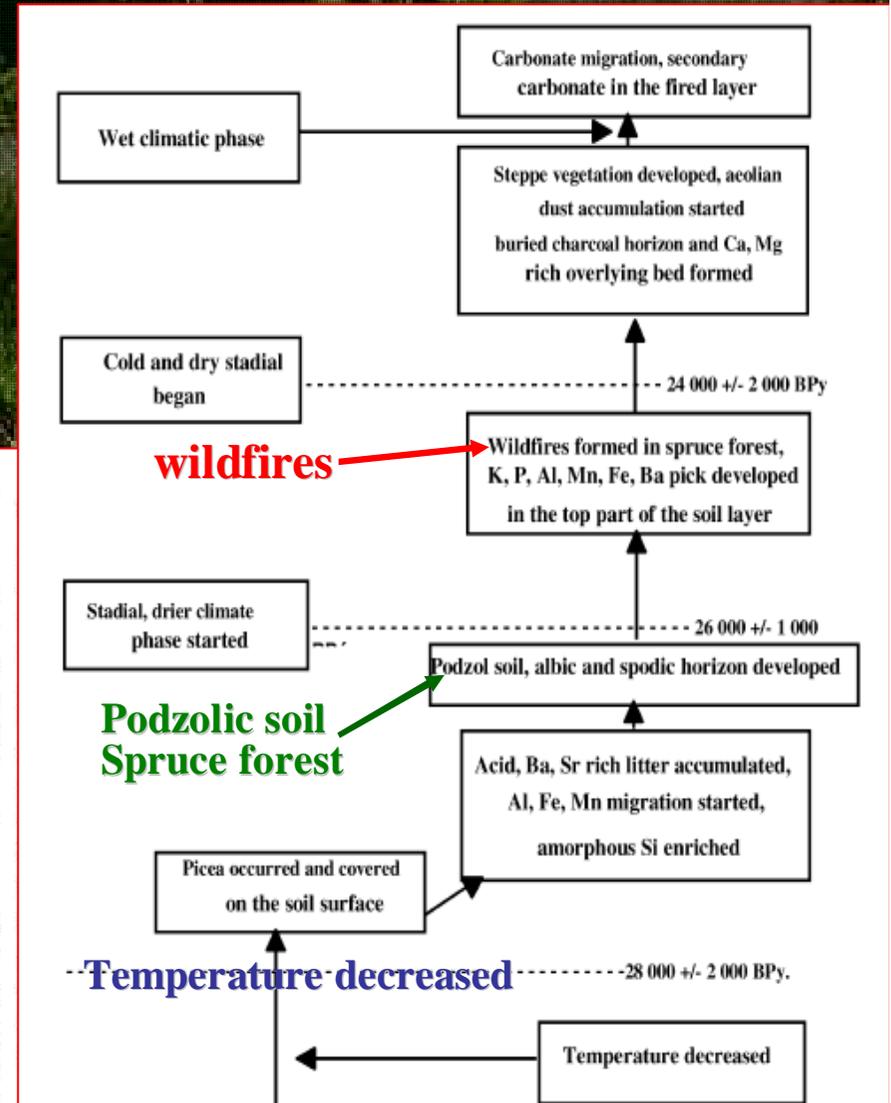
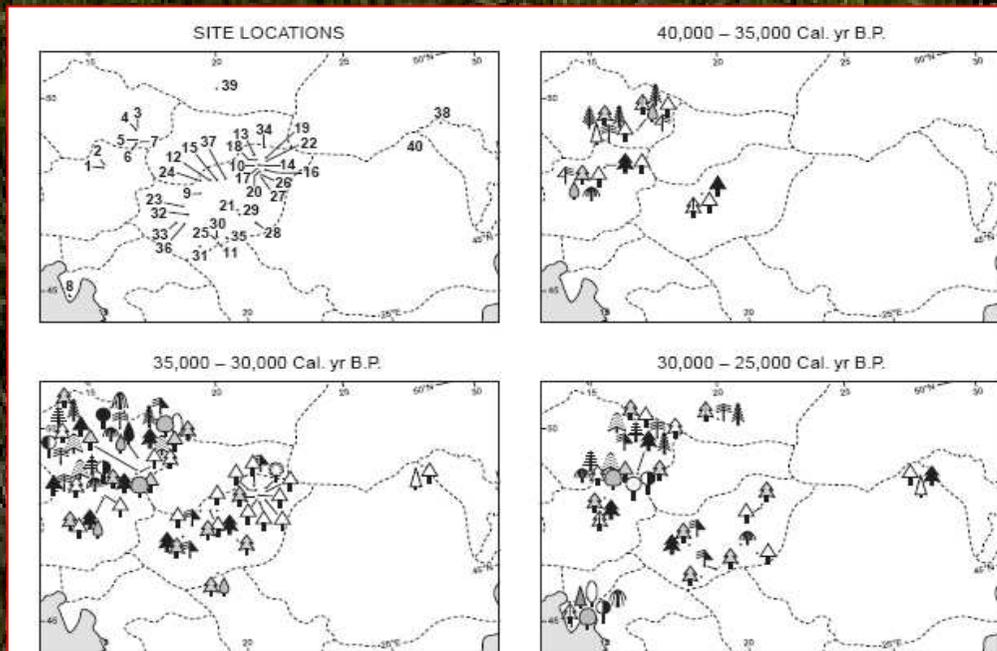
Between 22,000 and 20,000 yr BP: decline of thermophilous species and expansion of a kryo-xerophilous, xeromontane element, *Vallonia tenuilabris* was shown, together with the boreo-Alpine/montane *Columella columella*. The dominance of the kryophilous gastropods reached values of 80% in the northern parts of the Carpathian basin while dominance of the same group was about 40% in the southern parts. The "gastropod-thermometer" developed by Krolopp and Sümegei shows 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.

