Did human-mediated processes shape phylogeographic pattern of the Carpathian pine populations?

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The challenge to sustain biodiversity of the extreme ecosystems inquires detailed knowledge of the species' history and the trails of the recent population structure.

Summary

I. Native pine species of the Carpathians; biogeography, distribution, and habitat characteristics

II. Historical aspects and human mediated processes affecting natural range of pines

III. Phylogenetic pattern of the studied pine populations as consequence of the past events

I. Native pine species of the Carpathians; biogeography, distribution and habitat characteristics

Pinus – largest genus among the conifers

- around 176 taxa (Debreczi - Rácz 2011)
- Holartic distribution
- few species with large distribution northern boreal forests (e.c. *P. sylvestris* in Eurasia)
- higher species diversity in the Mediterranean (*P. halepensis*, *P. pinea*, *P. pinaster*, *P. brutia*)

Europe : 11 native species

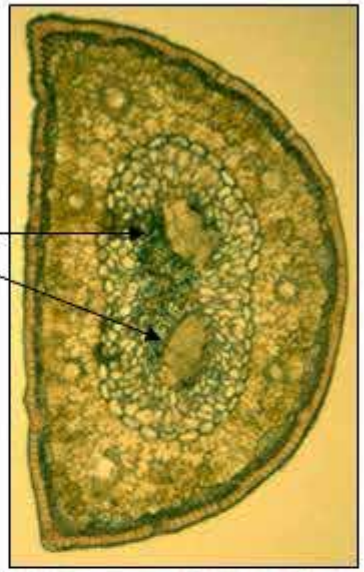
Carpathians: 4 native species

- forming climatically conditioned (subalpine) vegetation belt:
  Pinus mugo Turra
- having narrow distribution, relict population:
  Pinus cembra L.
  Pinus sylvestris L.
  Pinus nigra subsp. nigra var. banatica

Pinus sylvestris L.– Scots pine

Two needle pine

Diploxylon type



section Pinus, subsection Pinus

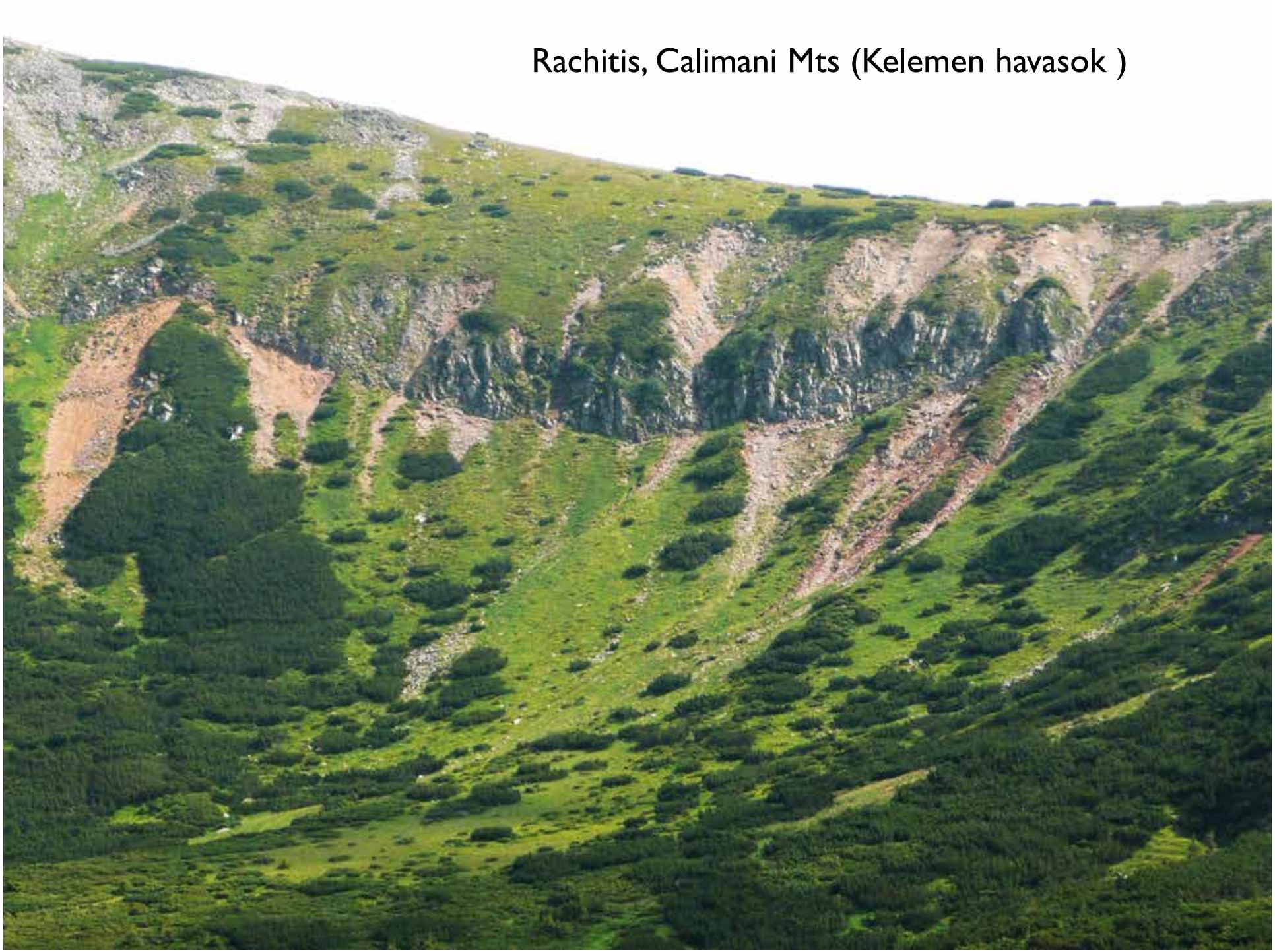

Lower Tatra Mts, river Vag


Fenyőkút (Korond), Transylvania


Mohos peat bog, Csomád Mts Eastern Carpathians

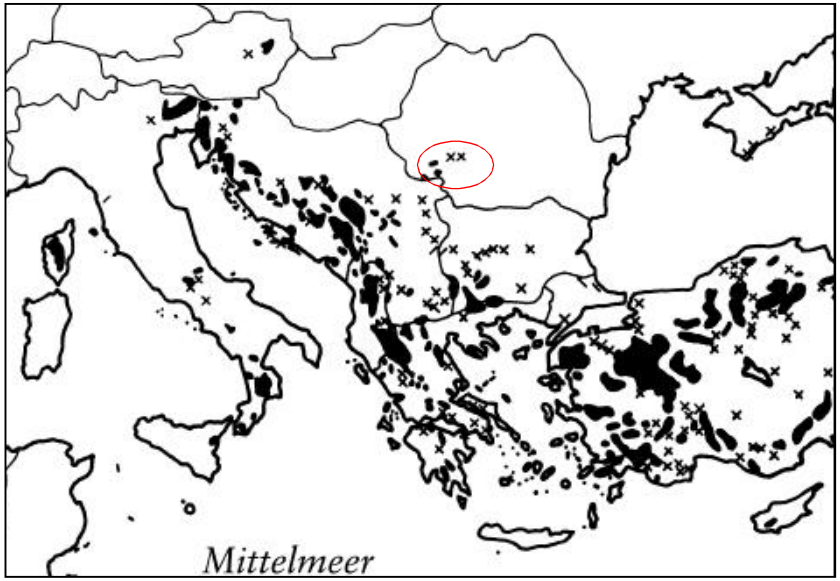
Pinus mugo Turra – dwarf pine


Retezatul Mic Mts



Rachitis, Calimani Mts (Kelemen havasok)

Pinus nigra *var. banatica* J. Arnold - black pine

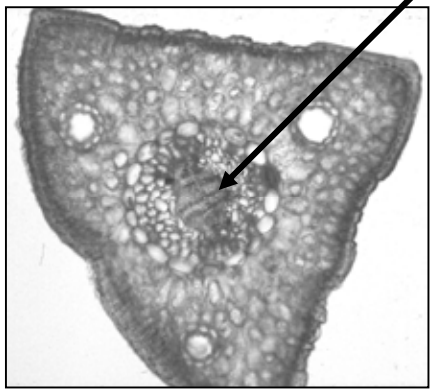



Mt. Domogled Baile Herculane (Herkulesfürdő)
P. nigra subsp. nigra var. banatica (Georgescu & Ionescu)

