UNIVERSITY OF ZAGREB
FACULTY OF SCIENCE
Department of Biology
DIVISION OF BOTANY

HrZZ
Croatian Science Foundation

Filogeografija biljaka na Balkanskom poluotoku

Biokovo, Croatia

& BalkBioDiv

International Symposium on "Evolution of Balkan Biodiversity"

Zagreb, Croatia
June 28th - 30th 2012

Balkbiodiv - Insights into the plant diversity of the Balkan Peninsula

Home | Database

Project Balkbiodiv

Insights into the plant diversity of the Balkan Peninsula

The **Balkan flora** is not only the richest in Europe but comprises also many endemics. **Preservation of indigenous species** and their habitats is therefore not only of national, but also of international importance. While species richness is still the most widely used measure for biodiversity assessments, recent **molecular studies** have shown that much of the "hidden", **intraspecific diversity** is neither adequately reflected in taxonomy nor used in nature conservation. Another source of biodiversity is **polyploidy** (multiplication of chromosome sets), which was not only involved in the origin of most crop plants but is also considered one important mechanism allowing sympatric speciation. Ploidy level differences are not restricted to the species level, but also occur frequently within species. Polyploids have been shown to originate recurrently and to be successfully maintained, emphasising their evolutionary significance.
Applying a wide array of molecular techniques in combination with flow-cytometry, we aim to unravel the spatiotemporal evolution of three polyploid plant groups, which have their centres of diversity on the Balkan Peninsula, in order to uncover general mechanisms that contributed to the high levels of biodiversity of the Western Balkan countries. Several species included are important forage or ornamental plants, and some are of high nature-conservation priority in Balkan countries or are among top-listed in EU legislation.

Cerastium *Knautia* *Sesleria*

Our Team

Our team comprises scientists from the Universities of Innsbruck (Austria), Beograd (Serbia) and Zagreb (Croatia).

University of Innsbruck
Dr. Peter Schönswetter, project coordinator
Dr. Božo Frajman

University of Zagreb
Dr. Antun Alegro
Dr. Sandro Bogdanović
Dr. Ivana Rešetnik

University of Beograd
Dr. Dmitar Lakušić
Dr. Marjan Niketić
Dr. Gordana Tomović
Maja Lazarević
Nevena Kuzmanović

Spatiotemporal diversification of the Balkan flora: What do we know?

Peter Schönswetter, Božo Frajman: University of Innsbruck, Austria
Antun Alegro: University of Zagreb, Croatia

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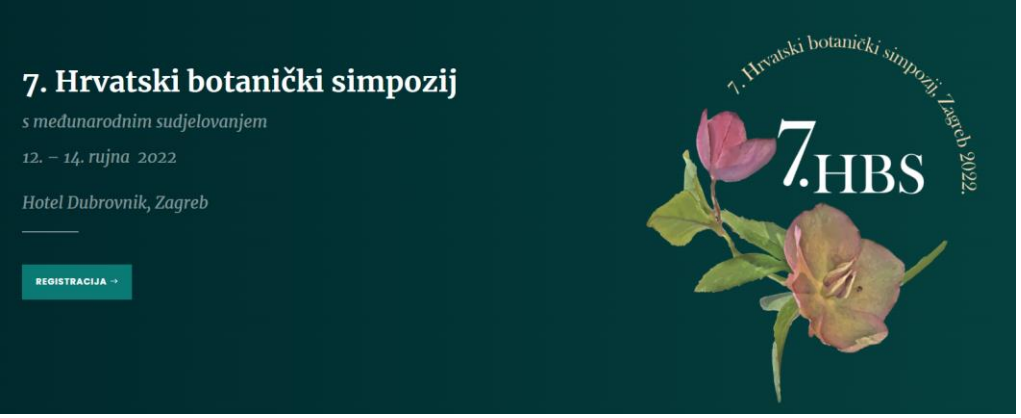


17:00-18:00 Okrugli stol / Round-table (moderatori / moderators: Ivana Rešetnik, Nevena Kuzmanović & Sandro Bogdanović)

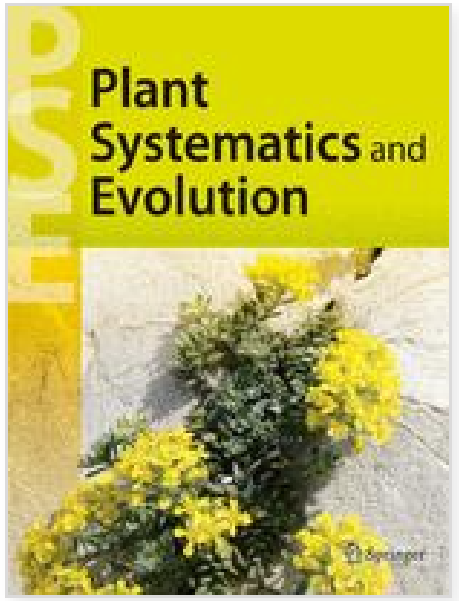
I. Rešetnik: PLANT PHYLOGEOGRAPHY OF THE BALKAN PENINSULA: AN OVERVIEW (predavanje / lecture)

Plant Systematics and Evolution
All Volumes & Issues

Plants of the Balkan Peninsula in Space and Time

ISSN: 0378-2697 (Print) 1615-6110 (Online)

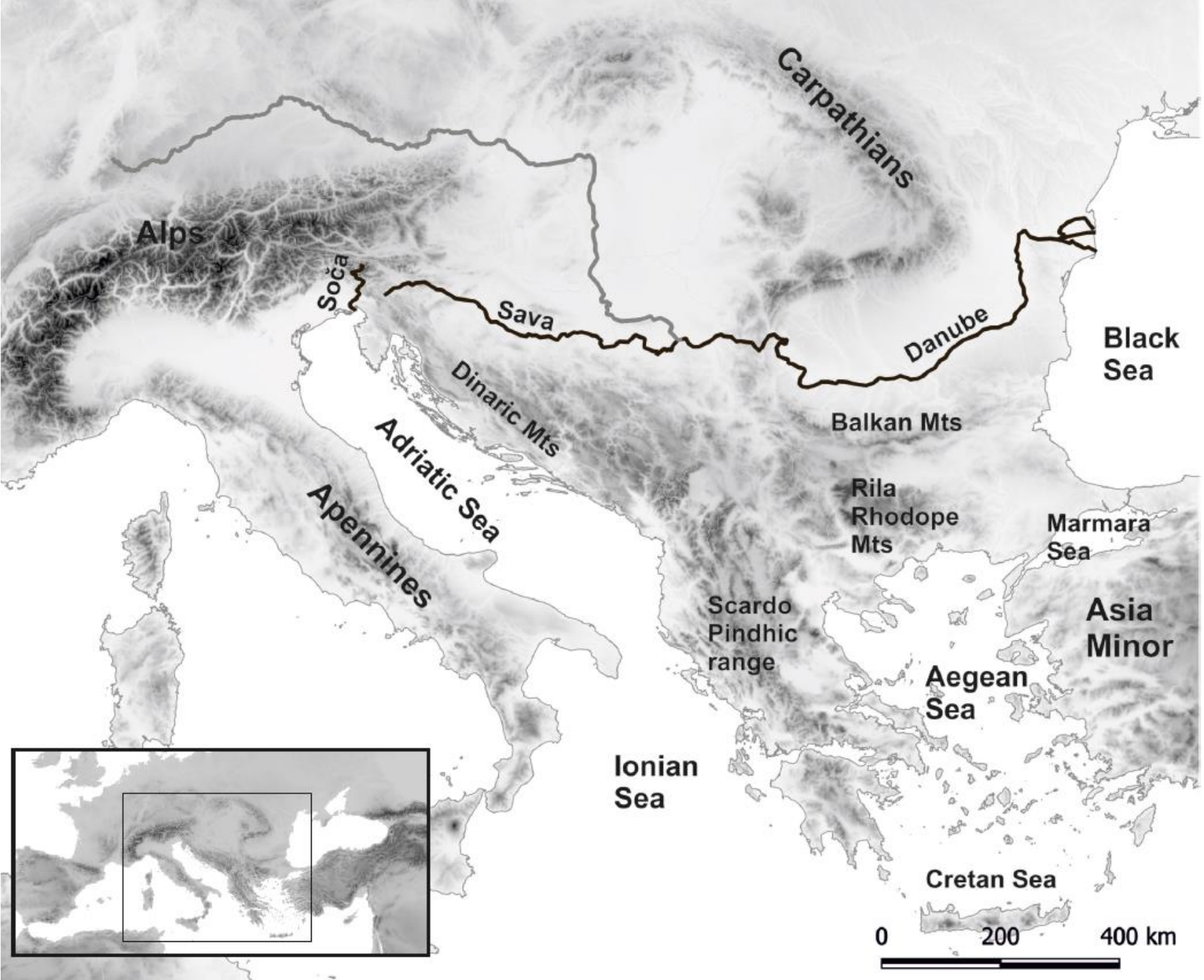
In this topical collection (22 articles)



2012

Some thoughts…

- there is still much to be discovered in the Balkans, most probably more than anywhere else in Europe
- a good balance of field work and molecular-based work is needed
- cooperative efforts on a larger scale should be preferred over regional/national approaches
- what is needed most urgently is a good representation of Balkan taxa in sound phylogenies
- we are ”standing on the shoulders of giants”, but this should not mean that traditional hypotheses on taxonomy, biogeography etc. should not be tested and – if necessary – rejected and abondoned

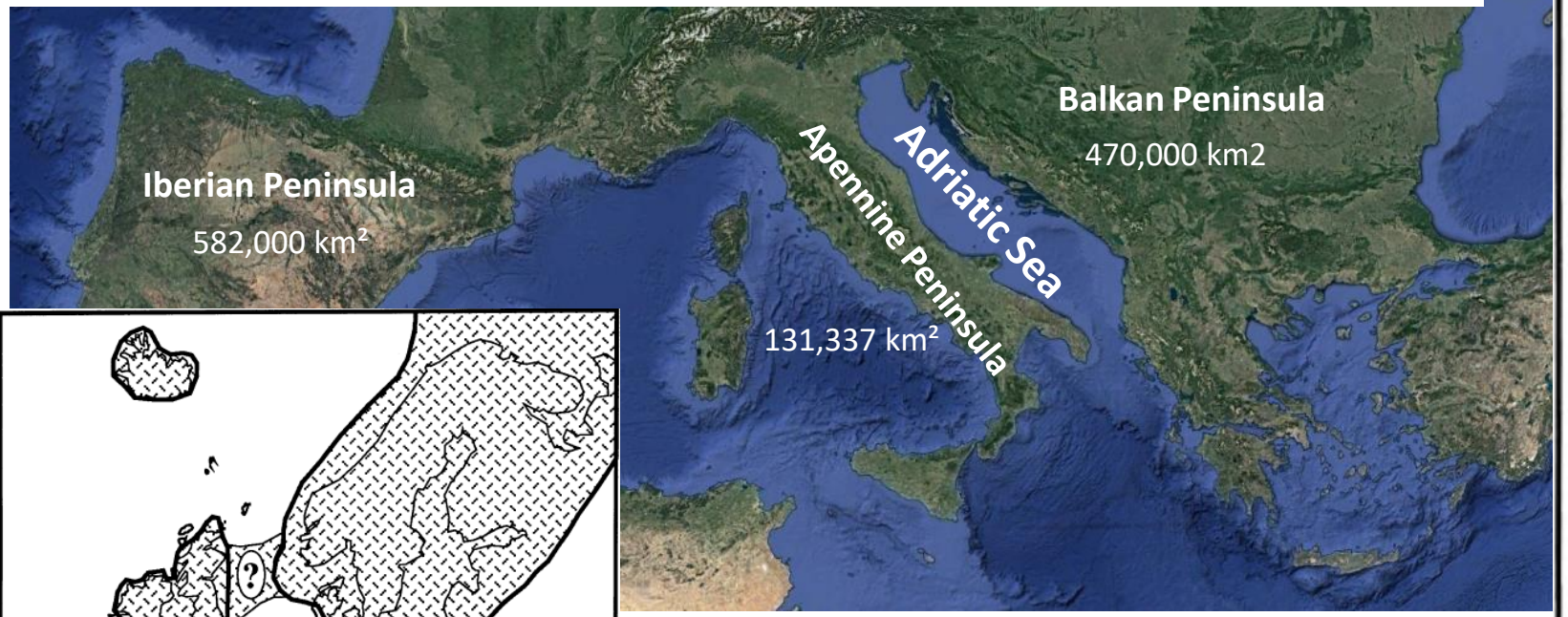


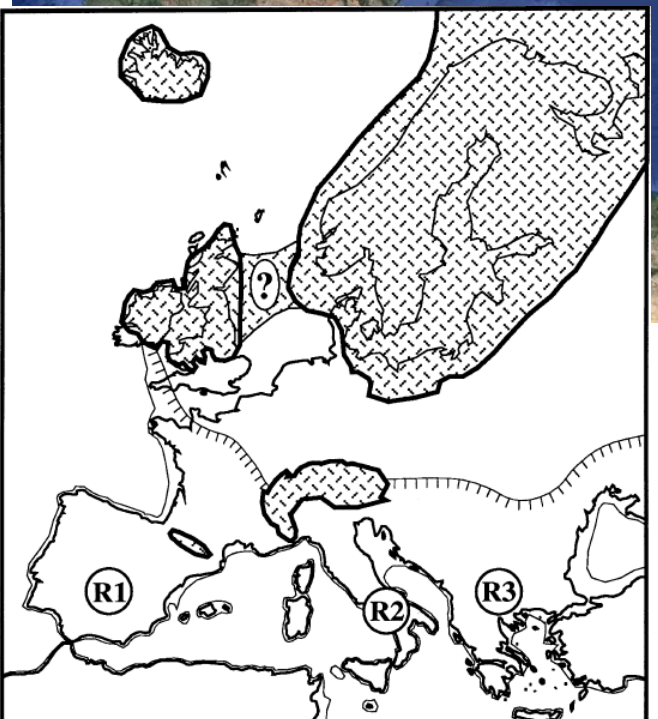
- complex geological history
- geographic heterogeneity
- diverse mosaic habitats
- high environmental stability over long periods
- Pleistocene climatic fluctuations
- **major glacial refugium**
- great species diversity
- high percentage of endemism
- major sources for the postglacial colonisation of central and northern Europe
- crossroad between Asia Minor and the rest of Europe