Biogeographical connections of Pannonian steppic woods

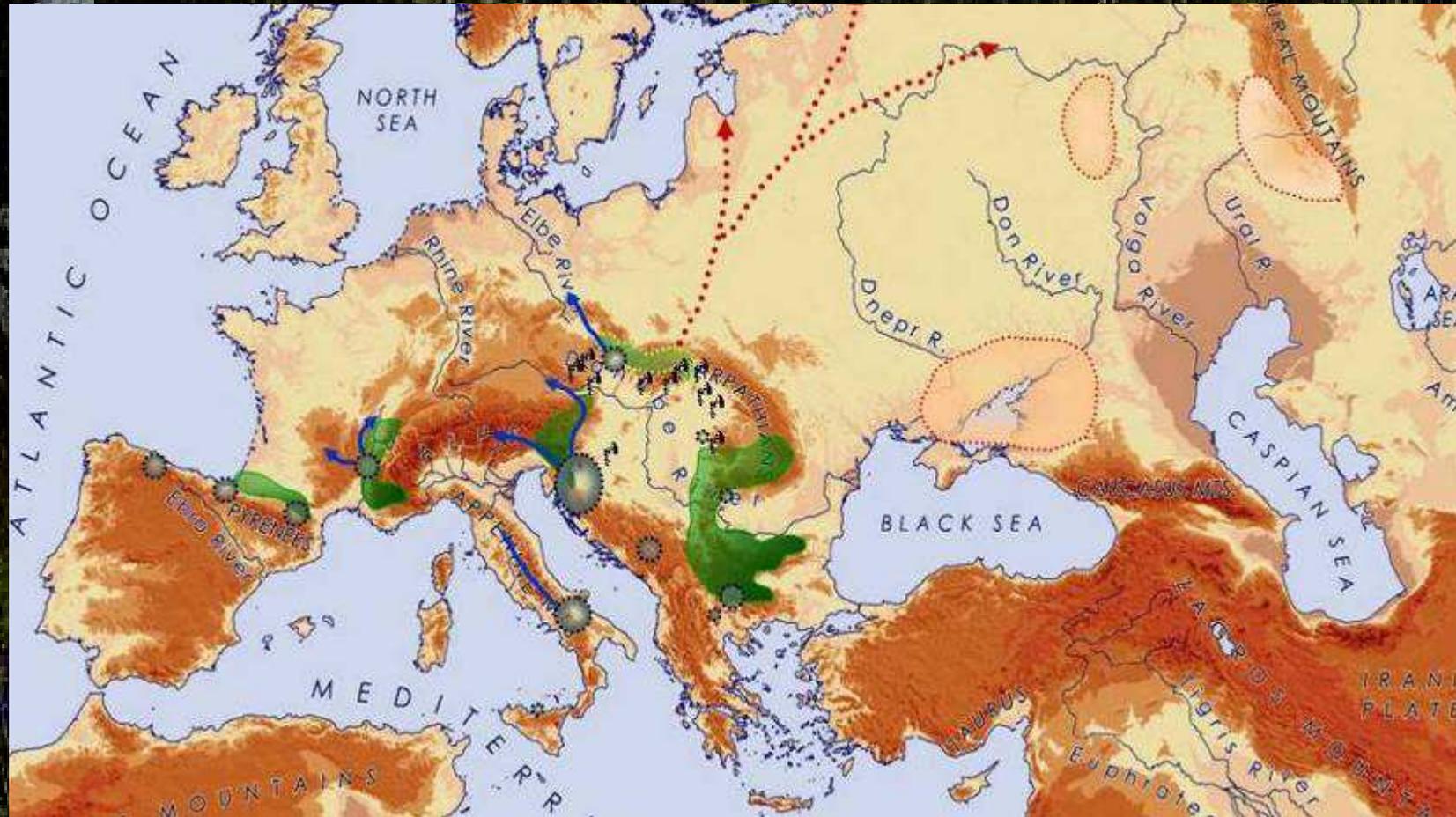
E and S Carpathians have been repeatedly pointed out as an *important glacial refuge area*, from which trees started to migrate at the beginning of the Holocene (e.g. Huntley & Birks 1983; Bennett *et al.* 1991; Huntley 1993; Willis 1994).