Pinus cembra L.– Swiss stone pine

Five needle pine

haploxylon type,



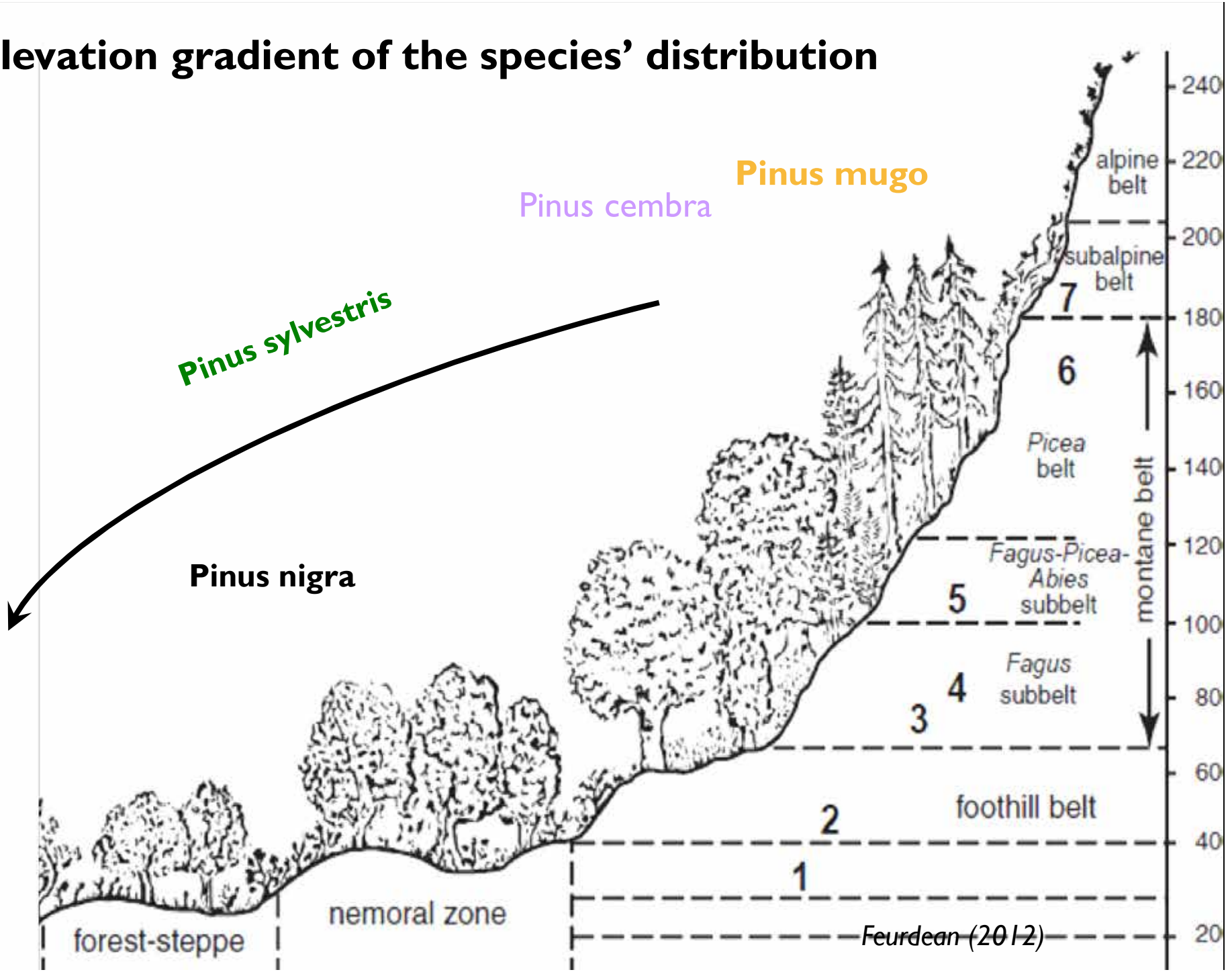
section Strobi, subsection Cembrae

closed cones, wingless seeds, dispersed by birds


Mt. Rodnei

Ineu (Ünőkő) Mt. Rodnei

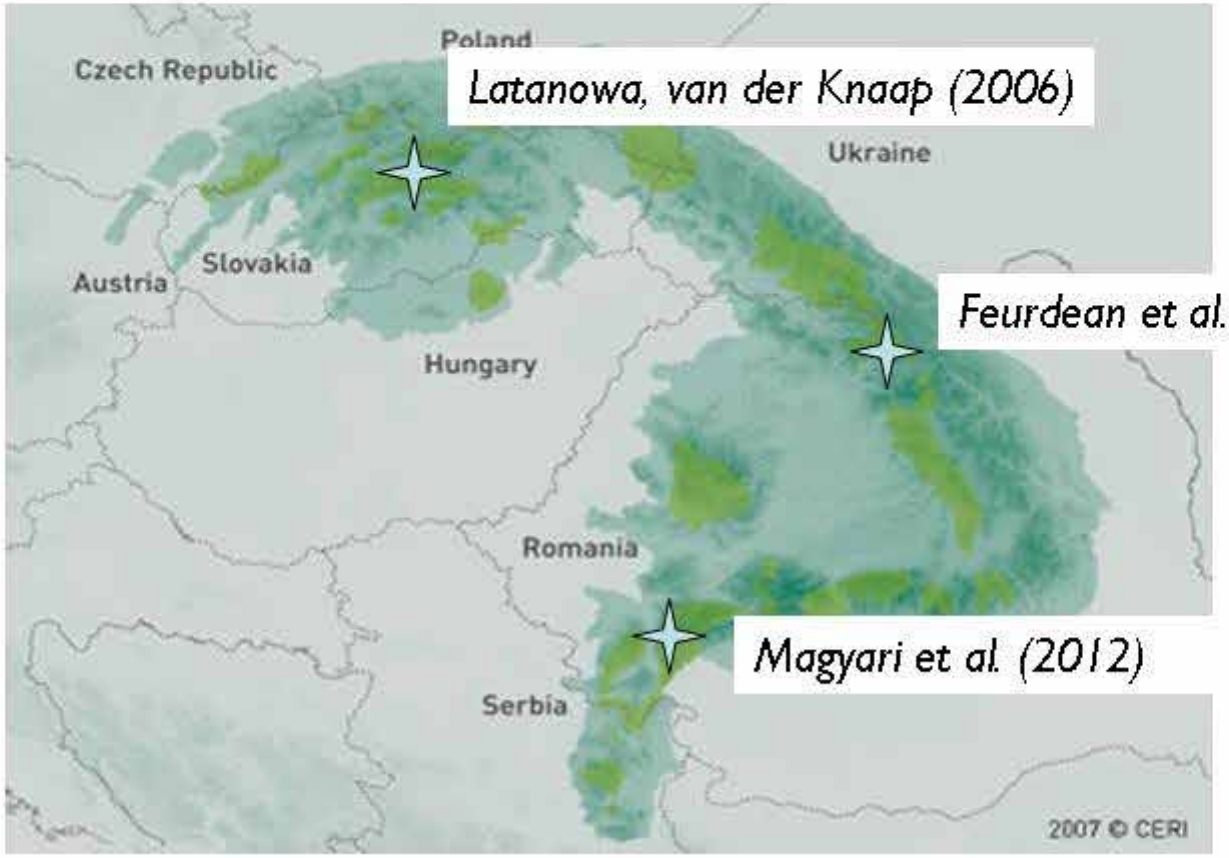
Elevation gradient of the species' distribution

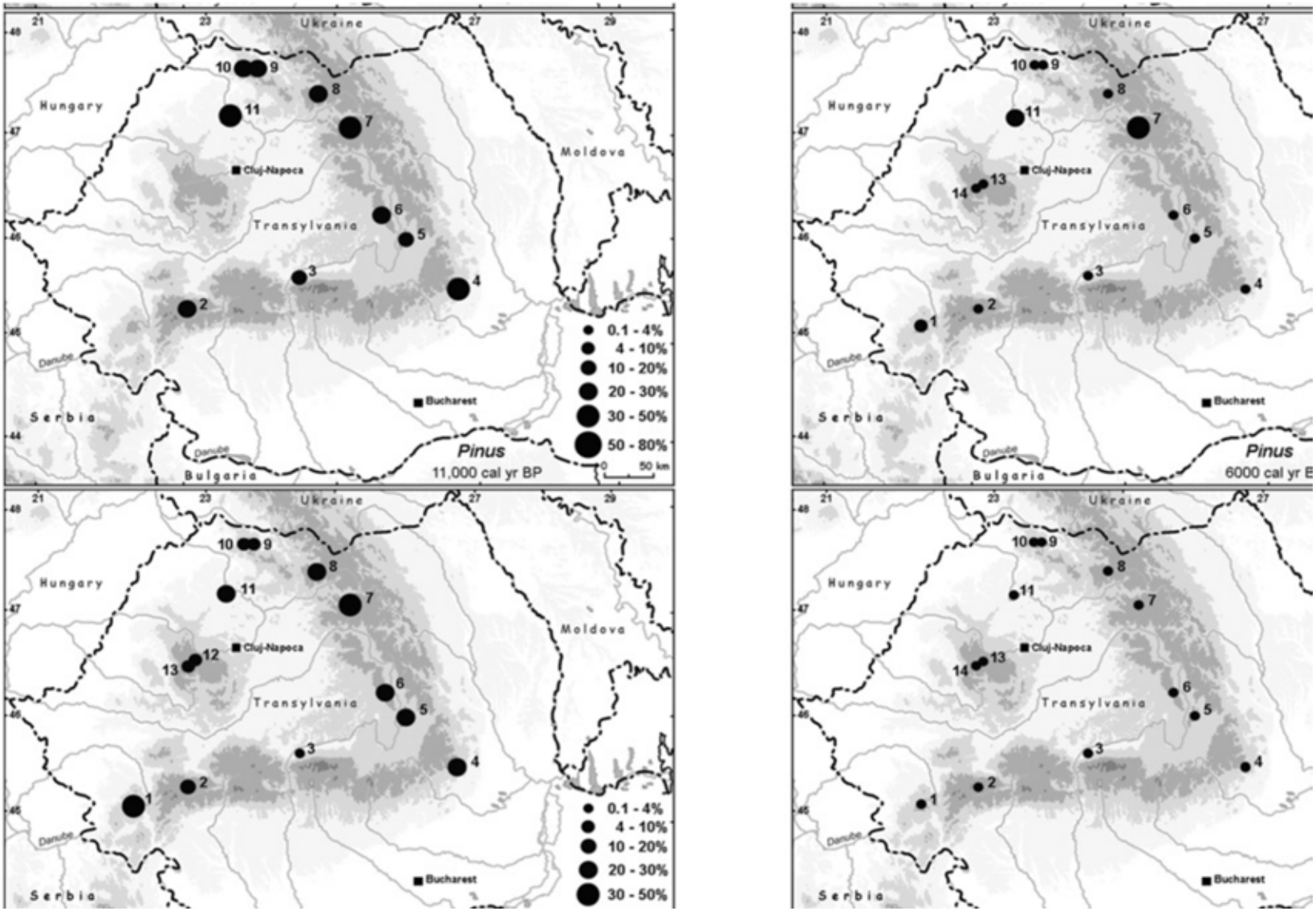


Feurdean (2012)

Preliminaries: Late glacial - early Holocene history

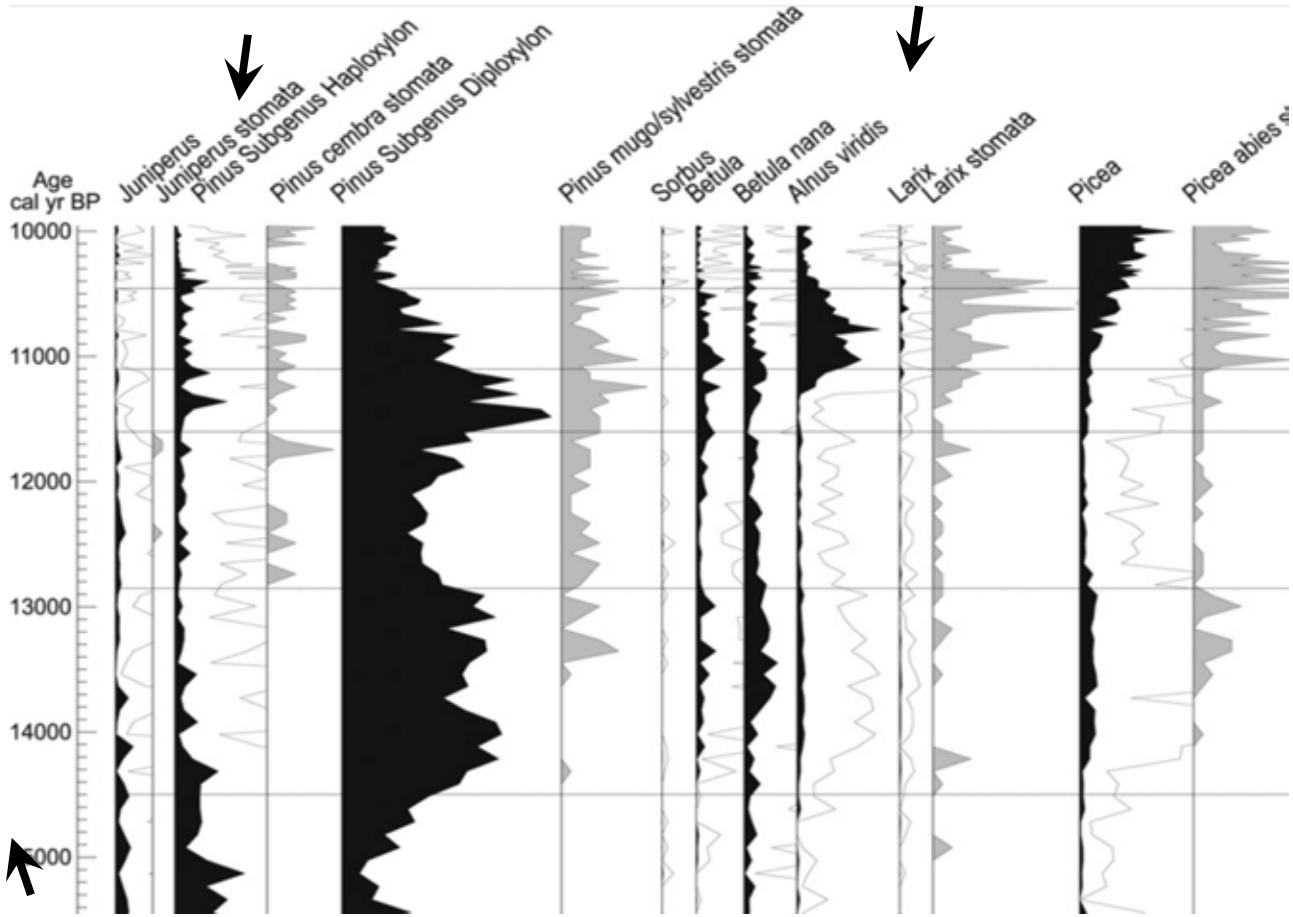
„…the predicted potential LGM ranges of six species (*Abies alba*, *Alnus glutinosa*, *Betula pendula*,*Corylus avellana*, *Fagus sylvatica*, *Taxus baccata*) are the same or smaller than today, **whereas the predicted potential LGM ranges of *Juniperus communis*, *Picea abies*, *P. omorika*, *Pinus cembra*, *P. mugo*, and *P. sylvestris*** are greater than today's ranges. These ensemble model predictions suggest therefore that **some trees, all conifers, may have had greater potential ranges in the LGM than today."** (Birks- Willis 2008)