Molecular Ecology (1998) 7, 453–464

Comparative phylogeography and postglacial colonization routes in Europe

PIERRE TABERLET,* LUCA FUMAGALLI,† ANNE-GABRIELLE WUST-SAUCY,‡
JEAN-FRANÇOIS COSSON§





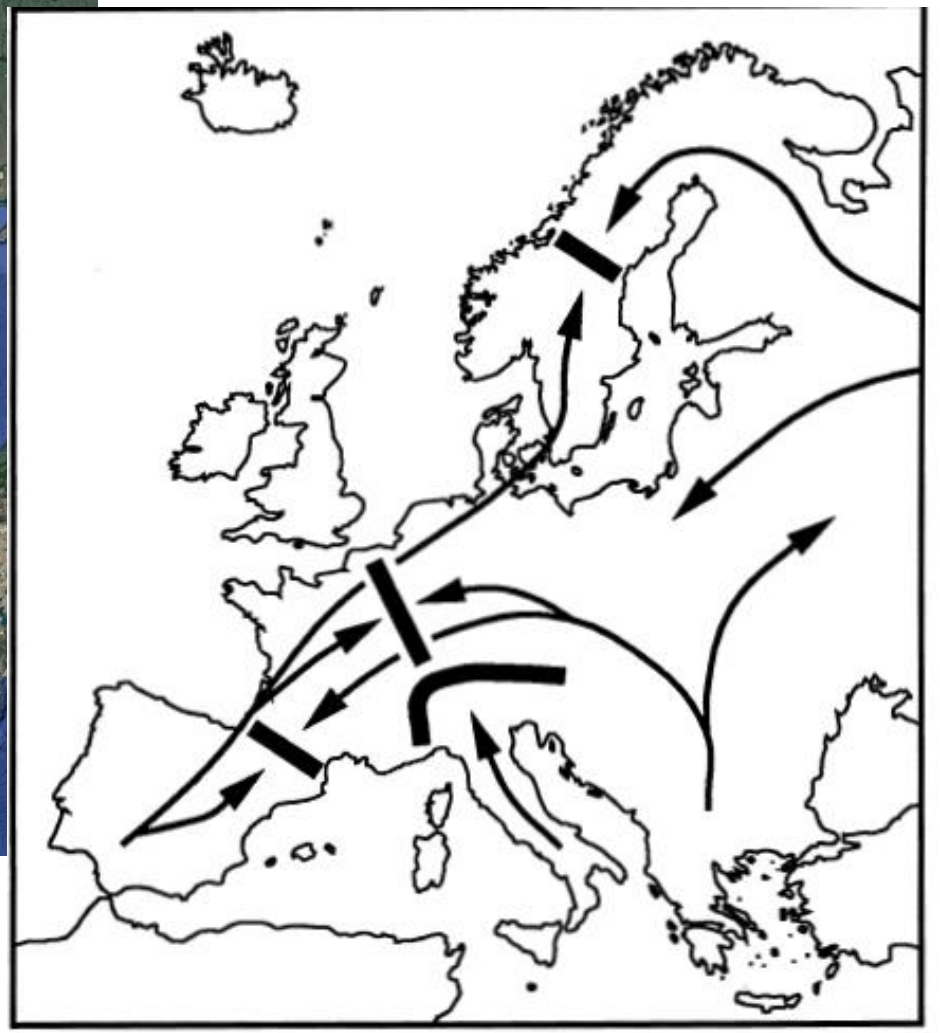
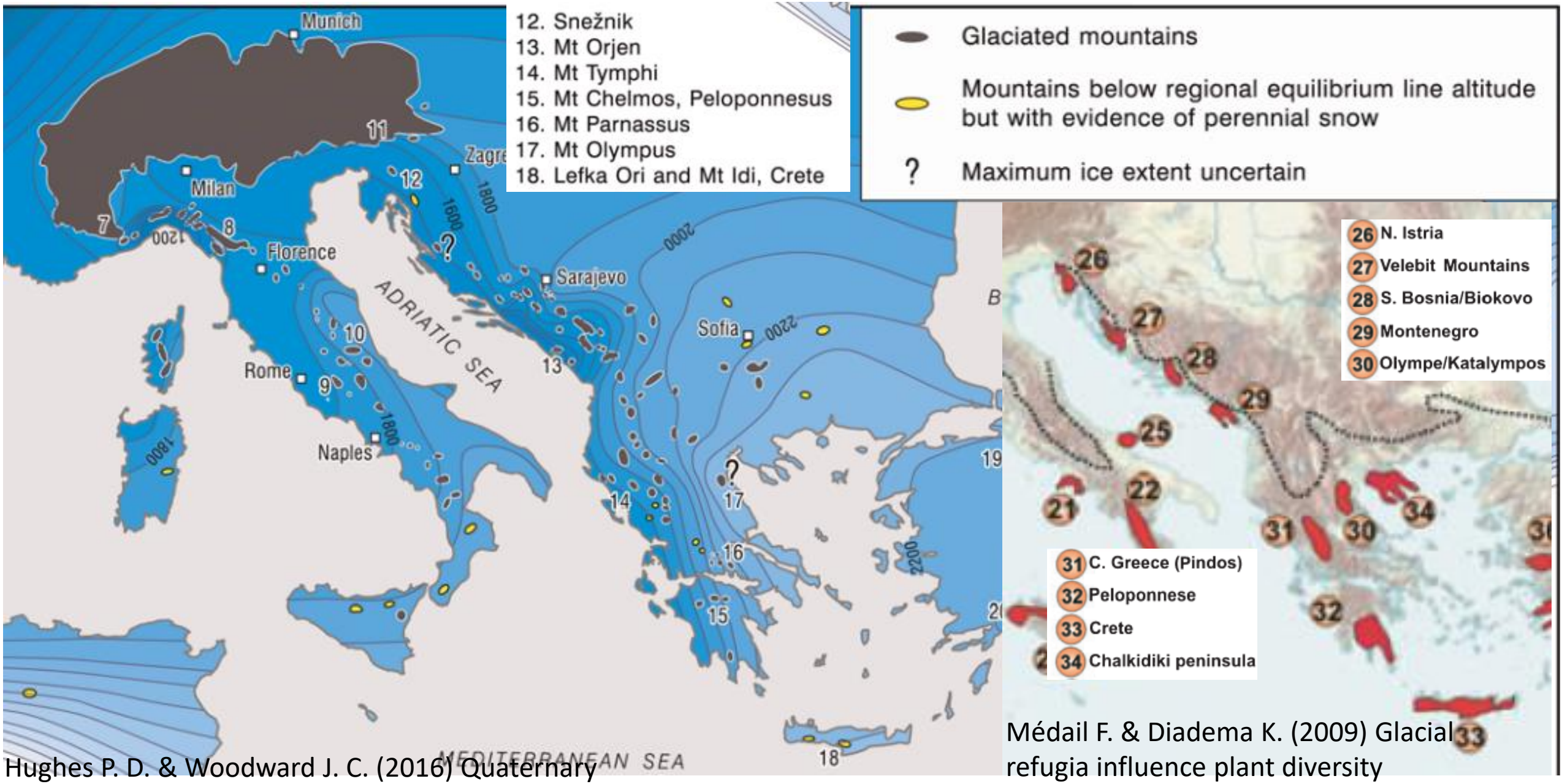


Fig. 6 Main postglacial colonization routes and subsequent suture zones in Europe.

Pleistocene climatic fluctuations → glaciation



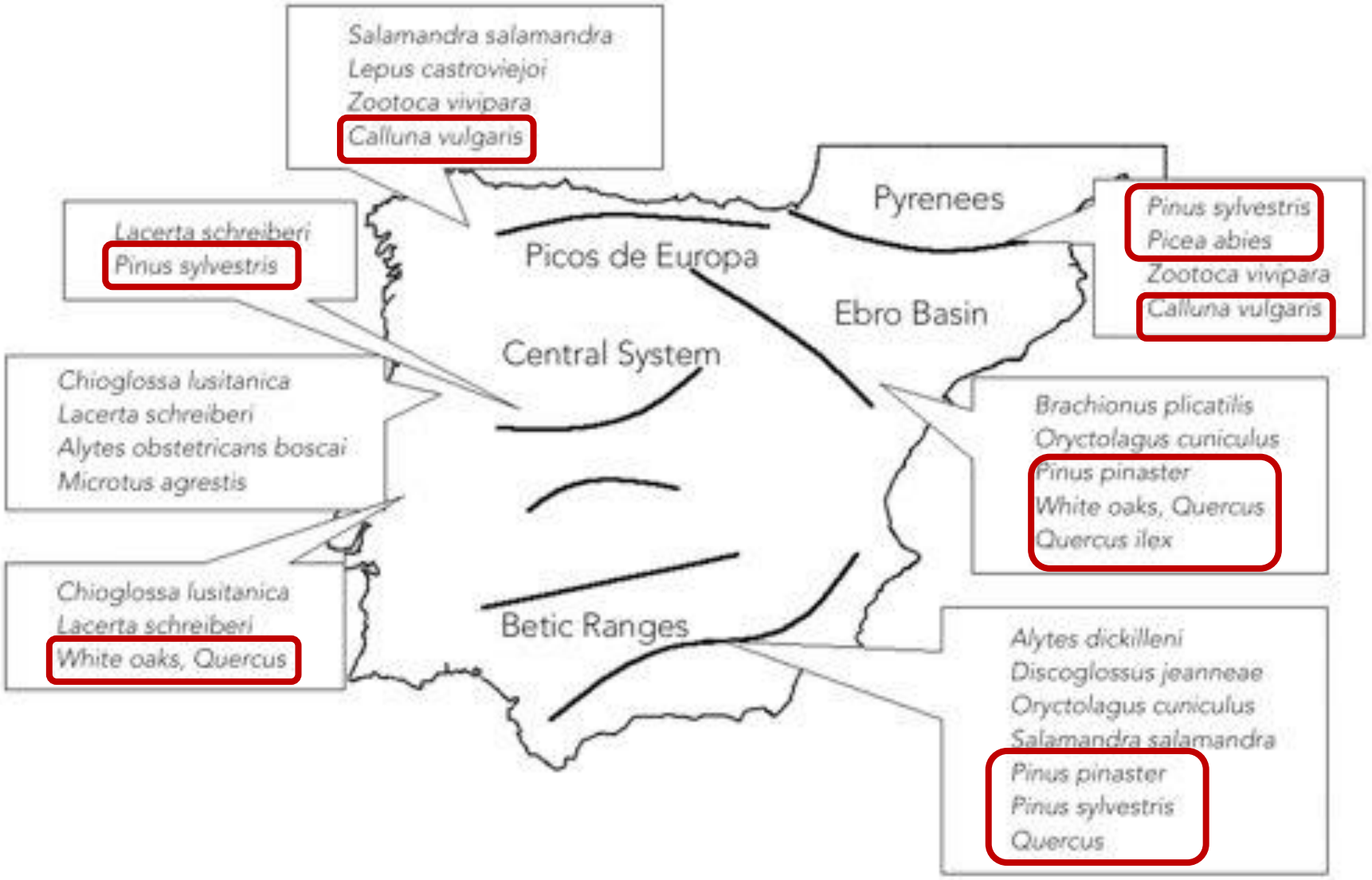
Hughes P. D. & Woodward J. C. (2016) Quaternary Glaciation in the Mediterranean Mountains