Dynamic change and mixture of taiga, steppe and tundra species has repeatedly occurred along a zone-ecotone of „mammoth-steppe and boreal forest with **high biodiversity and primary production** (Kretzoi 1977!).

"*Gastropod-thermometer*" (Krolopp & Sümegei): mean July temperature: 11-12°C in the N and 13-14°C in the S part of the basin during the *LGM*.

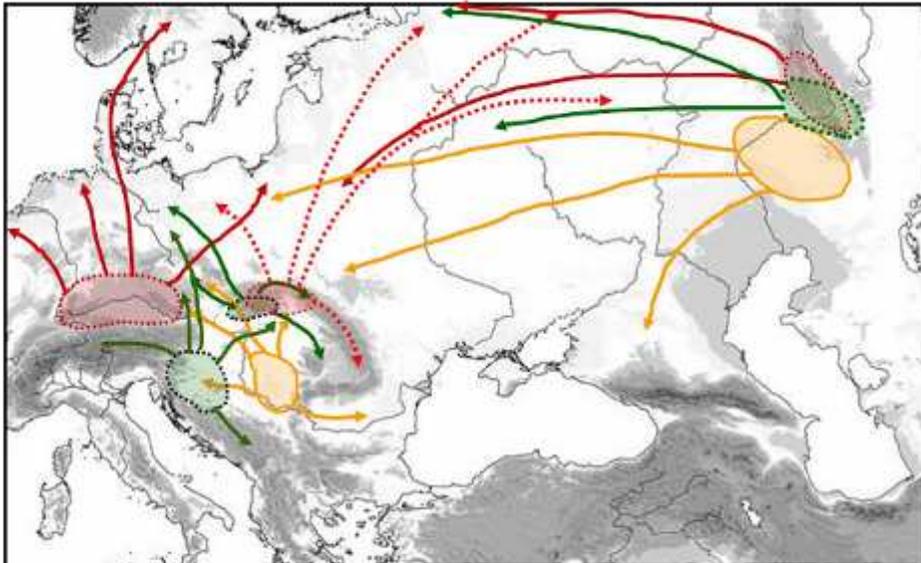


Biogeographical connections of Pannonian steppic woods



Dark green fields: European coniferous forest refugia (Schmitt & Haubrich 2008). Light green field with brown arrows: the Northern Carpathian arboreal refugium with expansion routes of boreal species (coniferous trees, Brown Bear, Bank Vole, etc.). Grey circles with blue arrows: refugia of the Beech with important post-glacial expansion routes (Magri *et al.* 2006; Magri 2007). Light brown patches: Eastern European boreal forest refugia during the LGM (from various sources).