Pinus pollen percentages were at their maximum (up to 75%) between 12,000 and 10,000 yr BP; (P. cembra only occurred in proportions <2%)

Feurdean et al. 2011,

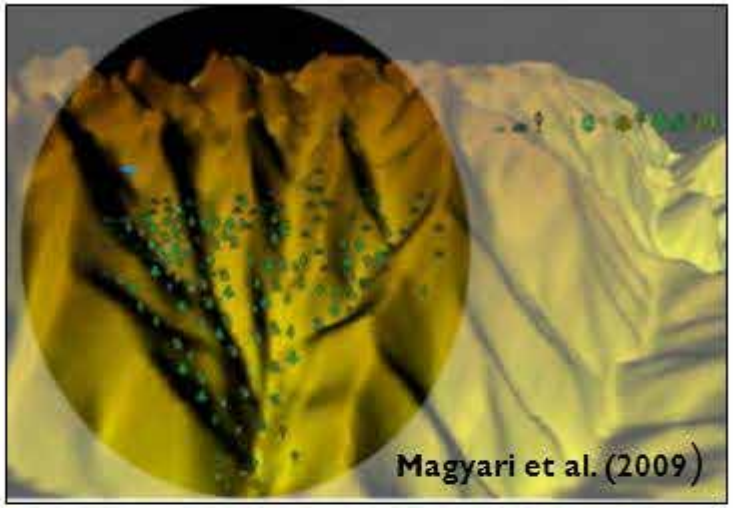


Magyari et al. 2012

Retezat Mts. Lake Brazi

Retezat Mts. South-Carpathians

refugial area for tree species



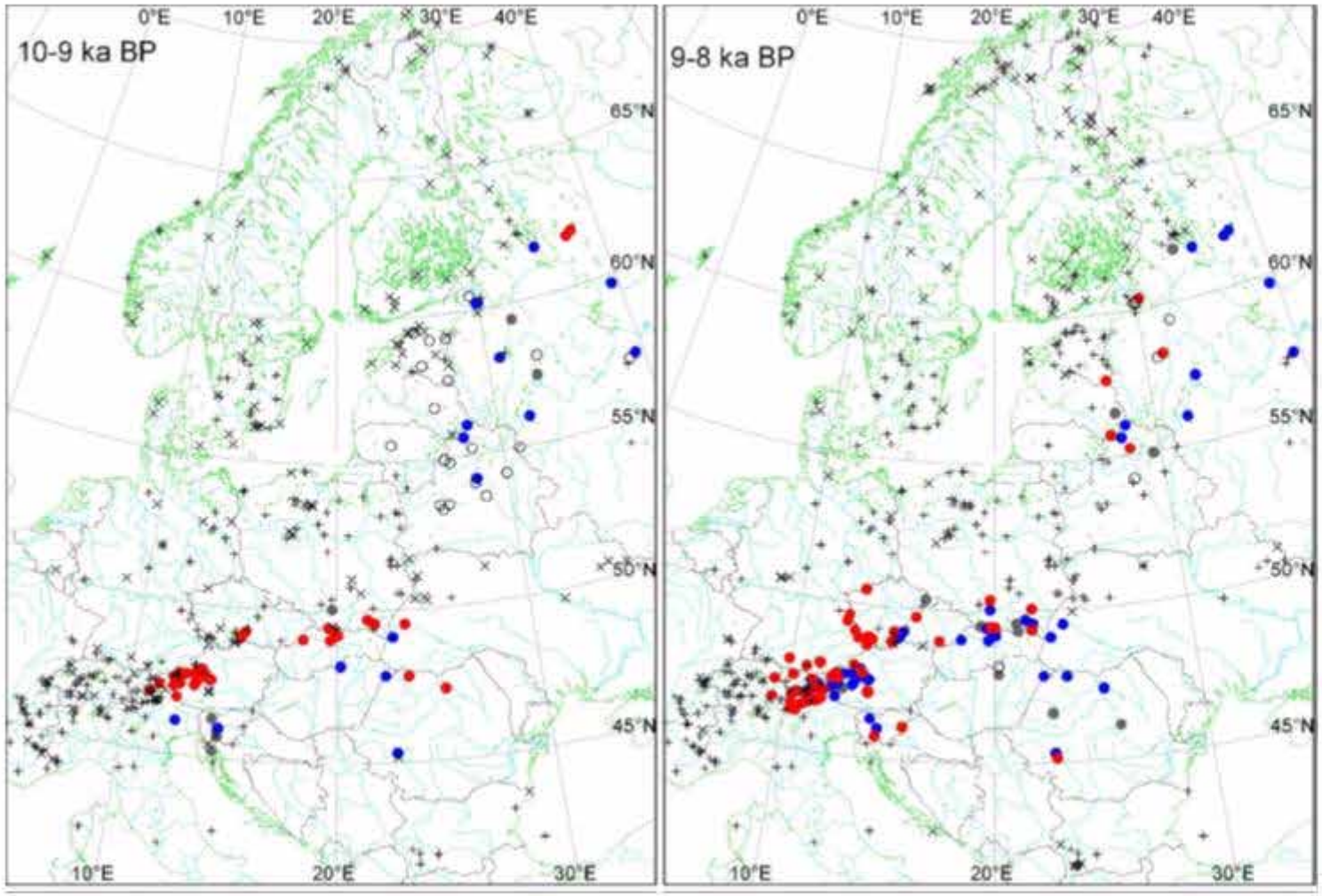
Vegetation reconstruction from the Late glacial interstadial period (~13,350 calyr BP) in the Retezat Mountains (Ro)

Magyari et al. 2012. QSR

lake Brazi (1740m asl),
~14200 cal yr BP. refugial populations of *Pinus mugo, P. cembra, Larix decidua, Picea abies*

by ~11,100 cal yr BP. in the early Holocene tree line reached 2000 m a.s.l. (higher than today) *P. mugo, P. cembra, P. abies* established around the upper lakes suggesting rapid increase in summer temperatures.

Lateglacial and Holocene expansion of *Picea abies* (L.) Karst.



The European range divided into a S and N part that come together in Poland

Distribution of Picea pollen >2% sites in the Holocene millennia 10–9, 9–8, cal yr. BP. Colours: red—expansion, blue—continuation, grey—the preceding millennium is not recorded.

Latanowa, van der Knaap 2006

II. Historical aspects and human mediated processes affecting natural range of pines

antropogenic impact on populations:

- pasturing
- mining activity
- wood industry, deforestations
- forest administration: planting

Pasturing – transhumance activity established by the Valachian culture

Nomad shepherds and extensive farming

Transhumance

„the alternate and periodic movement of pasturing animals between geographic and climatic regions - *from St George to St Demeter (St Michael)* -

Summer – on high mountain pastures,

Winter - on lowland pastures and visiting the markets (200-300 km migration)

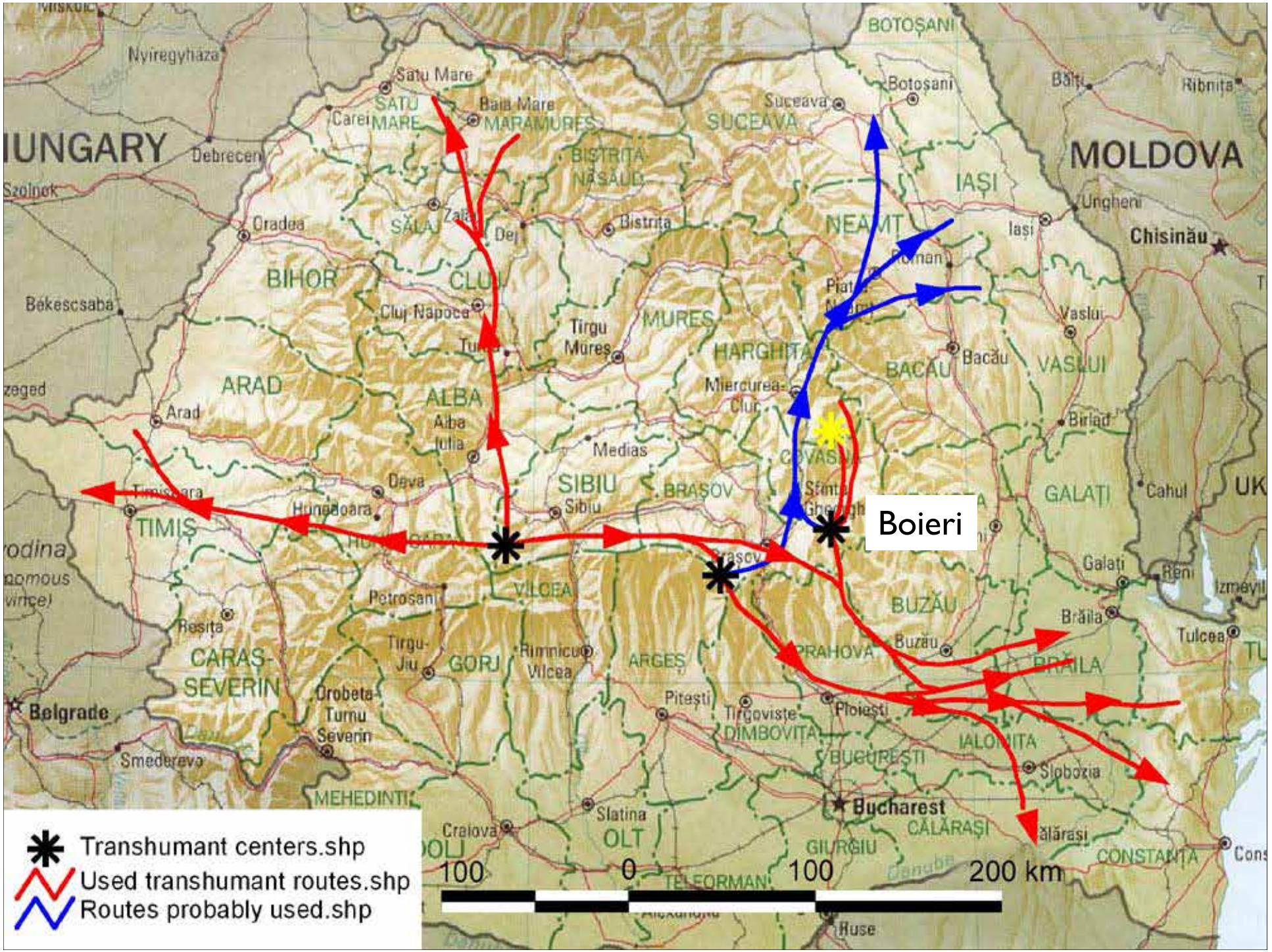
Reason: To avoid pasturing on more „productive" lowlands