Médail F. & Diadema K. (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin

Refugia within refugia: patterns of phylogeographic concordance in the Iberian Peninsula

2007

Africa Gómez and David H. Lunt



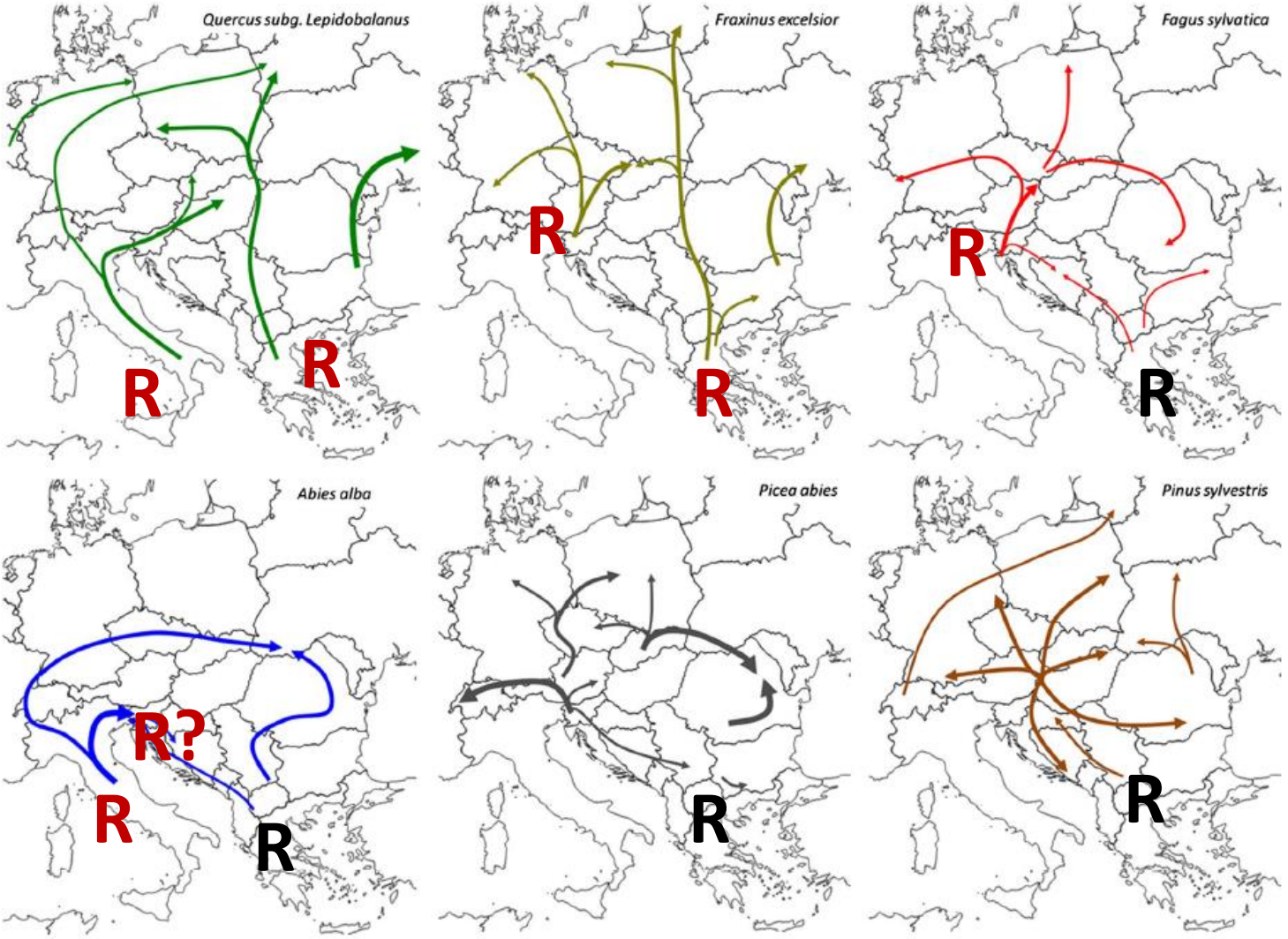
- many species and species complexes show strong genetic subdivisions indicative of past population isolation
- approximate location of putative inferred terrestrial refugia → broadly overlap with recognized areas of high endemism
- at least seven putative glacial refugia

Plant Systematics and Evolution (2020) 306:5
https://doi.org/10.1007/s00606-020-01647-x

ORIGINAL ARTICLE

The Balkans: a genetic hotspot but not a universal colonization source for trees

Dušan Gömöry[1] · Petar Zhelev[2] · Robert Brus[3]

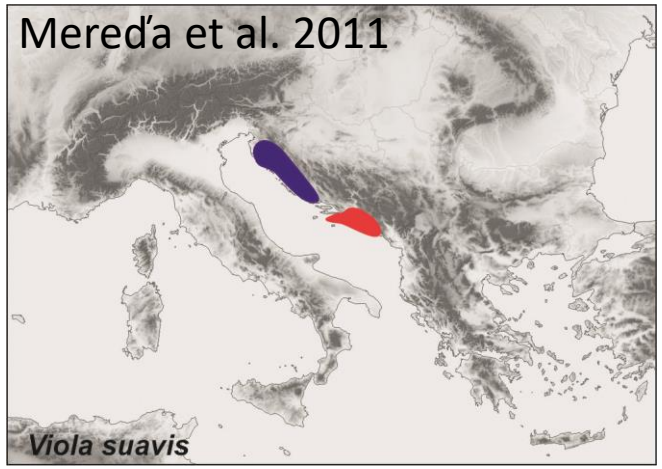


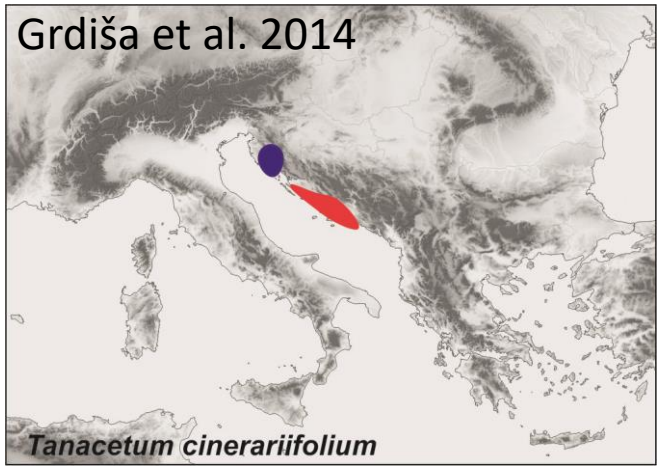
- high current diversity: roughly 90% of all European trees can be found in the Balkans, 75% in the Apennine Peninsula, 70% in the Iberian Peninsula, only about 35% in Scandinavia.
- glacial refugia of most European trees → high genetic diversity
- refugia within refugia pattern
- but in most tree species, the Balkan refugia have not effectively contributed to current gene pools

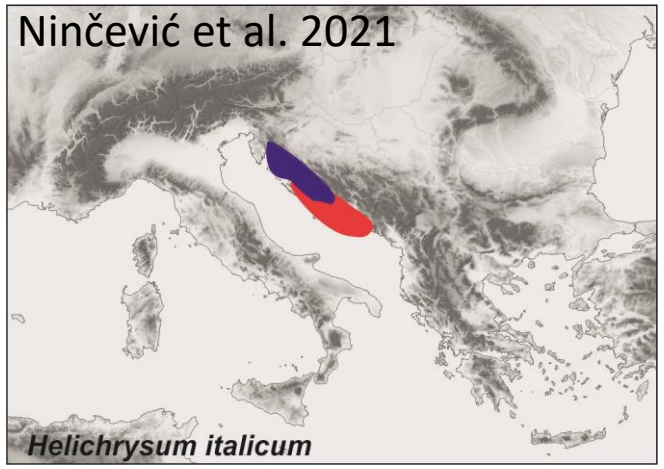
Phylogeographical patterns → Distribution of genetic lineages

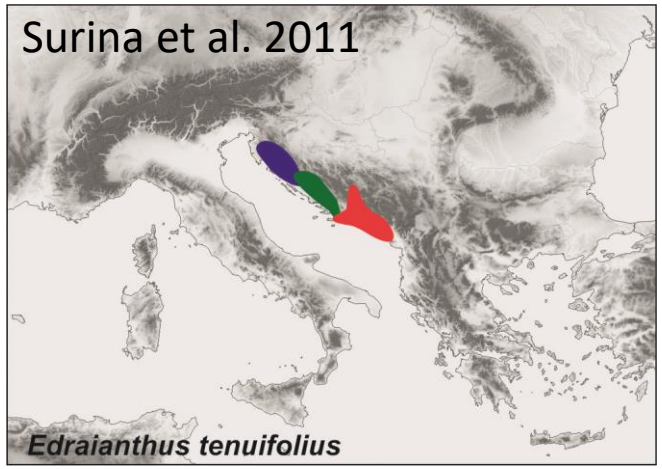
- phylogeographical studies encompass various temporal and spatial scales and their accumulation allows insights into the general drivers of biogeographical patterns → centred on the species level (within species or closely related species)

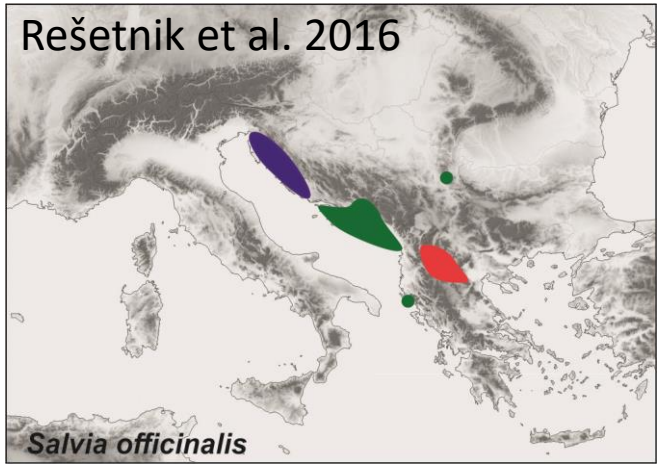
- thermophilic species in western Balkans → differentiation into two or three genetic lineages

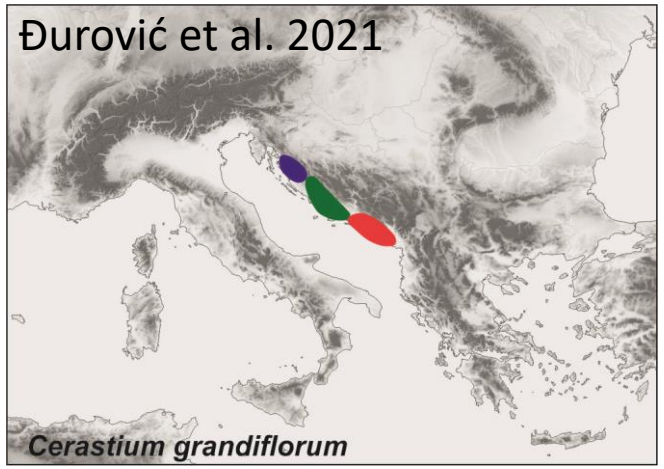








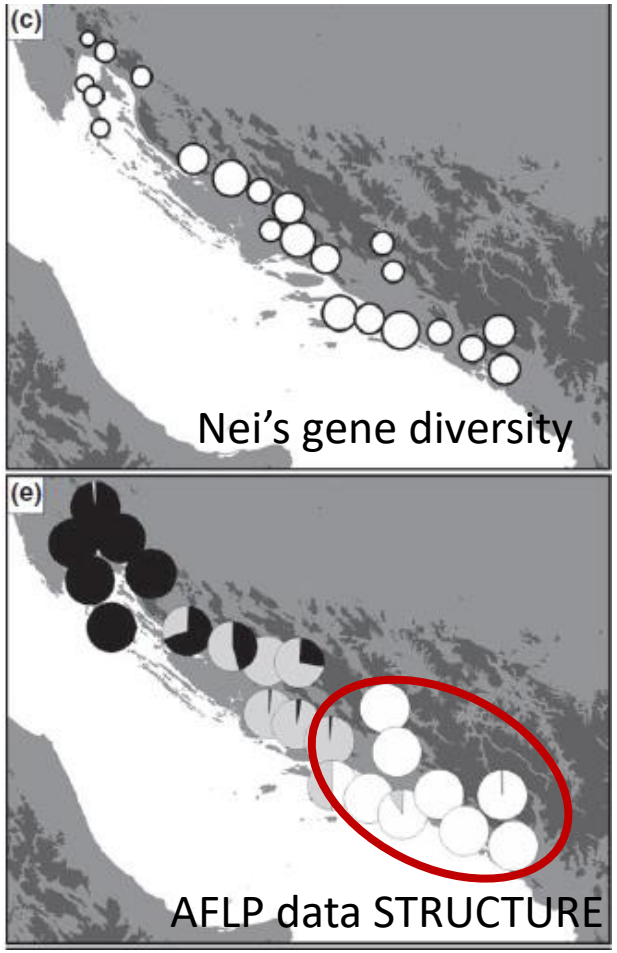




- **thermophilic species** - two main patterns of latitudinal genetic differentiation:

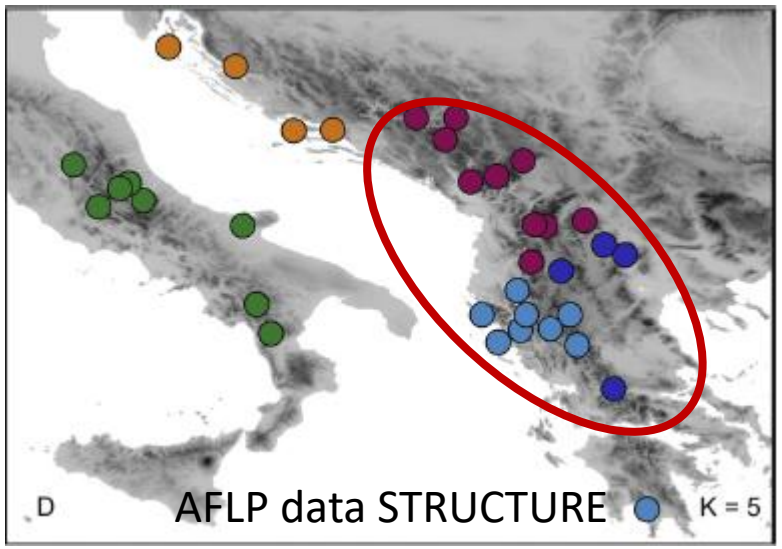
a) Southern richness – Northern purity hypothesis (Hewitt 2000)

Edraianthus tenuifolius



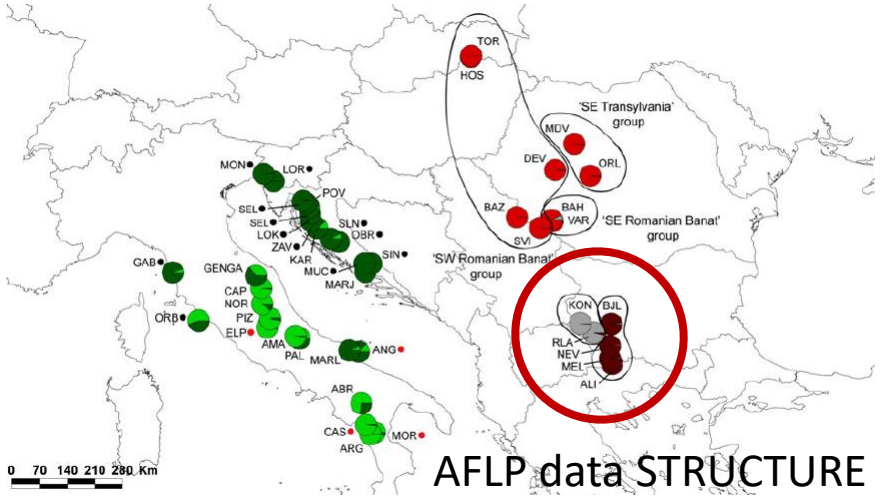
Surina et al. 2011

Euphorbia myrsinites



Falch et al. 2019

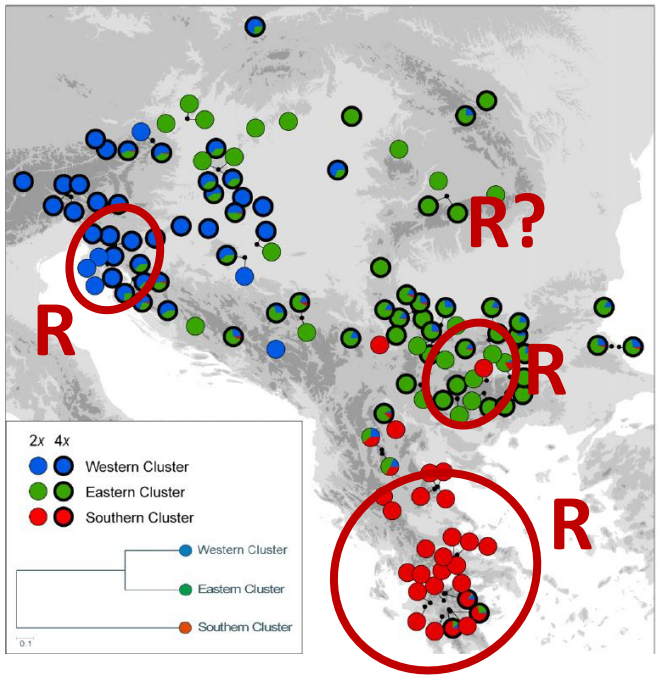
Onosma heterophylla s.l.



Kolarčik et al. 2010

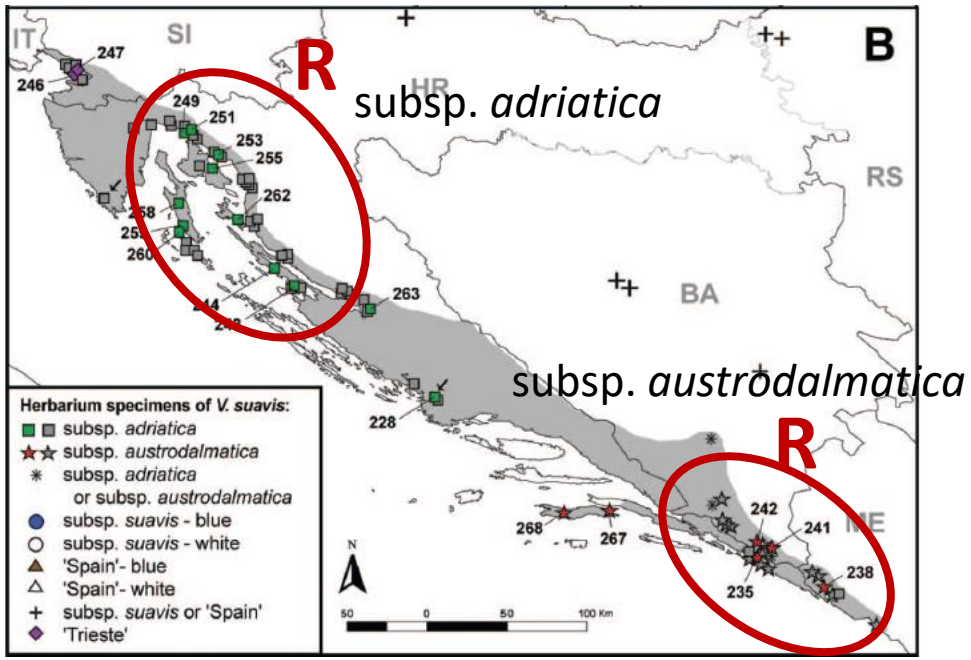
b) glacial persistence in both the north-western and southern Balkans - with equivalent and relatively high genetic diversity

Veronica chamaedrys group



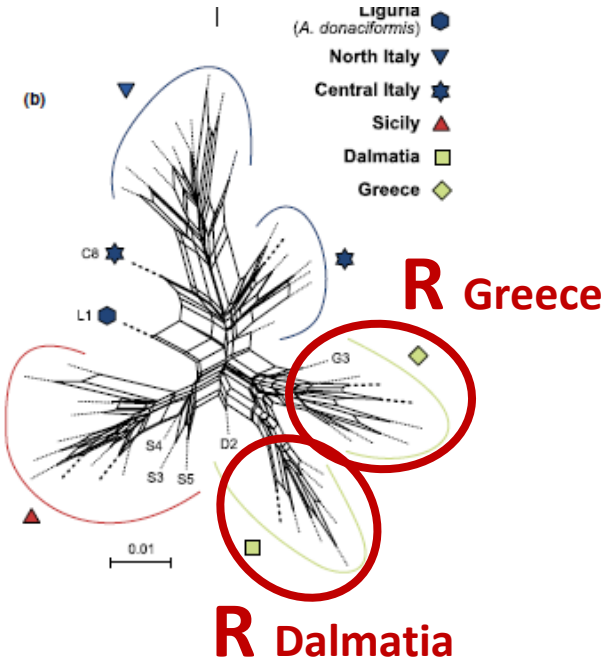
Bardy et al. 2010

Viola suavis s.l.



Mereďa et al. 2011

Arundo plinii

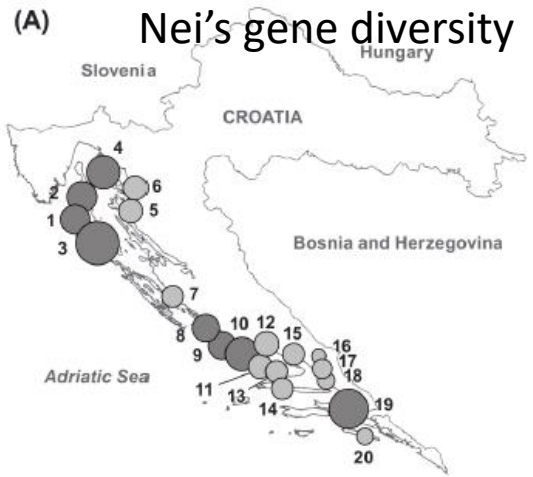


Hardion et al. 2014

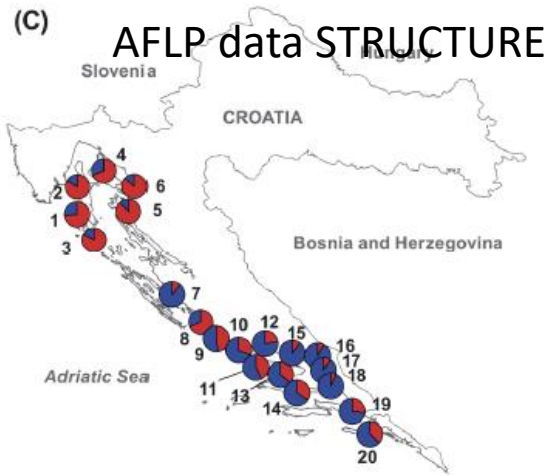
northern micro-locations as ecological sanctuaries