Biogeographical connections of Pannonian steppic woods



Sorex araneus, *Ursus arctos*, *Chlethrionomys rutilus*, *Cricetus cricetus*

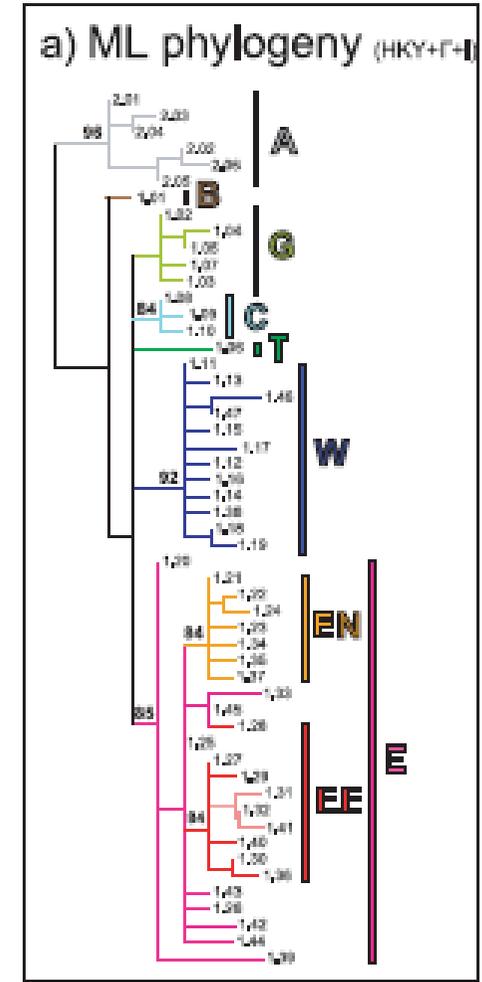
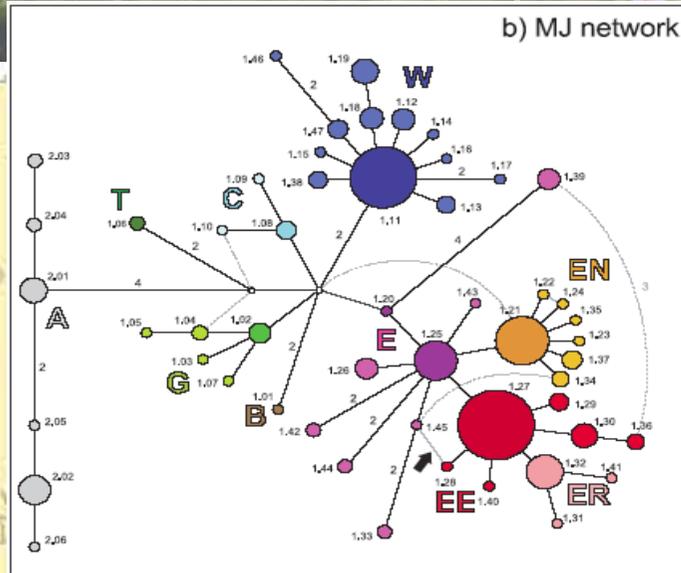
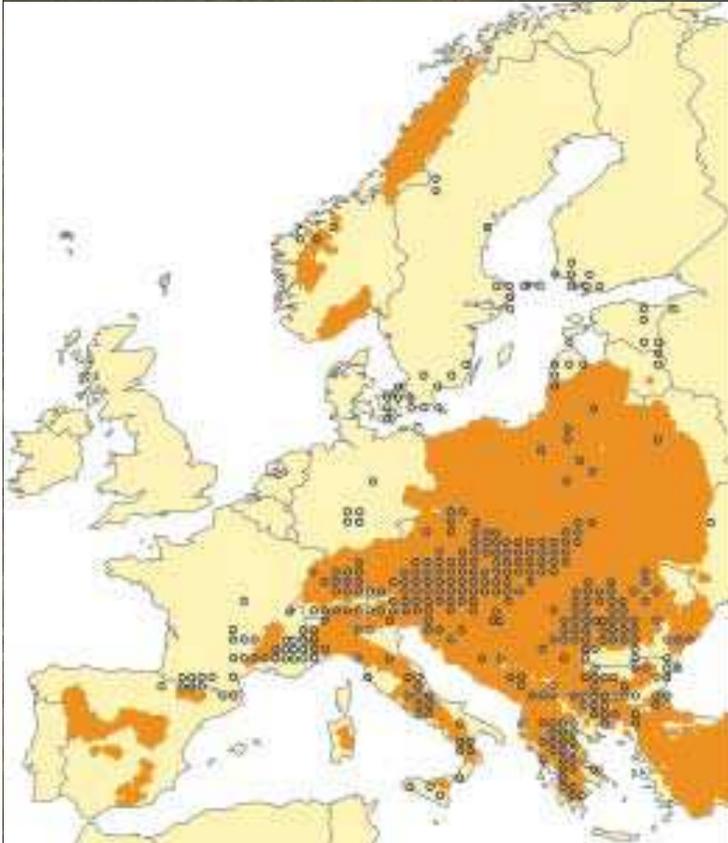
Extra-Mediterranean refugia:

- 1 Dogger-, Channel-, Atlantic land (*Beirne*)
- 2 W of the W Alps (*Erebia medusa*)
- 3 Black Forest (*Microtus arvalis*)
- 4 Southern Moravia (*Pollen + Macrofossils*)
- 5 Northern Carpathians (*Vipera berus*, *Ursus arctos*, *Chlethrionomys glareolus*, *Parnassius mnemosyne*, etc.)
- 6 Bátorliget (*Pollen + Macrofossils*)
- 7 Mti Apuseni (*Lumbricidae*,
- 8 SE Carpathians (*Bombina variegata*)

- 9 S Carpathians (*Bombina variegata*)
- 10 Stara Planina – Thracian Massiv
- 11 SE Alps – Illyrian (*Bombina variegata*, *Rana arvalis*, *Erebia medusa*, *Vipera berus* ...)
- 12 Moesicum (*Cricetus cricetus*, *Mus spicilegus*,
- 13 W Greece – Macedonia (*Quercus* spp.,
- 14 S Urals (*Sorex araneus*, *Cricetus cricetus*, *Chlethrionomys glareolus*)



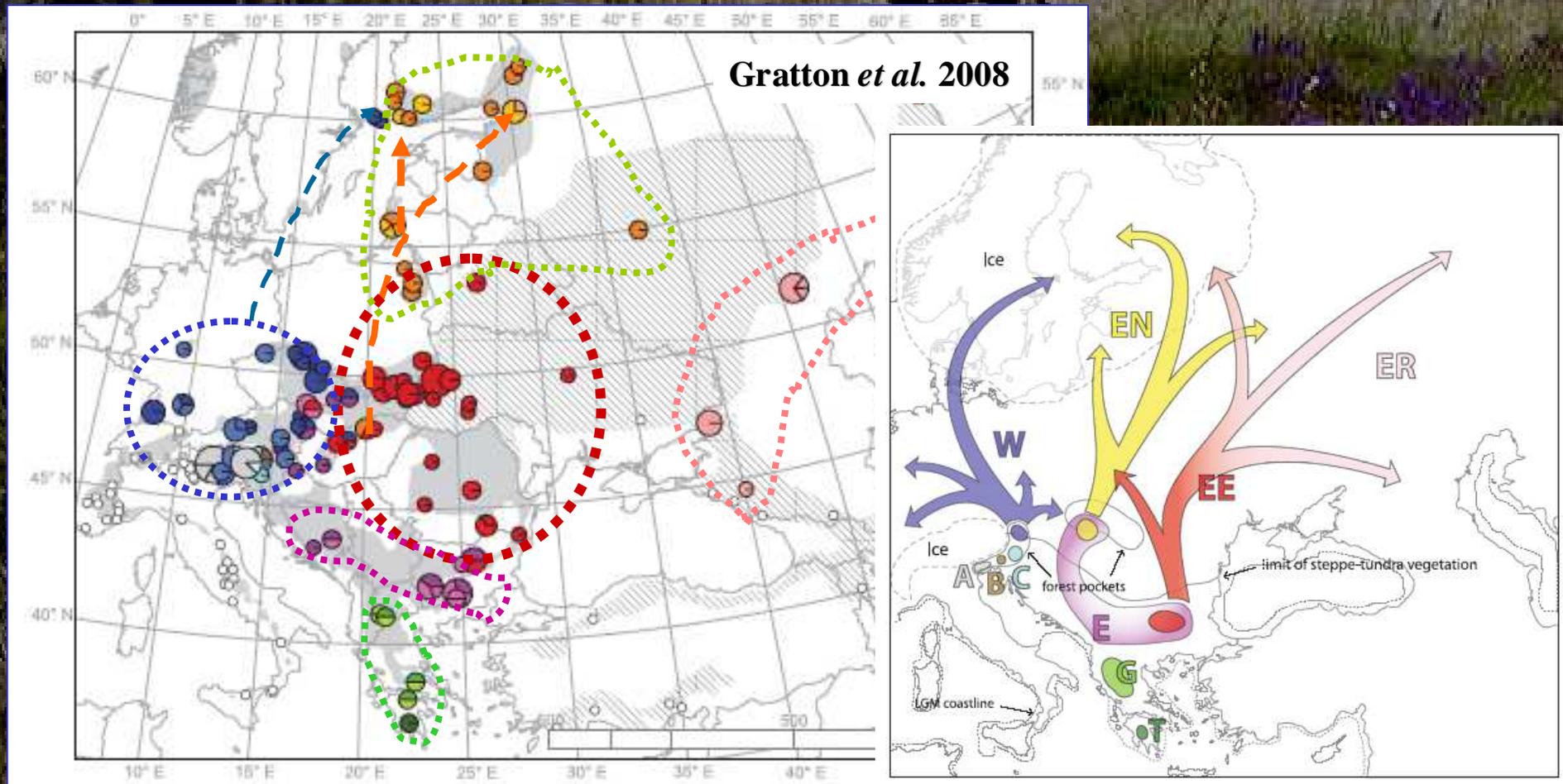
Biogeographical connections of Pannonian steppic woods