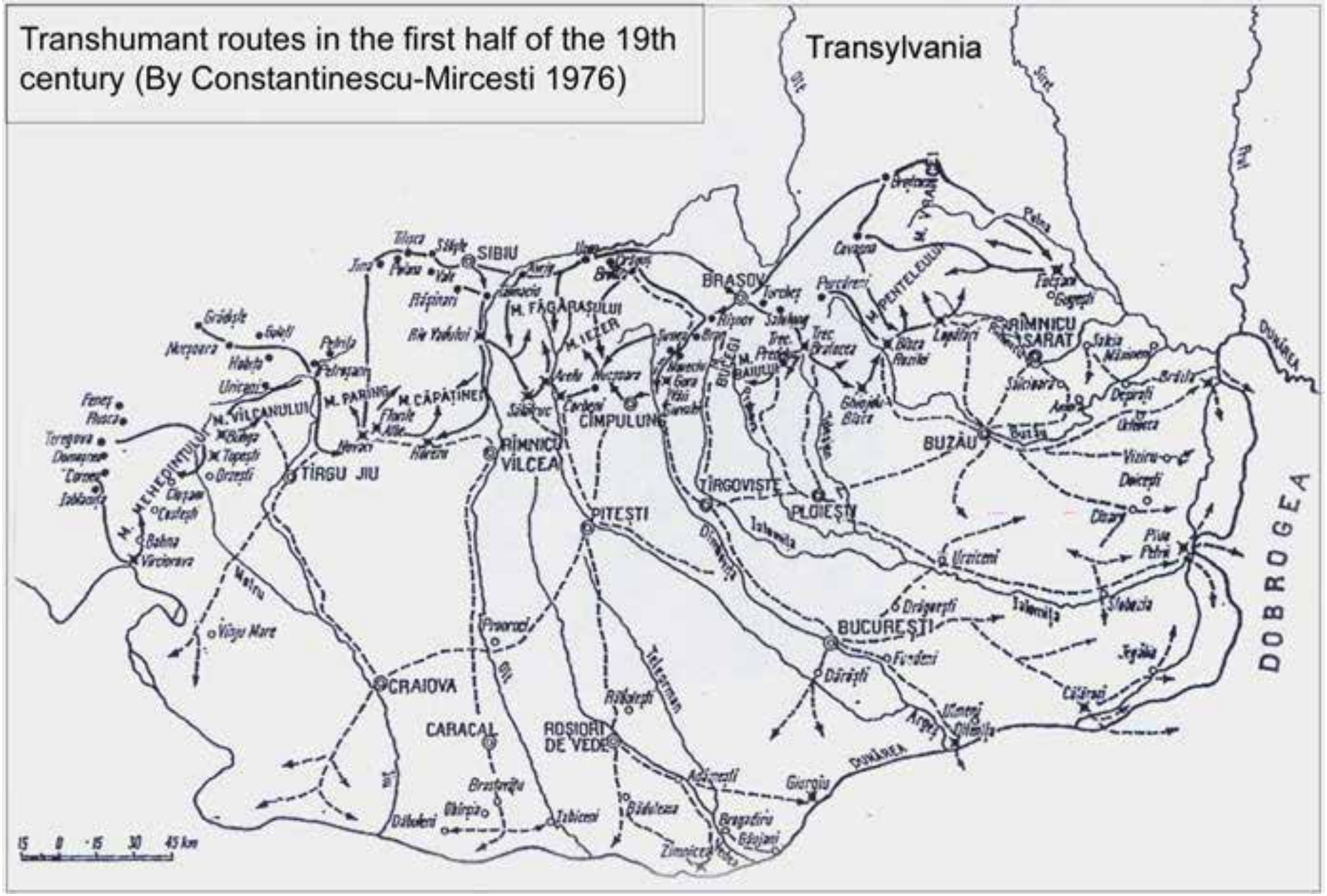
One of the most decisive human activity that shaped the high mountain vegetation of the Carpathians during the last 800 years

Mertens - Huband ***in:*** *Bunce et al. 2004 EU report,*

- early written documents – 12th century (but probably even much more earlier)
- from the Balkan penninsula migration to the north, all along from the southern Carpathians to Moravia
- Pasturing started on the lowlands, creating transhuman routes to the mountains by clearing forest used southern and eastern slopes

mainly sheep but also cattles
(in 1990 in Romania 15 millions, today 7.6 millions head)


Boieri
Transhumant centers.shp
Used transhumant routes.shp
Routes probably used.shp
100 0 100 200 km
HUNGARY
MOLDOVA
Nyiregyhaza
Debrecen
Szolnok
Satu Mare
Baia Mare
Carei
SATU MARE
MARAMURES
BOTOŞANI
Botoşani
Suceava
SUCEAVA
Bălți
Ribnița
Chisinău
Ungheni
Iași
IAȘI
NEAMȚ
BISTRIȚA NĂSĂUD
Bistrița
Dej
Zalău
SĂLAJ
Oradea
BIHOR
CLUJ
Cluj Napoca
Bekescsaba
Târgu Mureș
MUREȘ
HARGHITA
Miercurea-Ciuc
BACĂU
Bacău
VASLUI
Vaslui
Birlad
ARAD
Arad
ALBA
Alba Iulia
Medias
SIBIU
Sibiu
BRAȘOV
Deva
Hunedoara
Timișoara
TIMIȘ
GALAȚI
Cahul
Galați
Reni
Izmayil
Brăila
Tulcea
BUZĂU
Buzău
PRAHOVA
BRĂILA
Petroșani
VÎLCEA
Reșița
CARAȘ-SEVERIN
Târgu-Jiu
GORJ
Râmnicu Vîlcea
ARGEȘ
Pitești
Târgoviște
DÎMBOVIȚA
Ploiești
IALOMIȚA
BUCUREȘTI
Slobozia
Belgrade
Drobeta Turnu Severin
Smederevo
MEHEDINȚI
Slatina
OLT
Craiova
Bucharest
CĂLĂRAȘI
GIURGIU
CONSTANȚA
TELEORMAN
Ruse


Transhumant routes in the first half of the 19th century (By Constantinescu-Mircesti 1976)
Transylvania
SIBIU
BRAŞOV
RÎMNICU SĂRAT
BUZĂU
TÎRGU JIU
RÎMNICU VÎLCEA
CÎMPULUNG
PITEŞTI
TÎRGOVIŞTE
PLOIEŞTI
BUCUREŞTI
CRAIOVA
CARACAL
ROŞIORI DE VEDE
DOBROGEA
DUNĂREA
Mureş
Olt
Siret
Prut
15 0 15 30 45 km


Parang Mts. (Southern Carpathians) 2013


Parang Mts. 2013

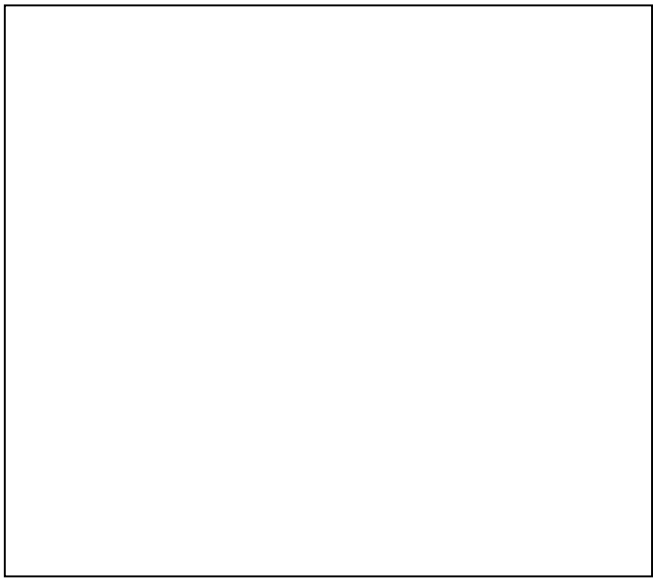

Retezat Mts. 2007

Northern Carpathians (Poland and Ukraine) – *Mróz et Olszanska* in *Bunce et al. 2004 EU report*

- There was no transhumance in the strict meaning of the term!
- Traditional pastoralism based on grazing of mountain grassland but overwintering lower in sheds, placed usually in the villages.

-The most important region **Podhale** – "under the Mountain meadows"
- Poland's southern region - short distance migration ➤

(15 million sheep at the end of the 19th century)



Góral people

Specific culture of the Ukrainian highlanders the **Hutsuls, Lemkos**

people pasturing in the North-Eastern Carpathian - Polonynas -
Transitional grazing grounds between the subalpine and lower settlements
of hay making animals were left there for winter

Before the II. World War pastures grassland covered 42% from the total area and arable land was just 3%

Mróz et Olszanska in *Bunce et al. 2004 EU report*

Consequences of overgrazing:

- degradation of the subalpine alpine habitats
- decreased of the *Pinus mugo* belt
- timberline changes
- increase of *Nardus stricta* and juniper rate
- acidic mires (*Deschampsia caespitosa*) and juniper
- grazed forest understory
- soil erosion

Rodnei Mts. Easthern Carpathians

pastures


Ciucas Mts.
grazed forest


Rodnei Mts

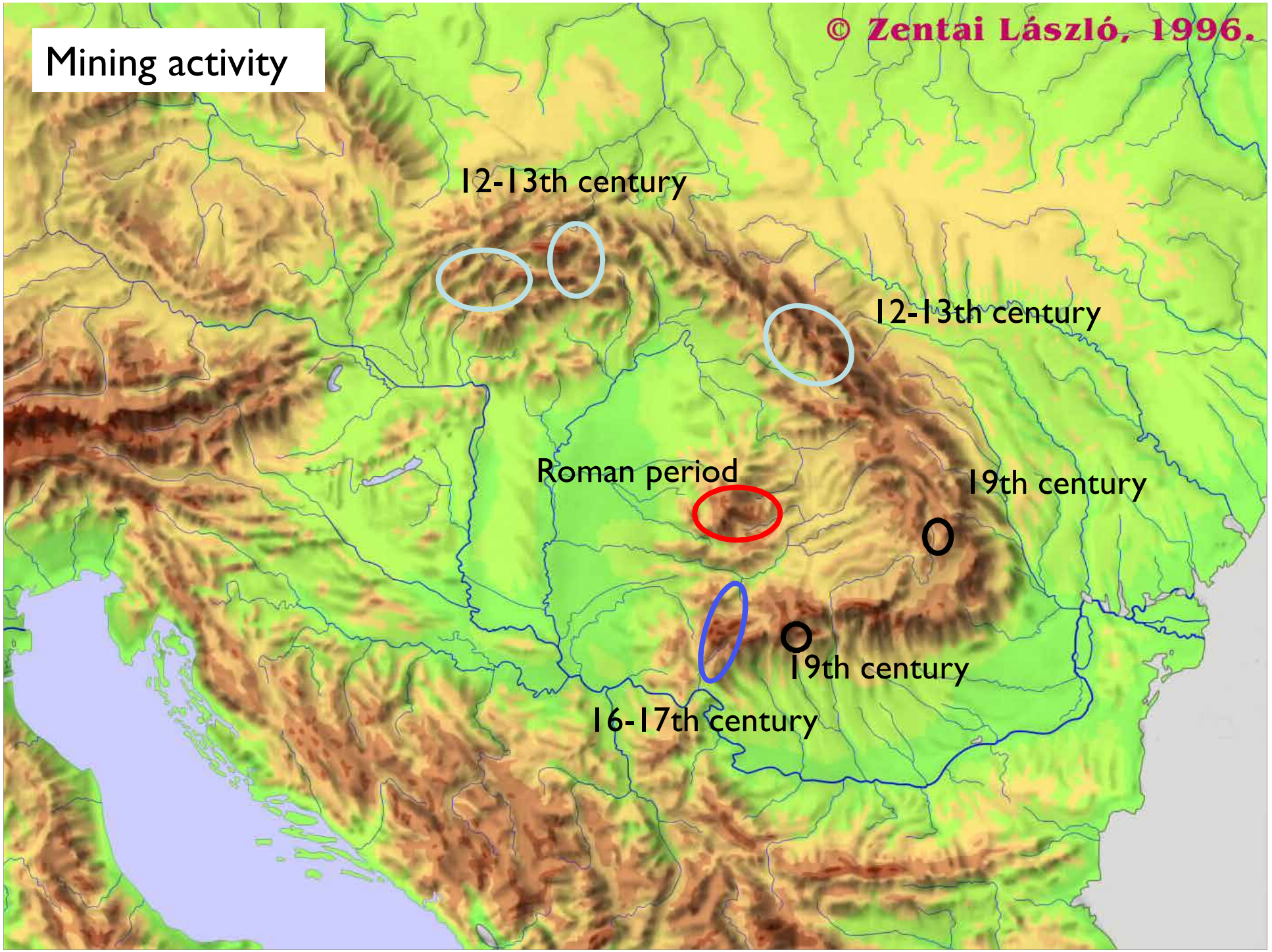
Benefits of grazing : increasing biodiversity of hay making meadows
'Underuse' – problem !