Tanacetum cinerariifolium

(A) Nei's gene diversity

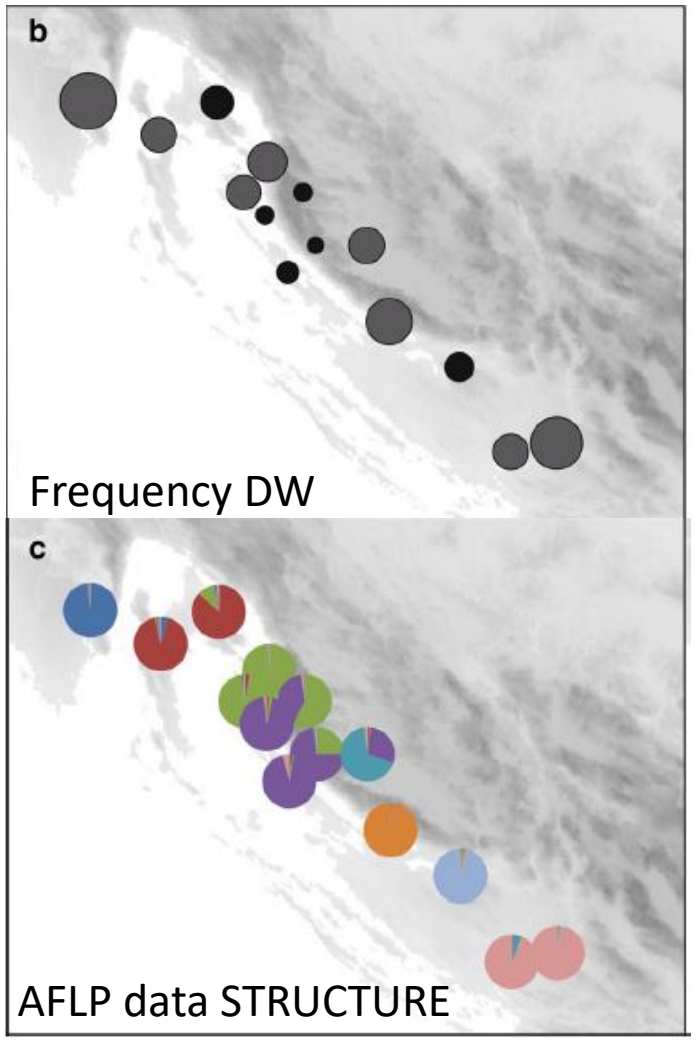


(C) AFLP data STRUCTURE



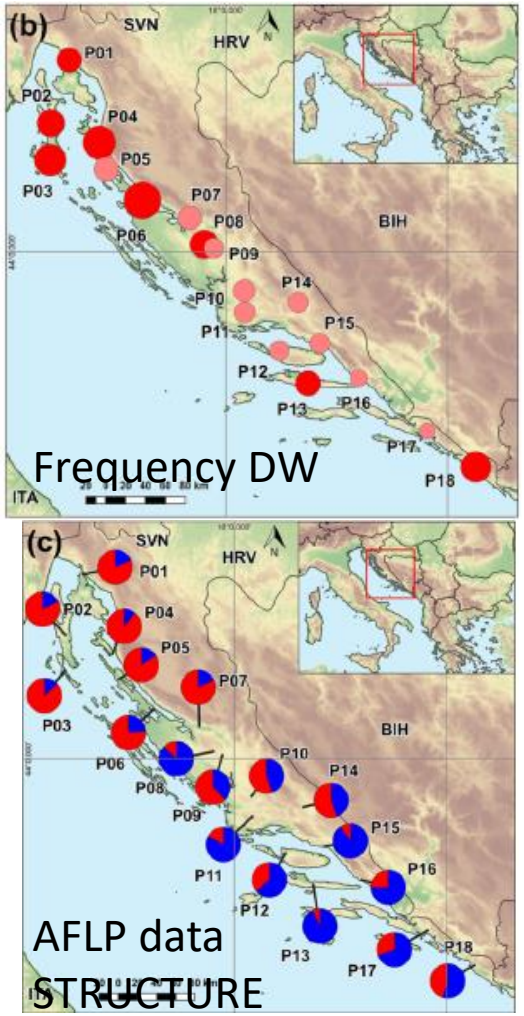
Grdiša et al. 2014

Campanula fenestrellata



Rešetnik et al. 2020

Helichrysum italicum

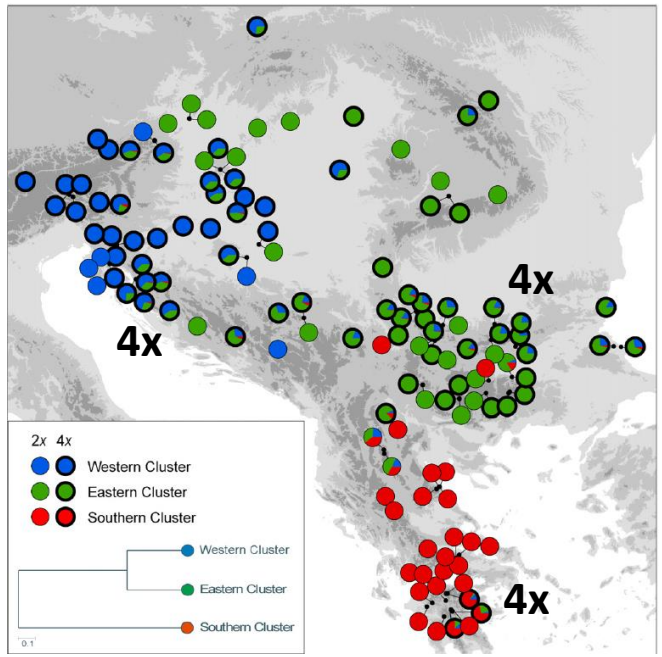


Ninčević et al. 2021

- **secondary contacts** - increased genetic diversity and admixed patterns:

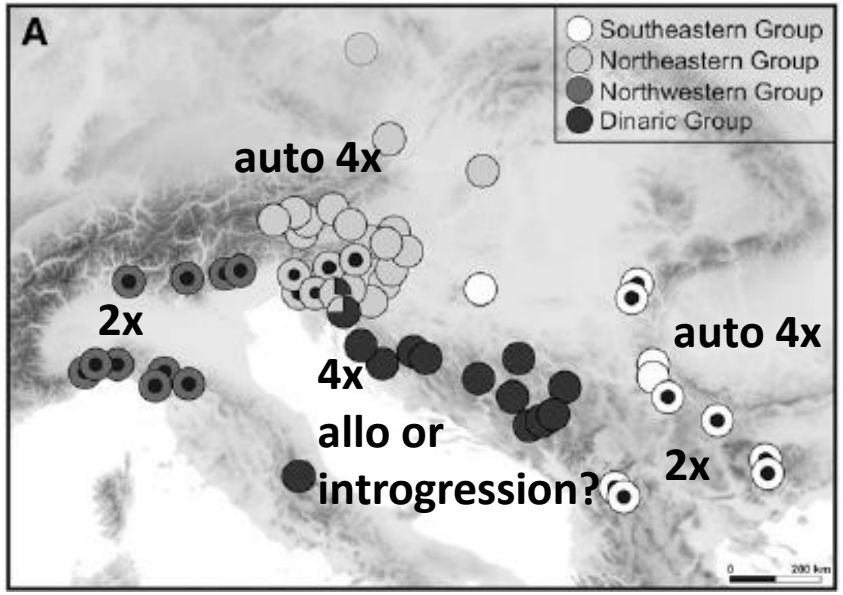
polyploidisation!

Veronica chamaedrys



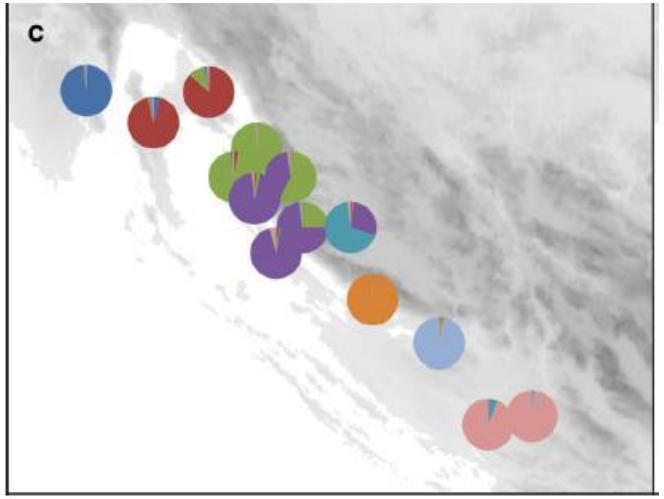
Bardy et al. 2010

Knautia drymeia



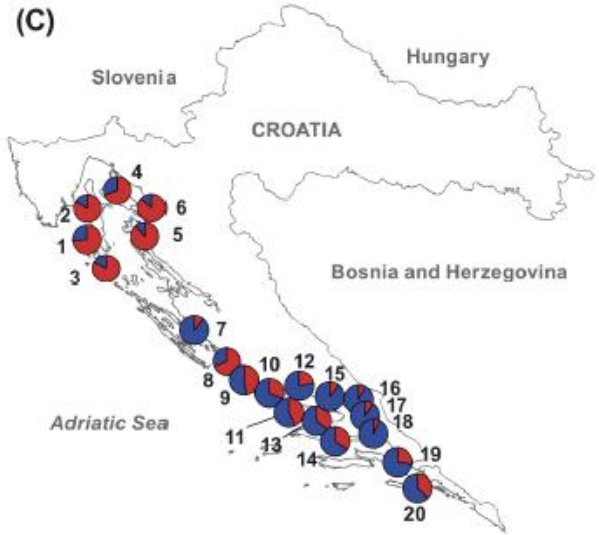
Rešetnik et al. 2016

Campanula fenestrellata



Rešetnik et al. 2020

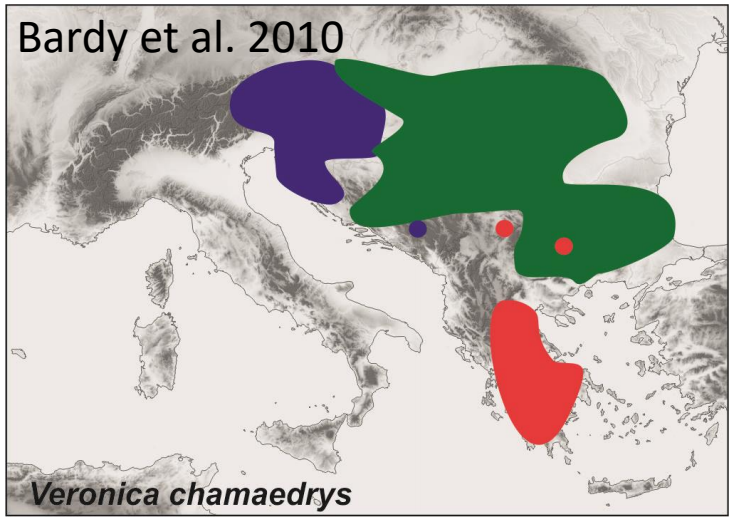
Tanacetum cinerariifolium

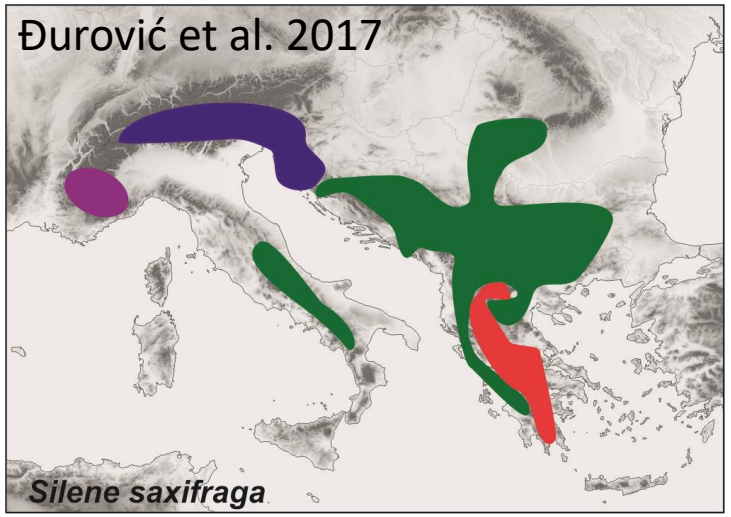


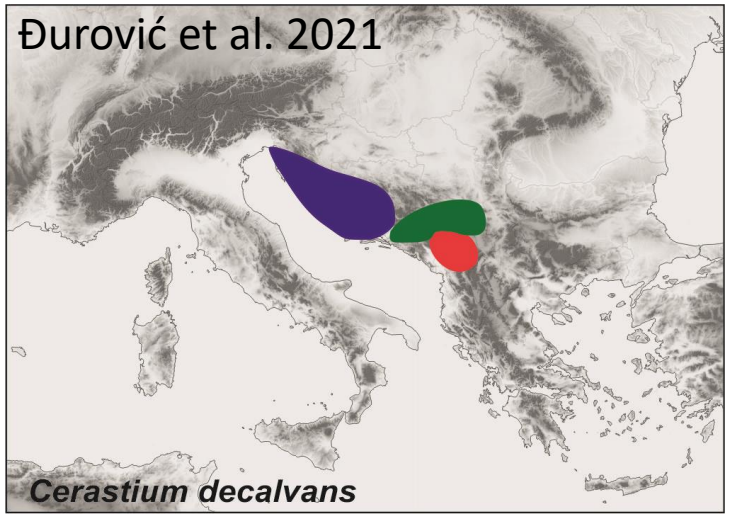
Grdiša et al. 2014

Phylogeographical patterns → Distribution of genetic lineages

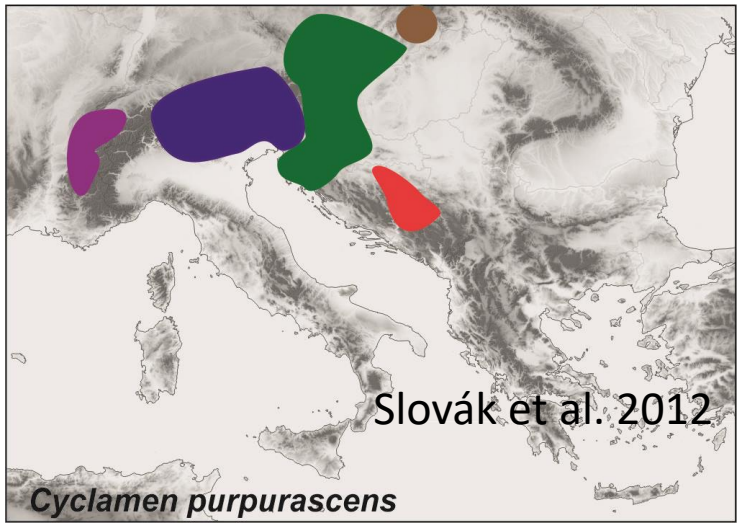
- species with wider elevational tolerance and wider geographical distribution → similar pattern