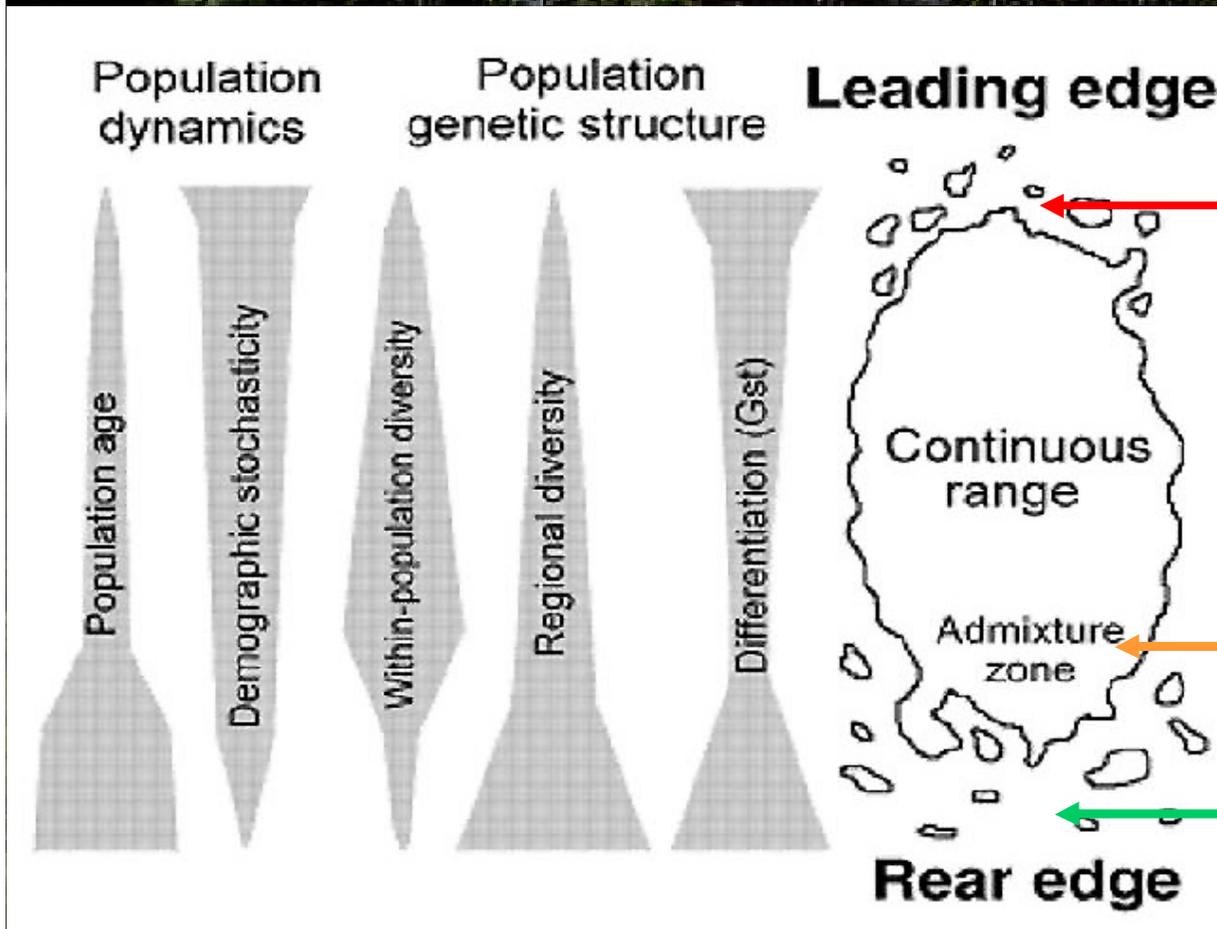
The eastern main clade of the Clouded Apollo (*Parnassius mnemosyne*) is subdivided into four (2 + 2 : BGCT/W and EN/EEER) main groups of mtDNS CO1 haplotypes. Outgroup: the W European main clade of the species (A)

Biogeographical connections of Pannonian steppic woods

From the four main mtDNA haplogroups of the eastern main clade of the Clouded Apollo (*Parnassius mnemosyne*) three occur in the Carpathian basin: a western subgroup expanding from the eastern margin of the Alps (blue), an eastern central European (red/pink), and also a northern subgroup expanding northwards from the Carpathian basin (orange/yellow). They are geographically and also ecologically separated from the southern Balcanic populations



Biogeographical connections of Pannonian steppic woods



Anatomy of the range

Long distance expansion
Founder events
Population growth
Cold stress

Merging of evolutionary lines

Stability of populations
genetic drift
Local adaptations
Aridity stress

Hampe & Petit 2003

Allopatric speciation is generally a slow process, thus strongly differentiated taxa can only evolve in refugia with survival potential both in cold and warm climatic phases ("double refugial effect"). Phylogeographic surveys have shown shallow differentiations only, contrasting with the strongly differentiated populations of lower latitudes.

Biogeographical connections of Pannonian steppic woods

Steppic woods and their contact grassland types are essential components of the Pannonian natural and traditional cultural landscape. They are habitat types with high national responsibility of Hungary as parts of our natural and cultural heritage.



A photograph of a grassy field with purple flowers and trees in the background. The text "Thank you for your attention!" is overlaid in the center in a red, serif font with a white outline.

Thank you for your attention!