Sitko –Troll 2008: 1933 timberline elevation was 1329m asl and in 2001 was 47m higher in Chornohora region

The area above the timberline decreased from 32km^2 to 22,5km^2 in 2001

The faster rising of the timberline is probably better due to the abandoned pastoral activity not because of the climate change

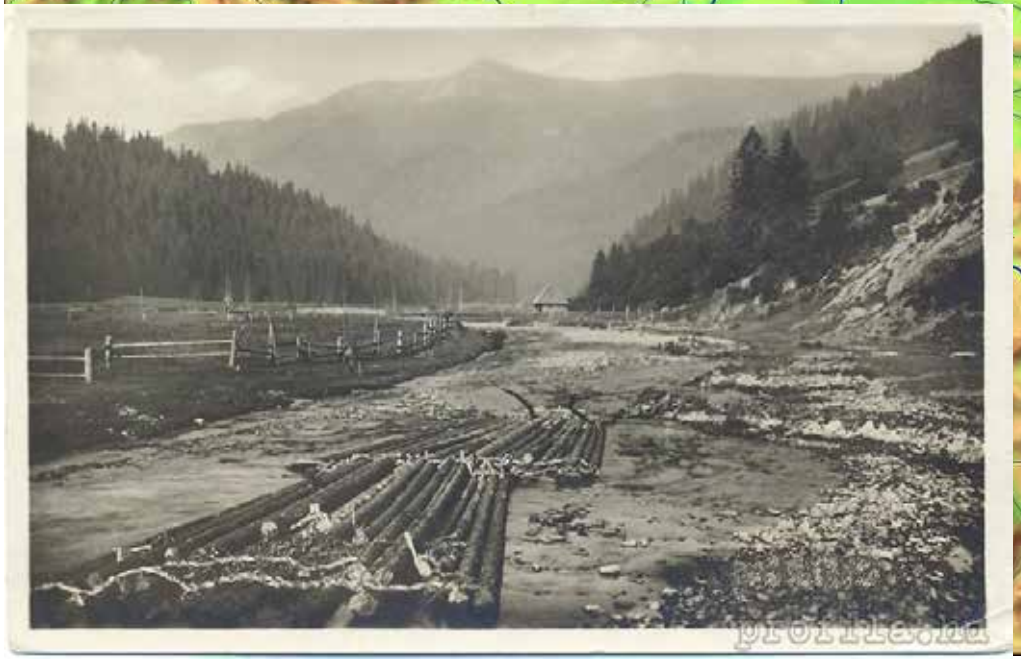
Horror in the Retezat Mts
(Adevarul, 12th July 2014)


Mining activity
© Zentai László, 1996.
12-13th century
12-13th century
Roman period
19th century
19th century
16-17th century

Torockó, Transylvania (1291, from Nieder Österreich iron, mining activity)

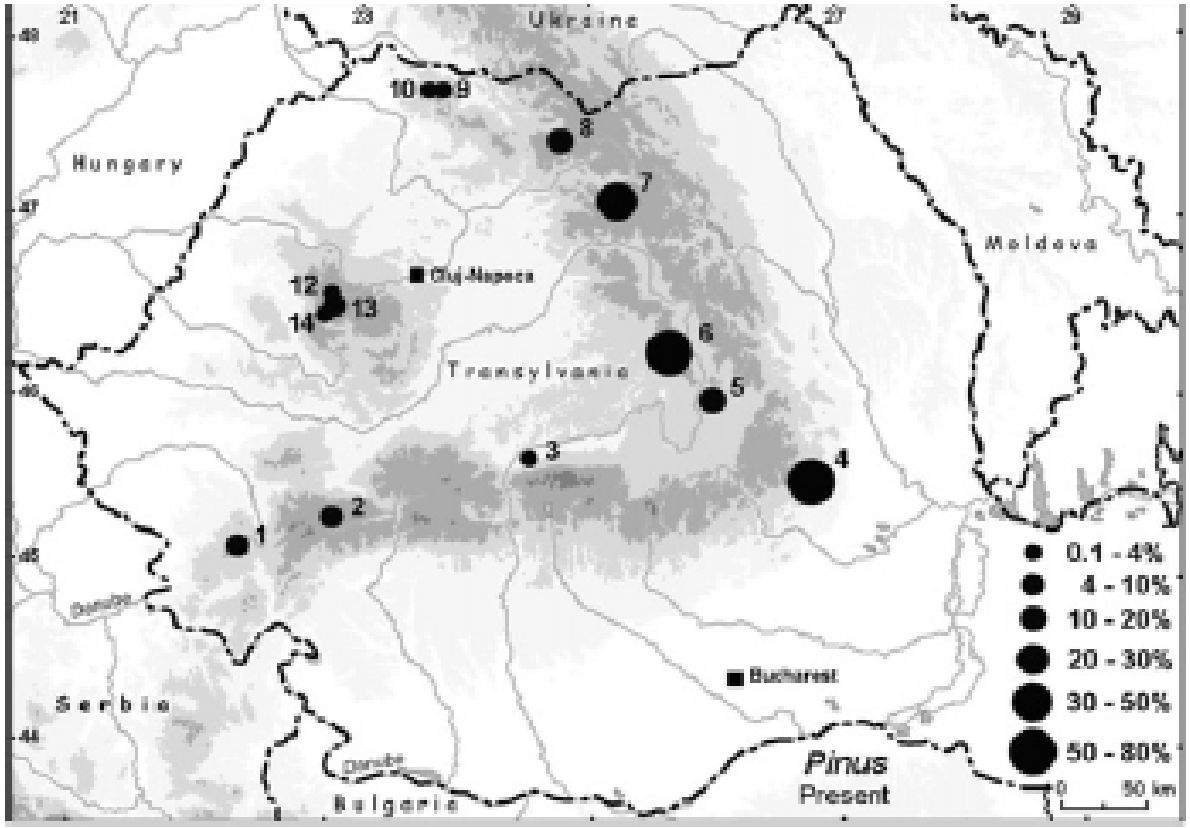
Wood industry

© Zentai László, 1996.




Negoiul Romanesc (Calimani Mts)

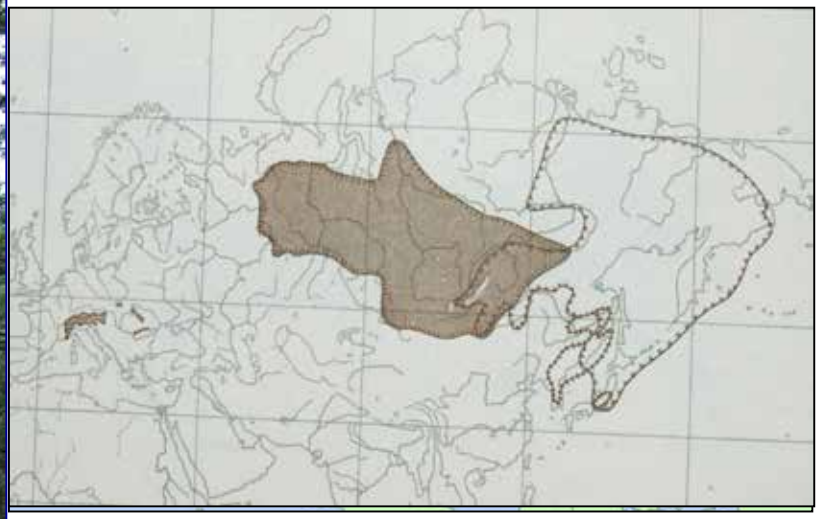
Negoiul Romanesc (Calimani Mts)



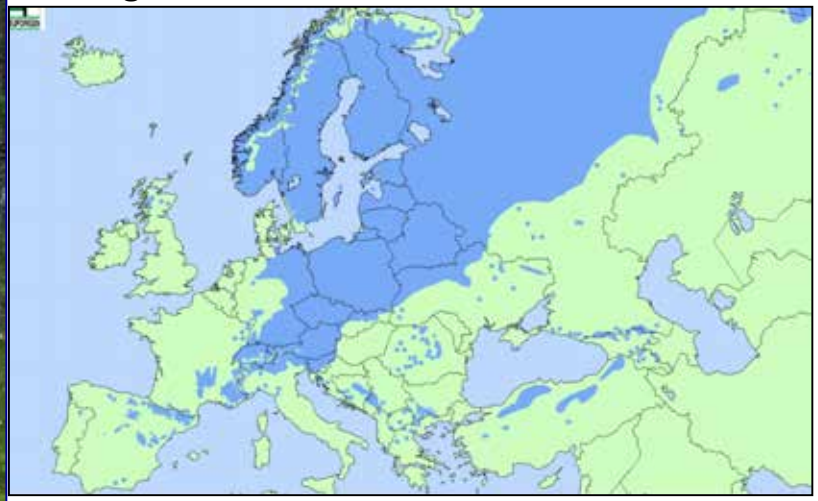
Feurdean et al. (2011)

Plantations?

III. Phylogenetic pattern of the studied pine populations as consequence of the past events



Euforgen



Pinus cembra L.

Swiss stone pine

Habitat: timberline ecotones, screes

Pinus sylvestris L.

Scots pine

Habitat: remnants of boreal forests along the Carpathians, raised bogs, and rocky outcrops

Relict species, with narrow distribution along the Carpathians

small populations, inhabiting only extreme habitats

Why *Pinus sylvestris*?

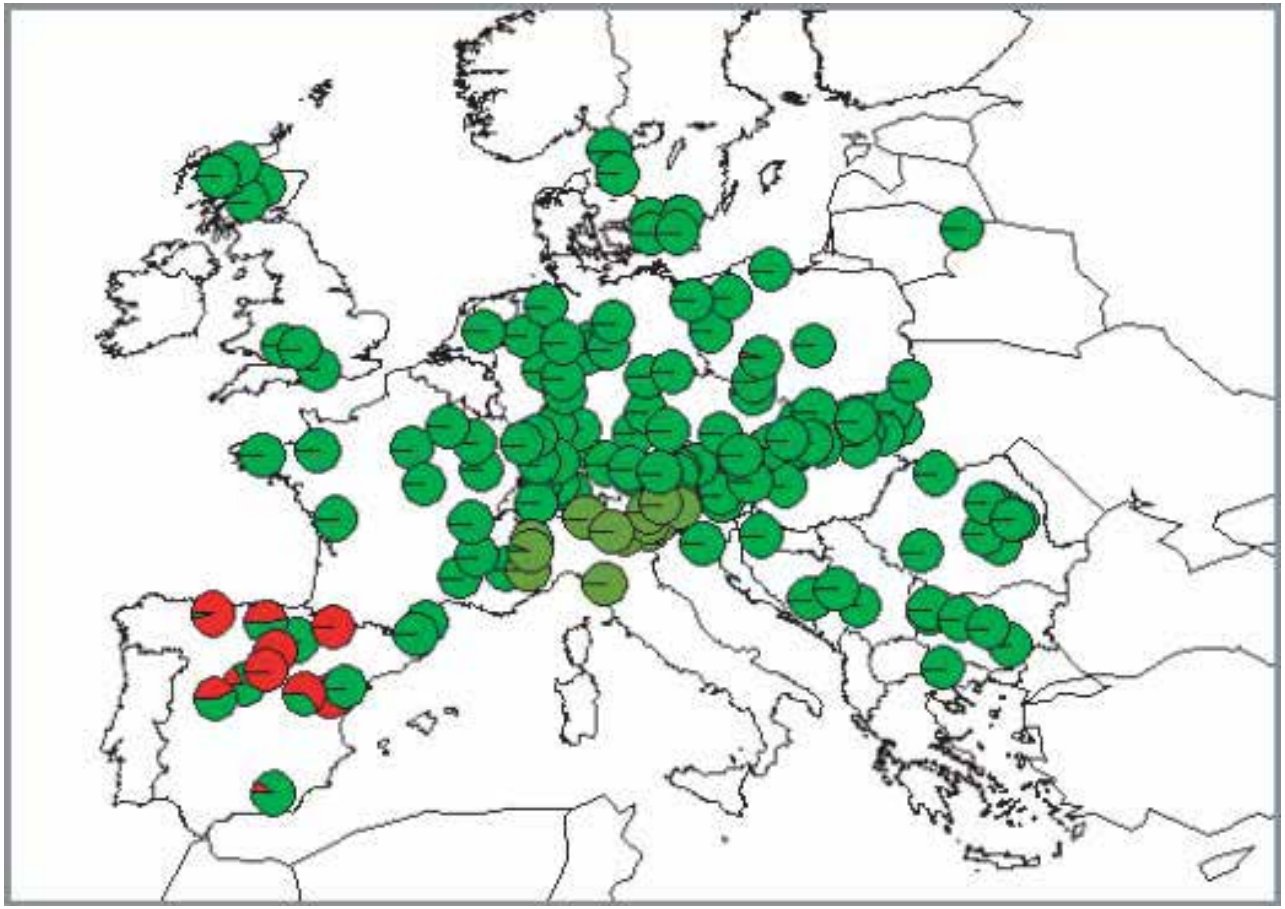
- Has the largest distribution among pines
(except *Juniperus communis*, also among the conifers)