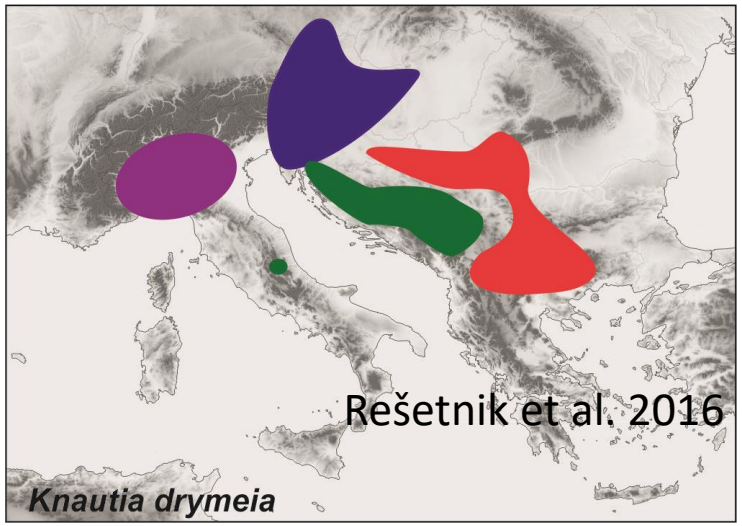






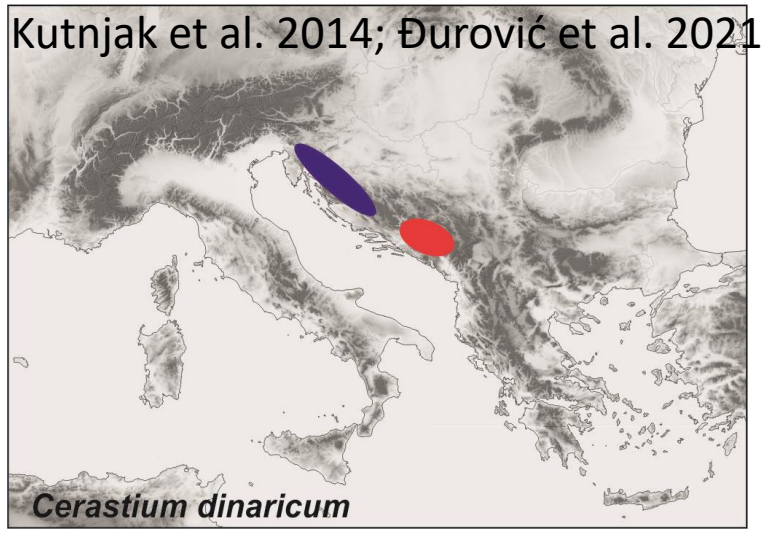
- species with wider elevational tolerance and wider geographical distribution - forest understory species → 4-5 allopatric groups

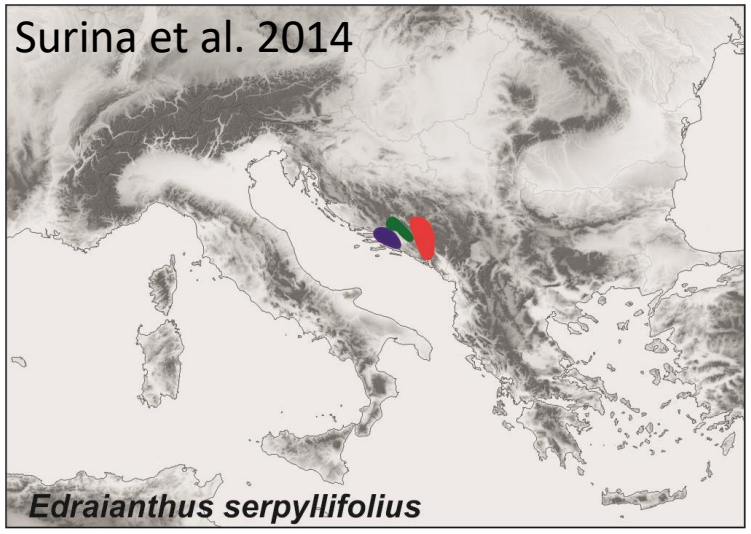


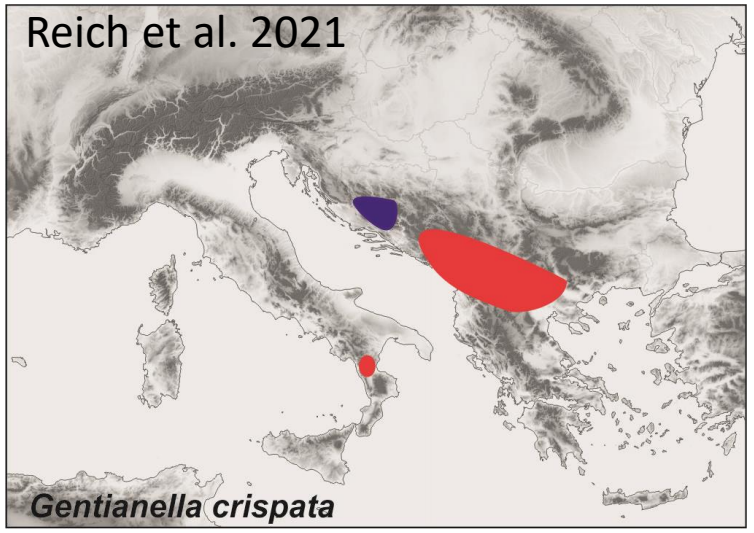


Phylogeographical patterns → Distribution of genetic lineages

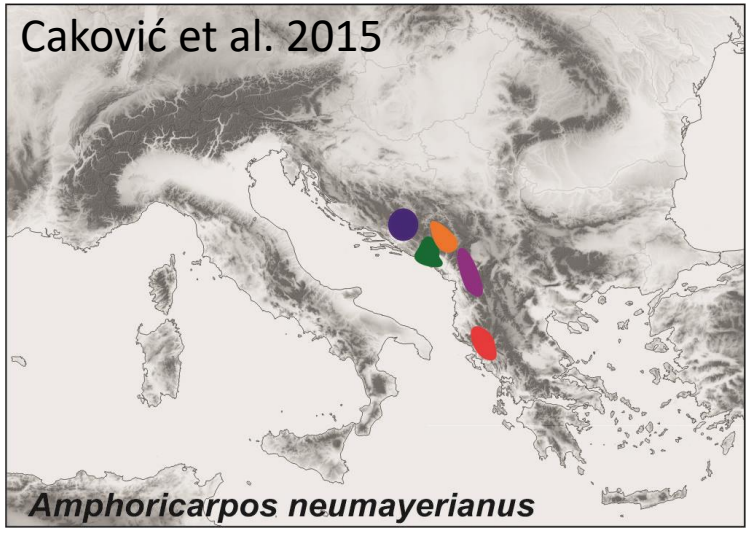
- alpine species → more restricted and disjunct distribution pattern

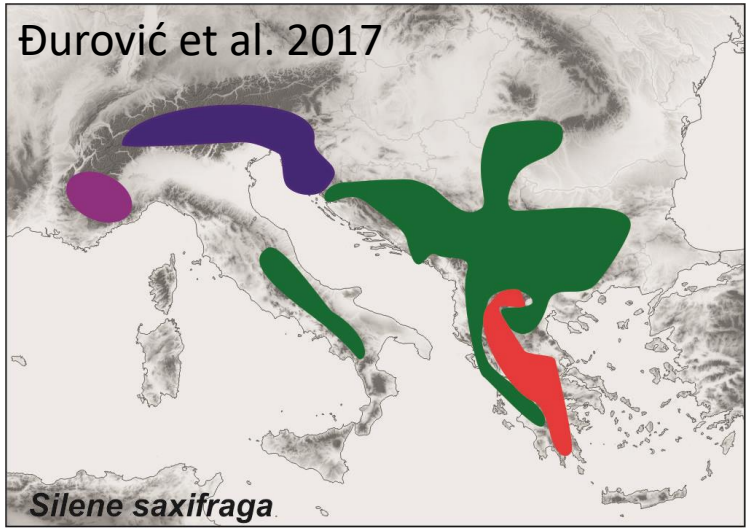


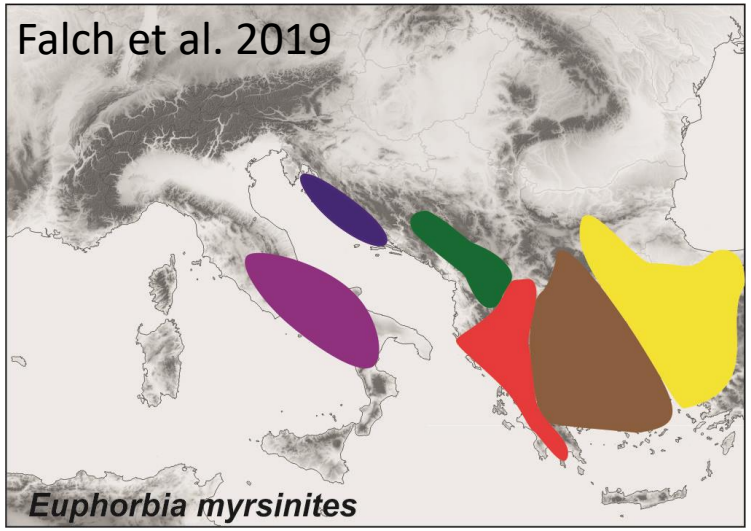




- borderline between Dinaric Mountains and Scardo-Pindhic range → spatially close but strongly differentiated genetic lineages







Journal of Biogeography (J. Biogeogr.) (2011)

ORIGINAL ARTICLE

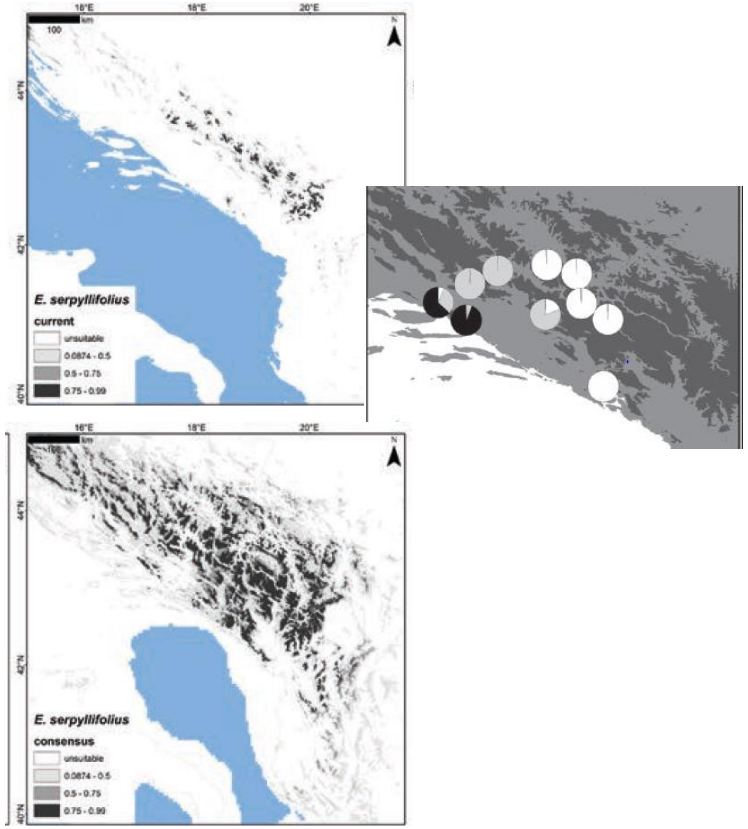
Quaternary range dynamics of ecologically divergent species (*Edraianthus serpyllifolius* and *E. tenuifolius*, Campanulaceae) within the Balkan refugium

Boštjan Surina[1,2], Peter Schönswetter[1,3] and Gerald M. Schneeweiss[1,*]

- Surina et al. (2011) proposed the hypothesis that cold-adapted species (*Edraianthus serpyllifolius*) experienced **altitudinal range shifts**, while the thermophilic species (*E. tenuifolius*) underwent **latitudinal range shifts**