- „*talking*" taxa (refugia and migration routes during the glacials and the Holocene, peripherial populations in the south)

- a „*big survivor*" with extremely high phenotypic plasticity, small stands on extreme habitats with probably good *fitness*

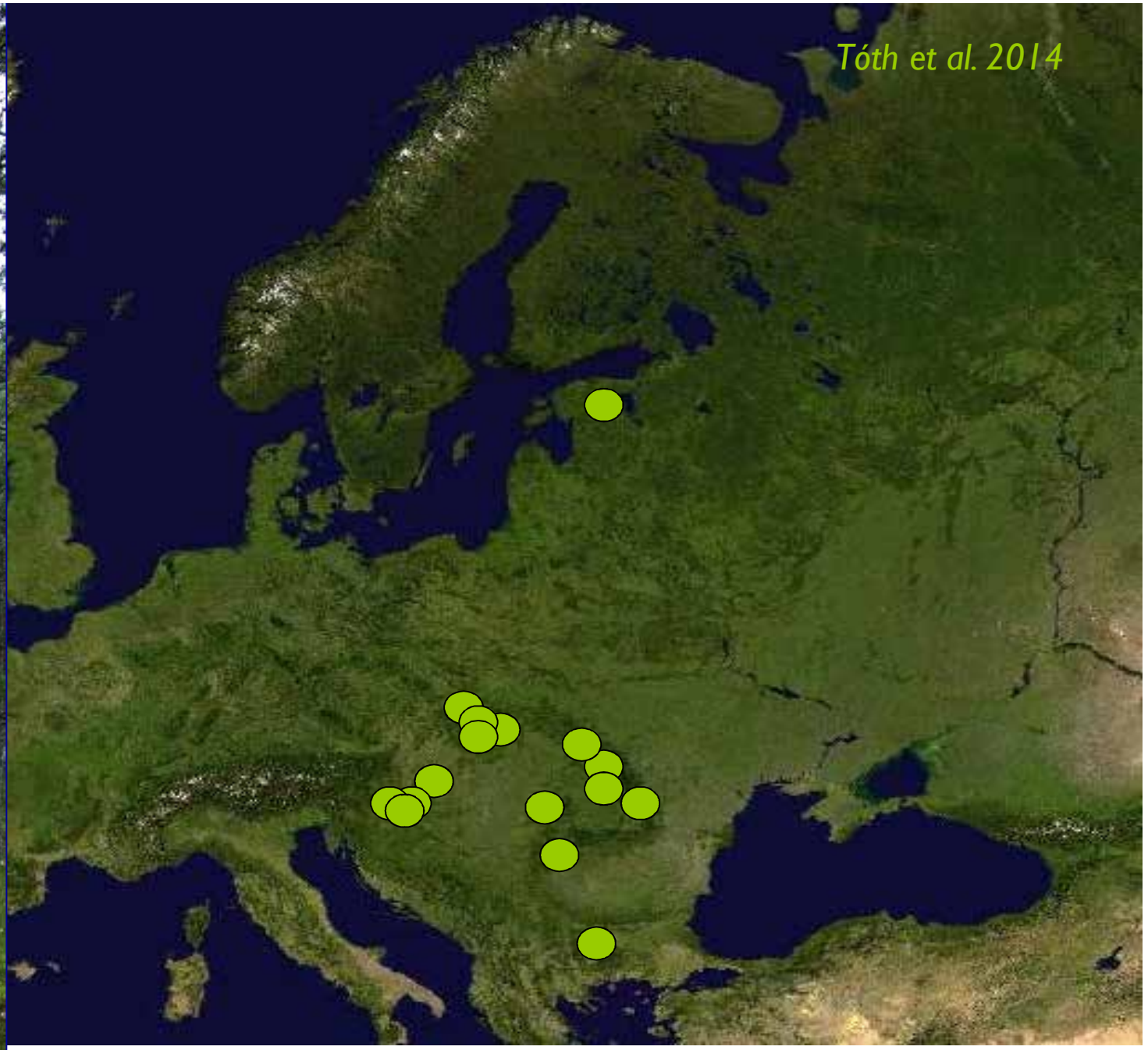
Many studies:

Mátyás 1994,
Sinclair et al. 1998, 1999,
Alia R. et al. 2001,
Vendramin et al. 2003,
Naydenov et al. 2005,
Cheddadi et al. 2006,
Pyhäjärvi et al. 2007,
Cerepovic 2009,
Ábrahám et al. 2010,
Sannikov – Petrova 2012



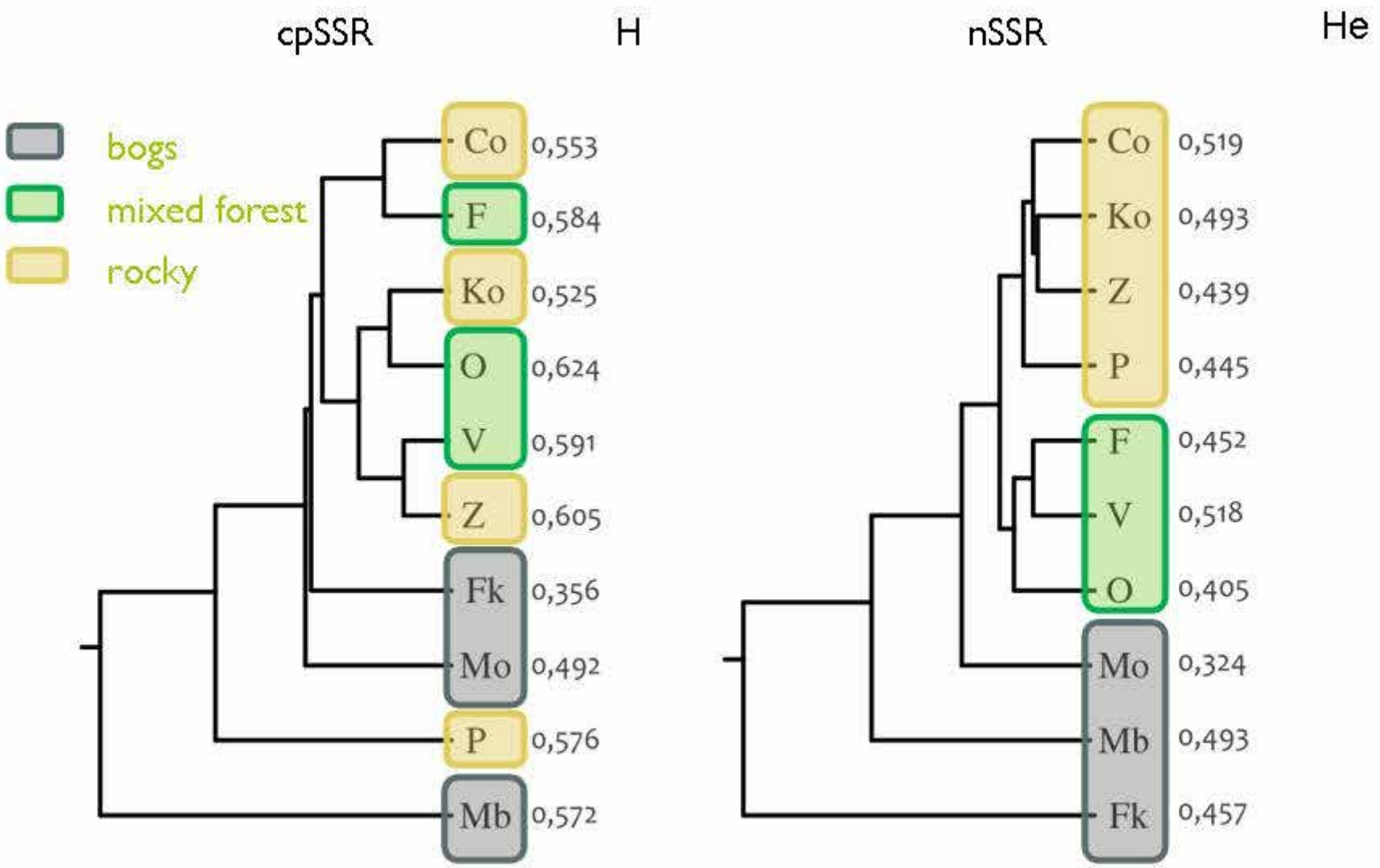
Survey of mitochondrial DNA of 106 populations of *Pinus sylvestris* showing three different haplotypes (red, dark green and light green).

Cheddadi et al. 2006



17 populations studied, 10 native to the Carpathians (N=342)

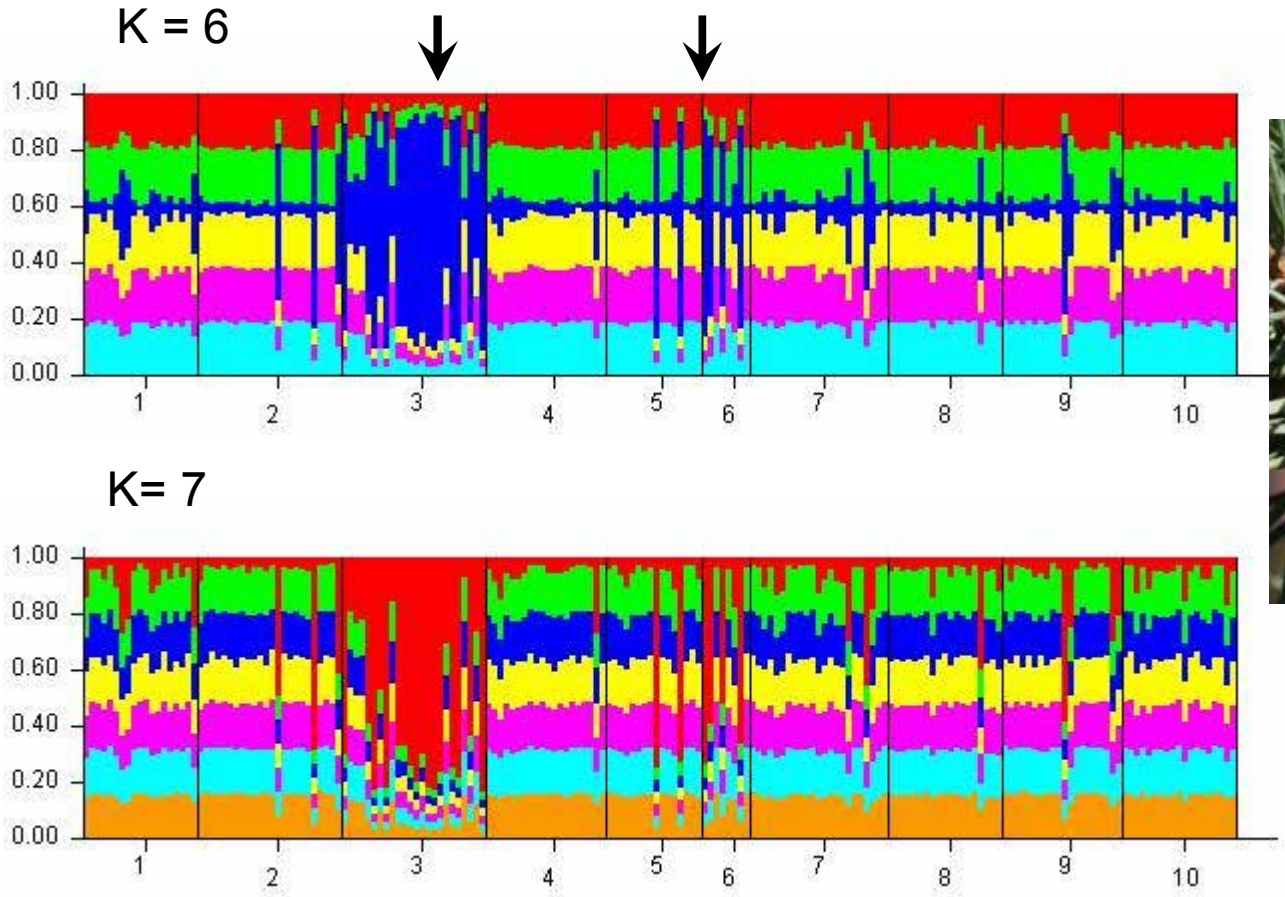
UPGMA dengrogram based on Nei's genetic distance



Tóth et al. 2014

7 tested nuclear SSR (4 polymorphic) – *Sorenzo et al. (1998), Sebastiani et al. (2012)*

STRUCTURE 2.3.4 with admixture model and correlated allele frequencies
'K' is the most probables number of clusters



Tóth et al. 2014

No of haplotypes, high: **60**

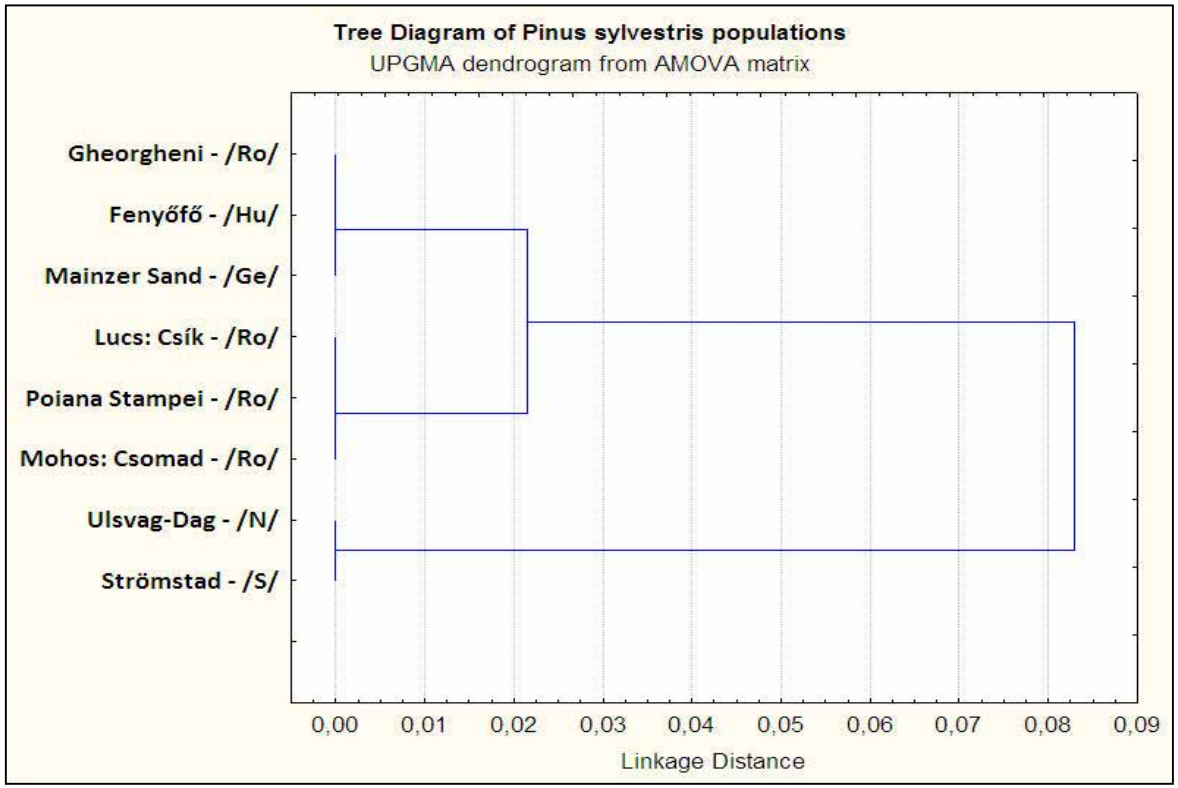
Mean haplotypic diversity: **H = 0.57**

AMOVA total variation 94,46% derived from within populations variation

Population divergence expressed by fixation index, low**: Fst = 0.05**

Mantel test: No geographical structuring!

UPGMA clustering shows groups of populations inhabiting the same habitat type.



Höhn et al. 2010

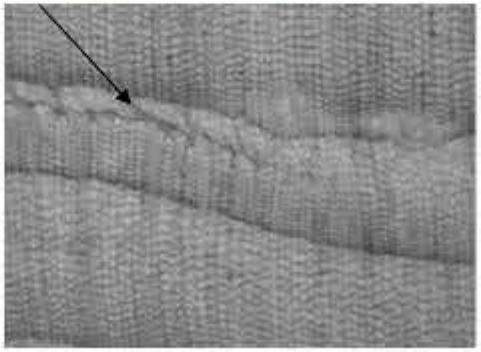
Pinus cembra L.

- Relict species, sparse occurence

- Glacial valleys, rocky surfaces on scheletic soils.

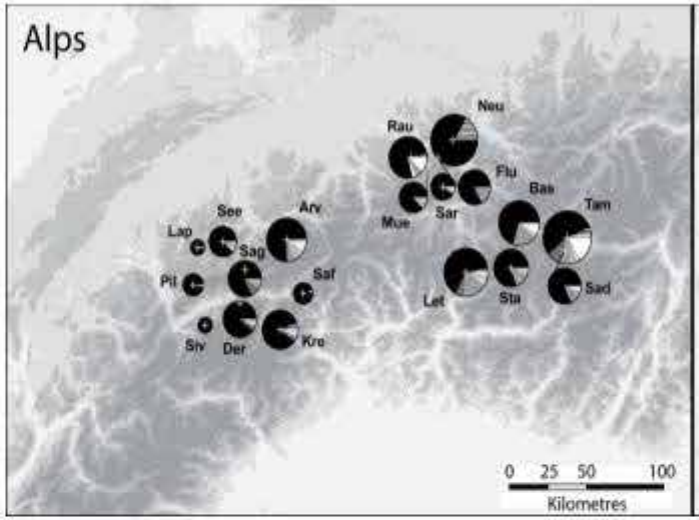
- Some of the oldest living trees found in the Carpathians It happens that one branch of the declined tree survives and grow further on forming a new trunk.

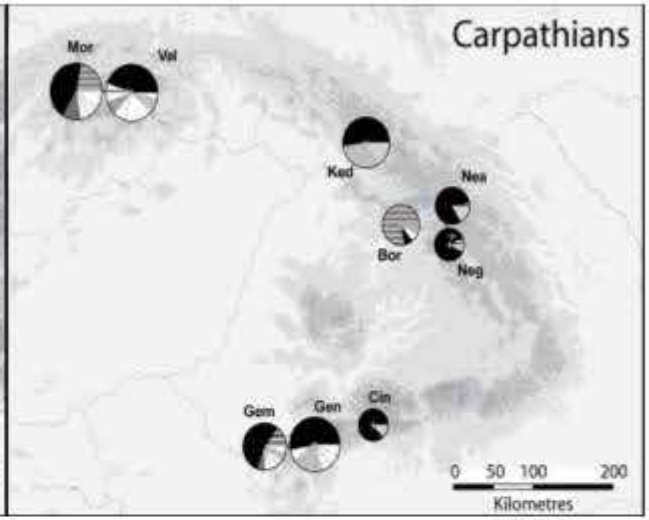
- High frost resistence of the trees but also some striking frost cracks inside the xylem of the old collapsed trees.

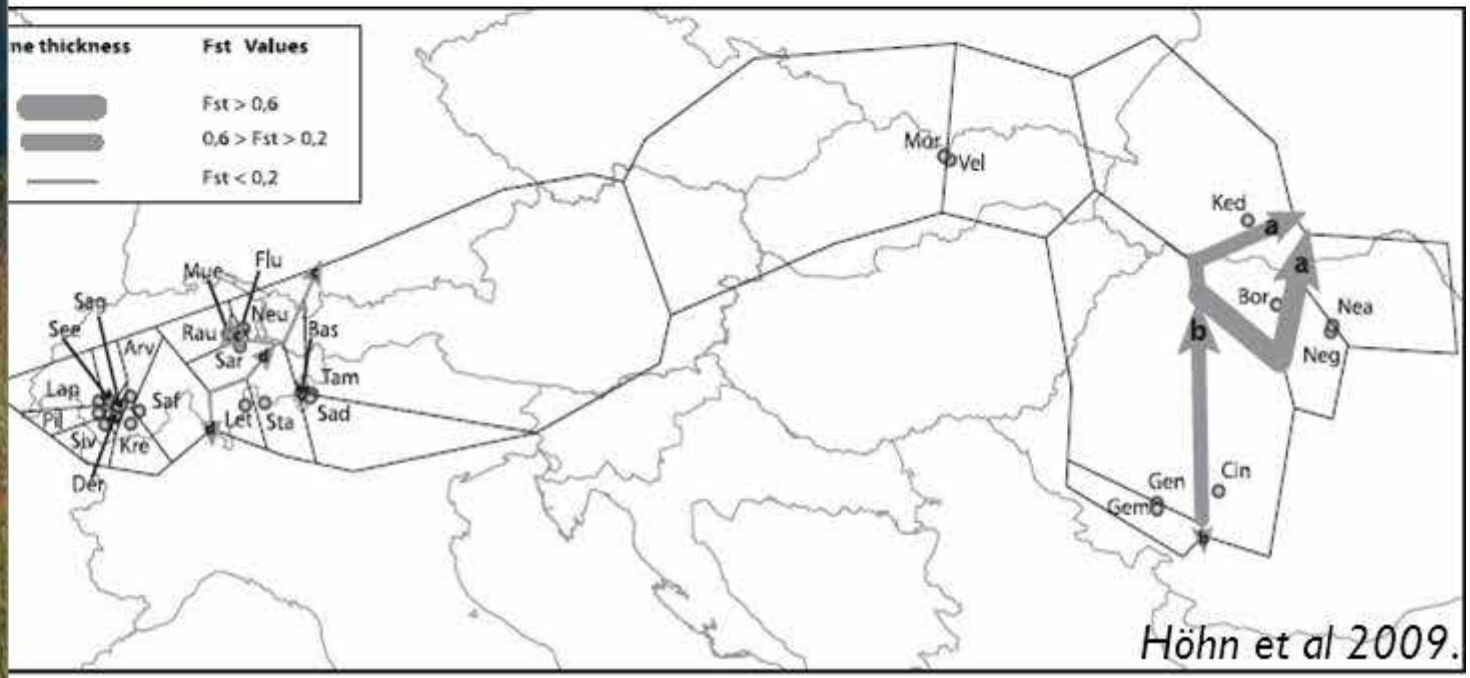


Popa – Kern – Nagy (2006)