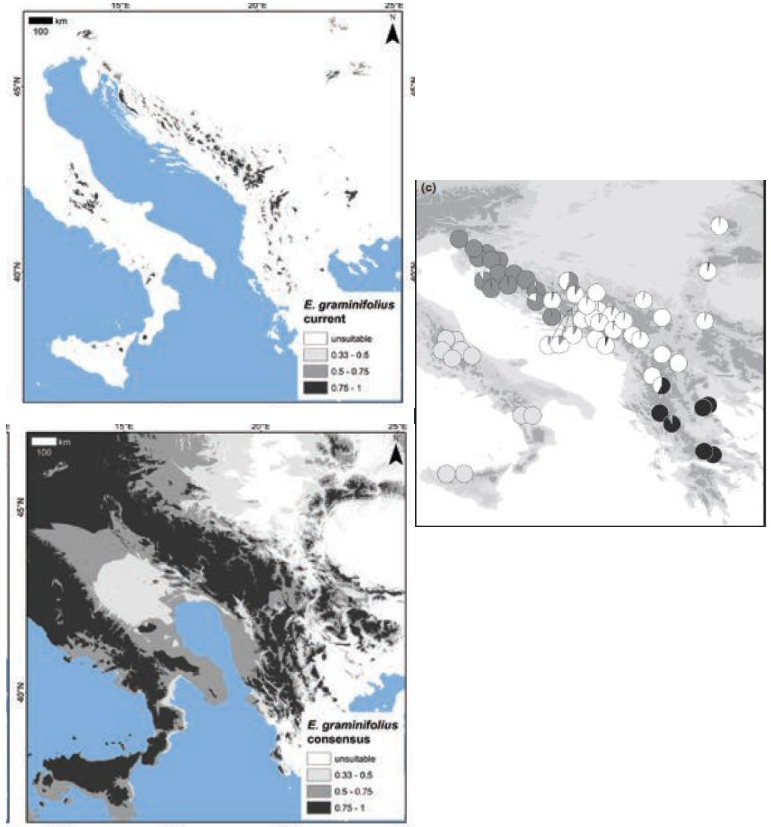
- **cold-adapted species** → more continuous distribution during cold stages
  → retreat into disjunct, higher elevations during periods with a warmer climate

Edraianthus serpyllifolius



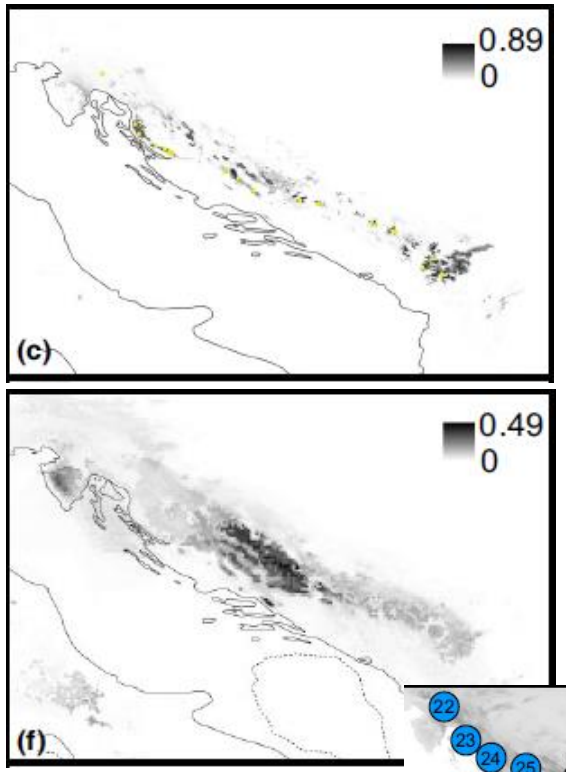
Surina et al. 2014, Glasnović et al. 2023

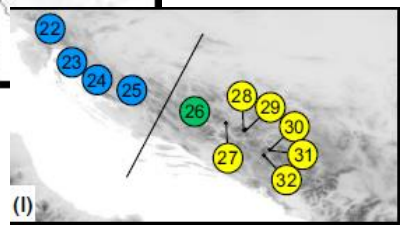
Edraianthus graminifolius



Surina et al. 2014

Cerastium dinaricum

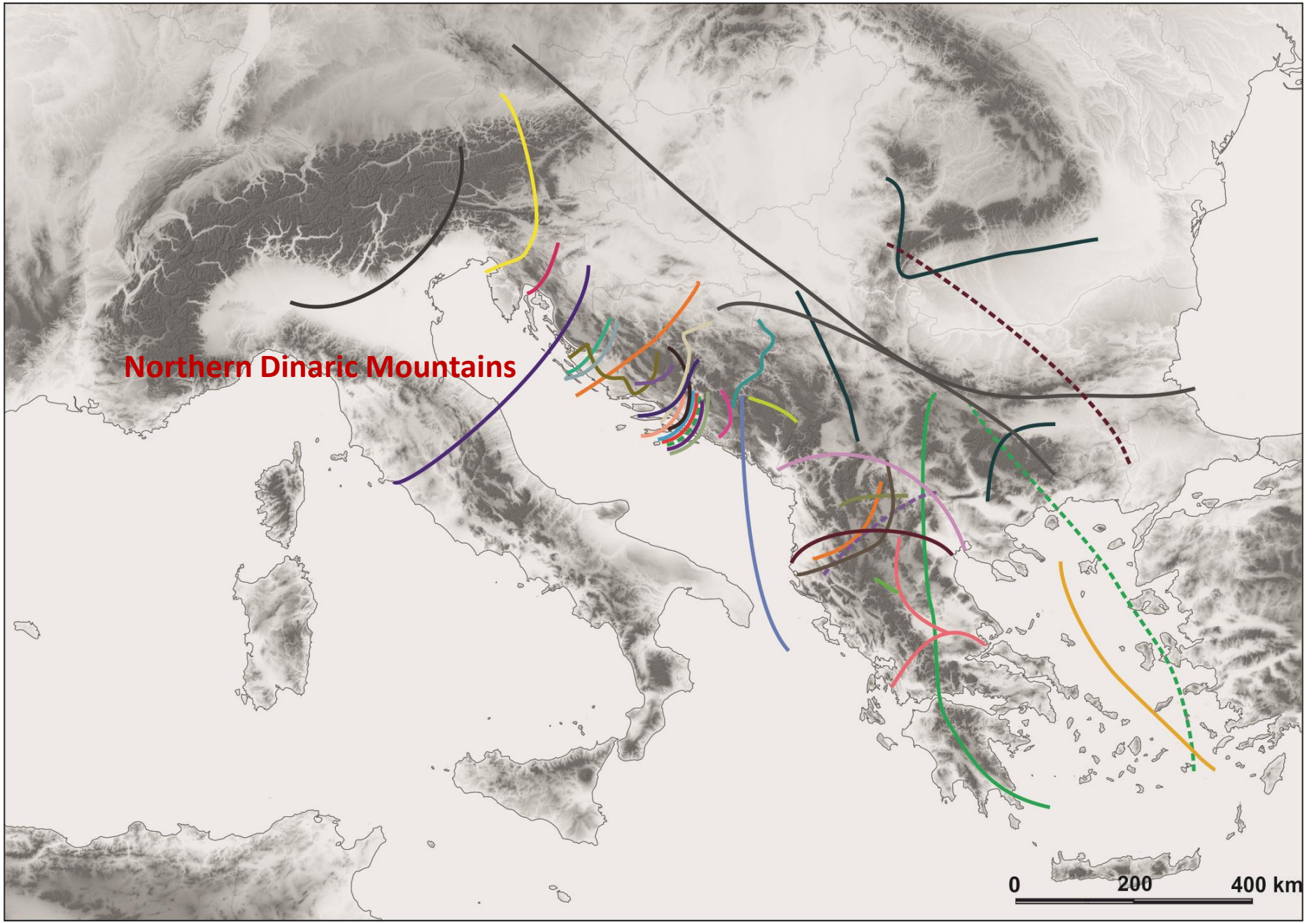




Kutnjak et al. 2014; Đurović et al. 2021

Phylogeographical patterns → Inference of major barriers

Astragalus onobrychis
Cyclamen purpurascens
Knautia drymeia
Silene saxifraga
Tanacetum cinerarifolium
Cerastium grandiflorum
Veronica chamaedrys
Edraianthus tenuifolius
Edraianthus graminifolius
Euphorbia verrucosa - E. montenegrina/E. serpentini
Gentianella crispata
Veronica orbiculata - V. dalmatica
Cerastium dinaricum
Cardamine maritima s.l.
Alyssum austrodalmaticum
Euphorbia myrsinites
Campanula pyramidalis - C. austroadriatica
Cerastium decalvans
Amphoricarpos neumayerianus
Heliosperma pusillum
Euphorbia spinosa
Campanula montenegrina - C. secundiflora
Carlina acanthifolia subsp. *utzka*
Sideritis scardica
Aurinia saxatilis
Campanula versicolor
Alyssum spruneri 'graecum'
Centaurea chrysocephala
Nigella arvensis
Sesleria rigida s.l.



Phylogeographical patterns → Inference of major barriers

Astragalus onobrychis
Cyclamen purpurascens
Knautia drymeia
Silene saxifraga
Tanacetum cinerarifolium
Cerastium grandiflorum
Veronica chamaedrys
Edraianthus tenuifolius
Edraianthus graminifolius
Euphorbia verrucosa - E. montenegrina/E. serpentini
Gentianella crispata
Veronica orbiculata - V. dalmatica
Cerastium dinaricum
Cardamine maritima s.l.
Alyssum austrodalmaticum
Euphorbia myrsinites
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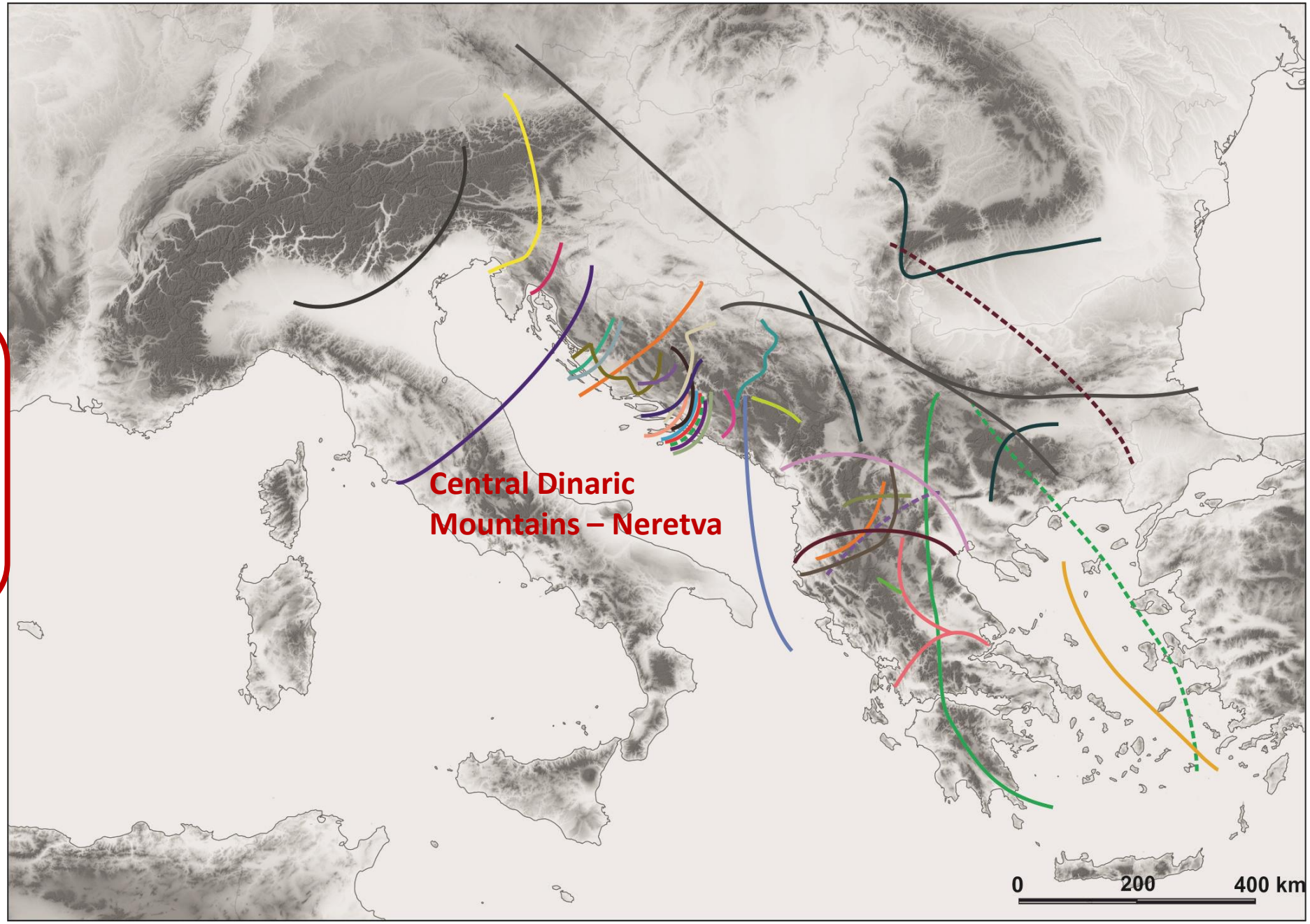
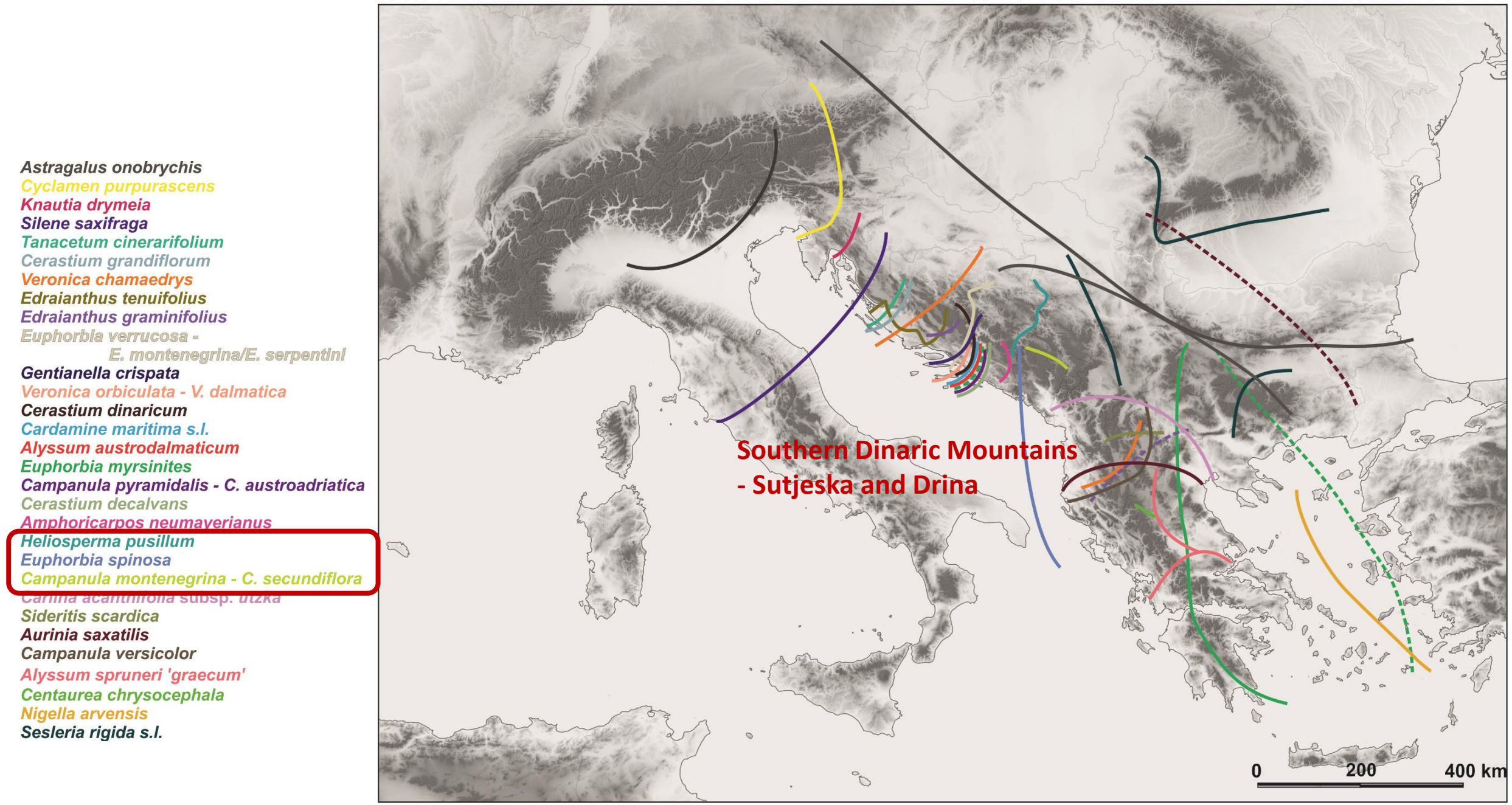