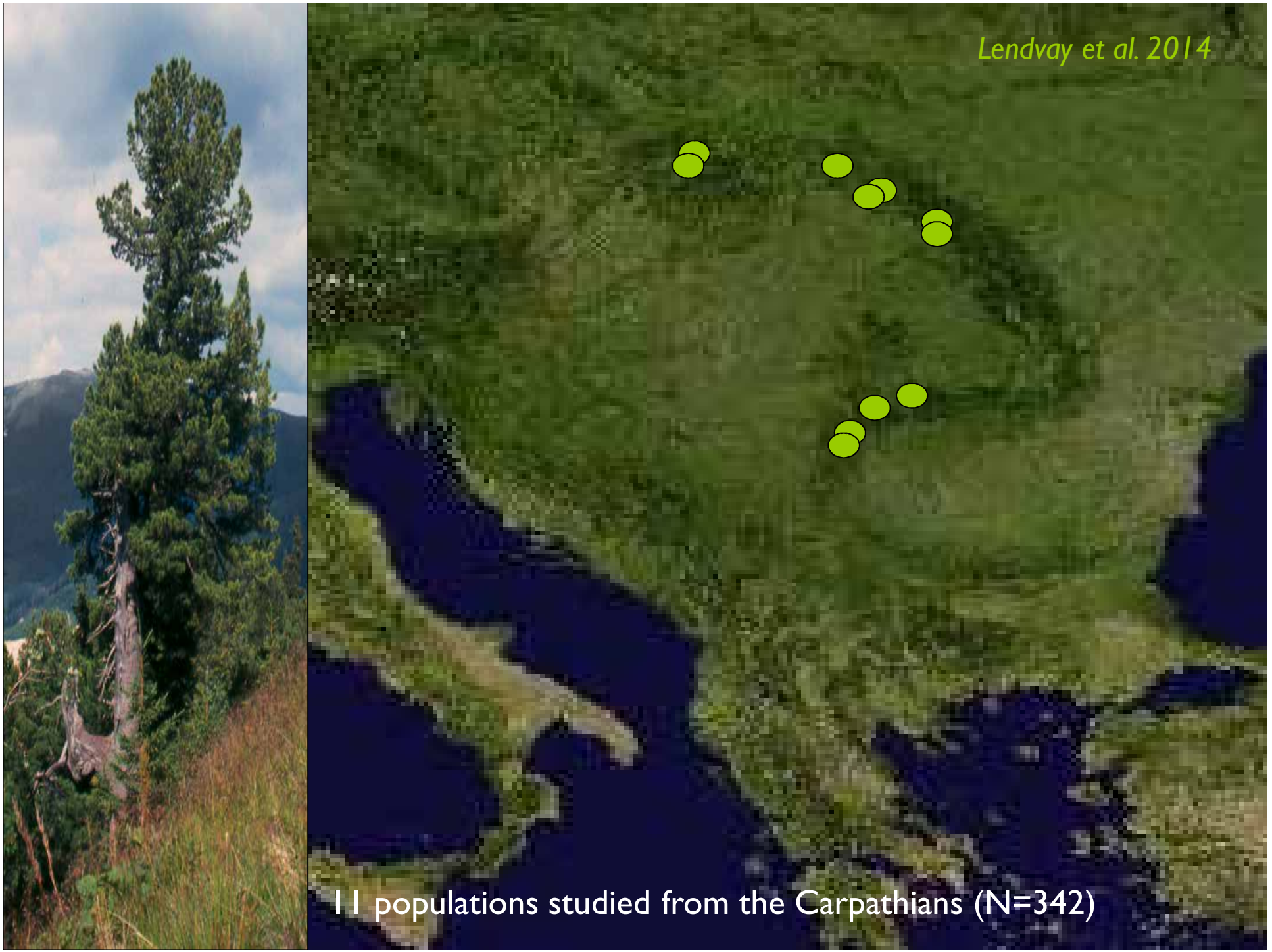
Population diversity along the two parts of the distribution range based on the cp SSR haplotype content



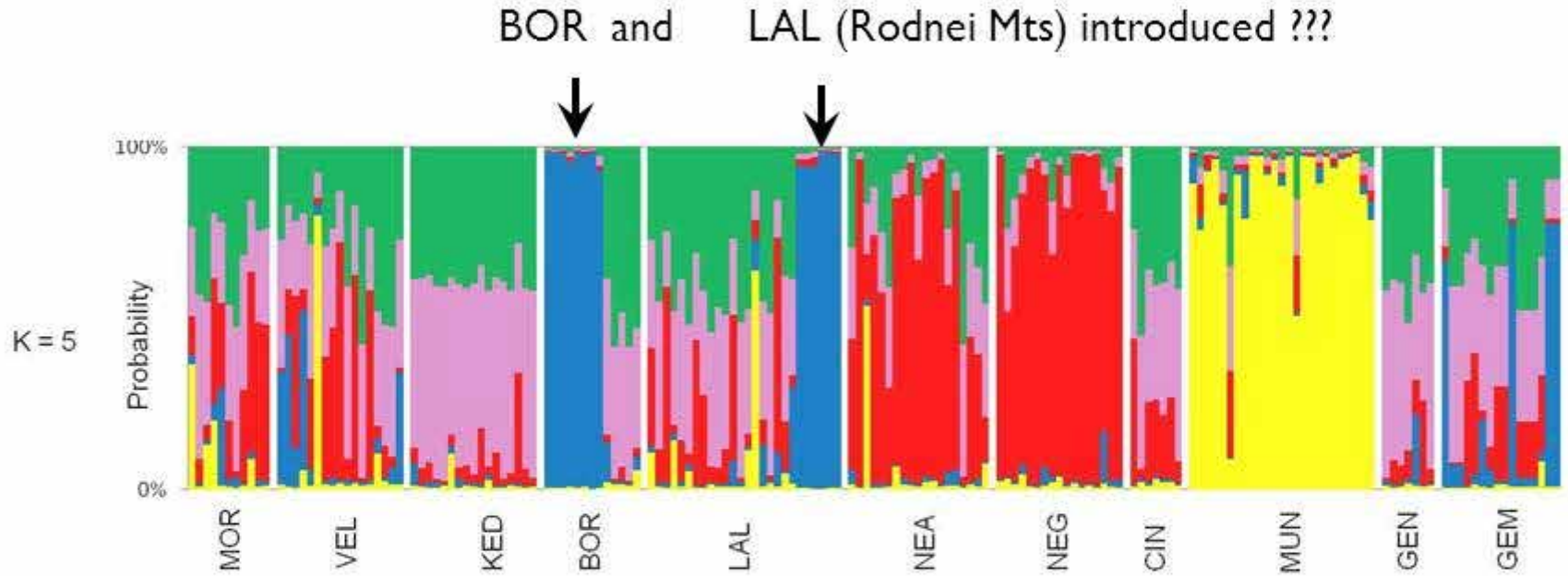




Höhn et al 2009.


Lendvay et al. 2014
11 populations studied from the Carpathians (N=342)

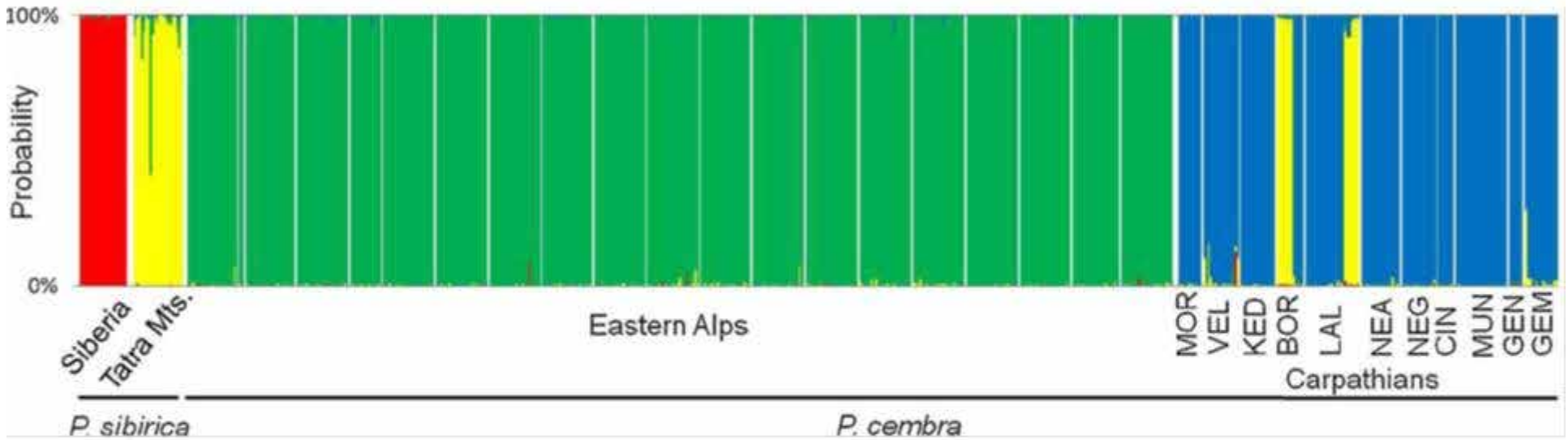
STRUCTURE 2.3.4 with admixture model and correlated allele frequencies,
'K' is the most probables number of clusters,
when K>2 two clearly distiguishing cluster



Lendvay et al. 2014

STRUCTURE 2.3.4

when K=4 two clearly distinguishing clusters in the Carpathians



Assignment of the non-native individuals from BOR and LAL populations using the USEPOPINFO model in STRUCTURE. Population of origin is predefined for the following groups: *P. sibirica* from Eastern Siberia (1), *P. sibirica* from the Tatra Mts. (2), *P. cembra* from the Eastern Alps (3) and *P. cembra* from the Carpathians

Lendvay et al. 2014


Valea Lala, Mt. Rodnei 2011

Valea Lala, Mt. Rodnei

Conclusions

1. Did human-mediated processes shape phylogeographic pattern of the Carpathian pine populations?

- ***Yes, the influence is manyfold.***

2. The Holocene reduction in the Carpathian pine area caused by the past global climatic changes and the ever increasing anthropogenic impact at the same time, is an important aspect that need to be known to understand present population structure.

3. The knowledge of the geological past, the human history and the genetic data altogether can provide valuable information for tree breeding, forest management and nature protection.

Conclusions:

- Carpathians are important in terms of accumulation of genetic diversity.

No correlation between genetic and geographic distance along the Carpathian range.

- Presumed multiple colonization routes from glacial refugia.

„However is still known that populations generally have strong ecological resilience, reasons of which clearly need to be better understood; evolutionary history, genetic system of species, epigenetics and phenotypic plasticity, or community dynamics."

Bertalan Lendvay

Endre Tóth

Klára Cseke

Levente Hufnagel

Project supported by OTKA K 101600

Péter Ábrán

Andrzej Pedryc

Júlia Ferenczi

Marcel Mandrescu

Sabine Brodbeck

Frederico Sebastiani

Giovanni Giuseppe Vendramin (CNR Italy)

Felix Gugerli (WSL Switzerland)