Phylogeographical patterns → Inference of major barriers



Phylogeographical patterns → Inference of major barriers

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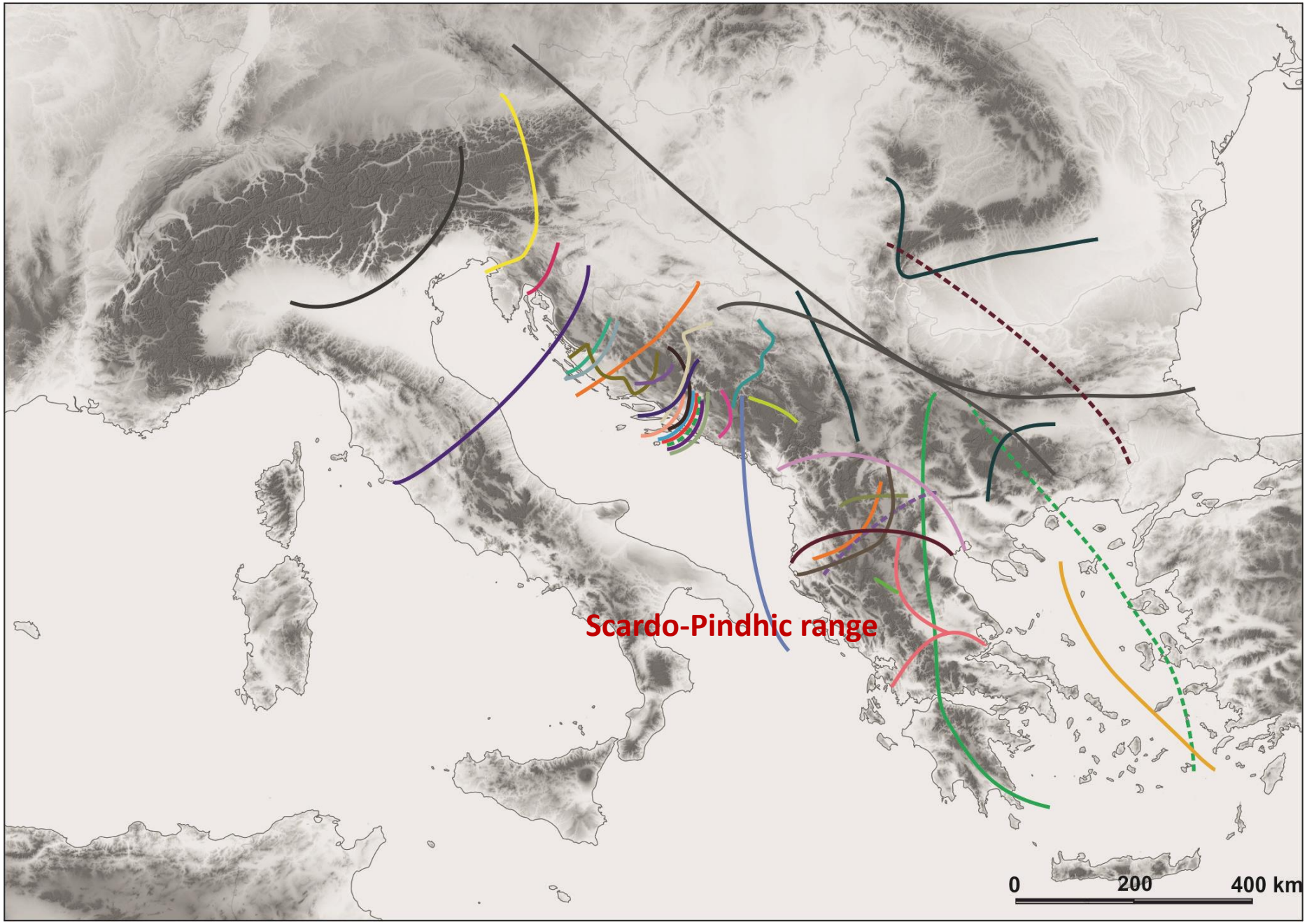
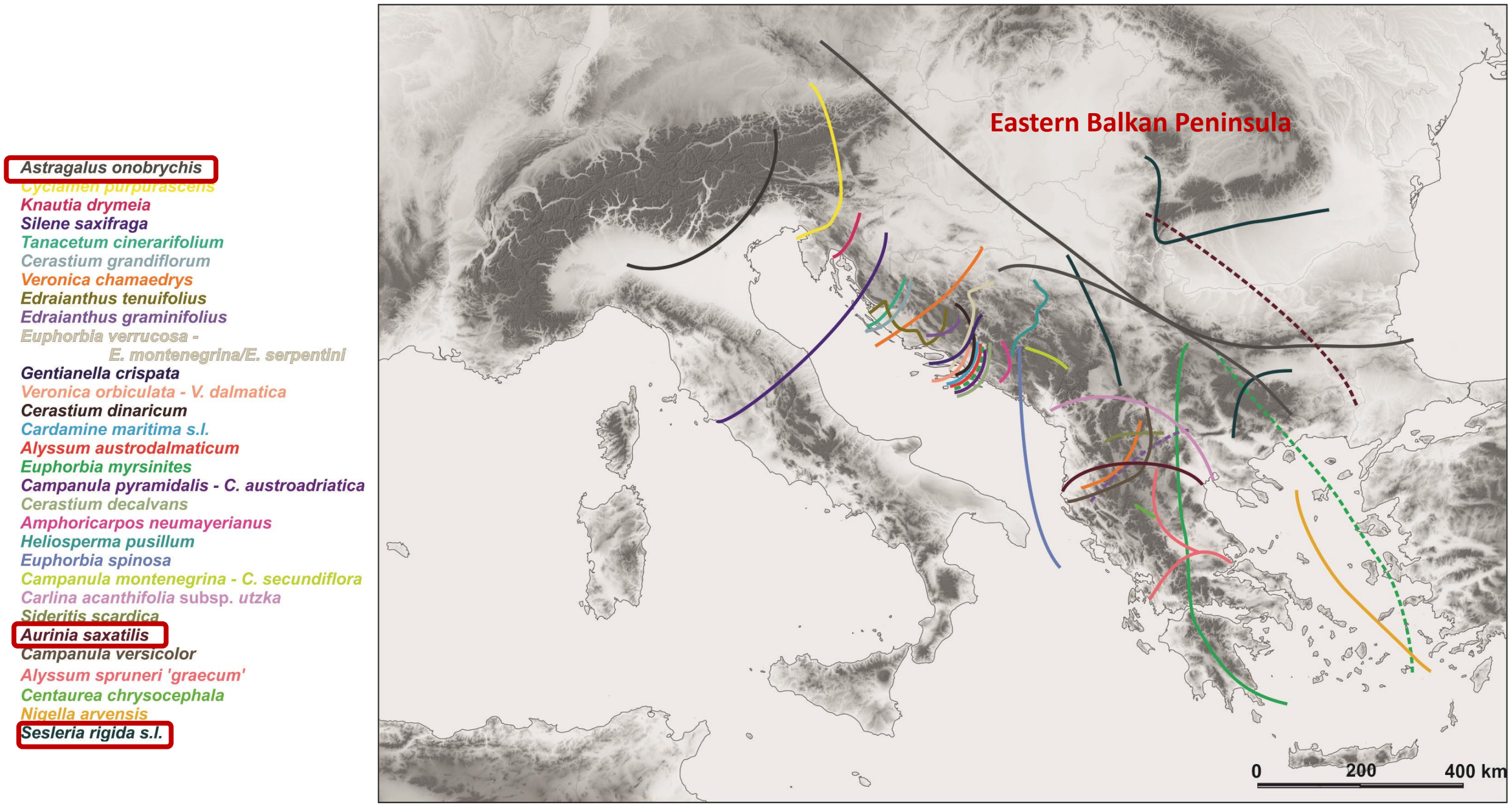


Phylogeographical patterns → Inference of major barriers



Phylogeographical patterns → Glacial refugia and their genetic imprint

- differentiation within species and closely related species groups most likely occurred in response to **Pleistocene** glacial oscillations
- only partially affected with glaciation – in LGM the mean temperature in July 5 ºC lower than today, snow line 1000 m lower
- warmer interglacial periods were shorter and characterized with higher temperatures than at present
- **"refugia-within-refugia"** model (Gómez and Lunt 2007) i.e. the existence of multiple refugia in the Balkan Peninsula
- Surina et al. (2011) proposed the hypothesis that cold-adapted species (*Edraianthus serpyllifolius*) experienced **altitudinal range shifts**, while the thermophilic species (*E. tenuifolius*) underwent **latitudinal range shifts**
- cold-adapted species had more continuous distribution during cold stages sufficient for gene flow to take place between the different mountain ranges - retreat into disjunct, higher elevations during periods of warmer climate: *Edraianthus serpyllifolius, Cerastium dinaricum, Sideritis scardica*
- thermophilic species - two main patterns of latitudinal genetic differentiation:

a) Southern richness – Northern purity hypothesis (Hewitt 2000): *Edraianthus tenuifolius, Euphorbia myrsinites, Onosma heterophylla* s.l.

b) glacial persistence in both the north-western and southern Balkans: *Veronica chamaedrys* group, *Viola suavis* s.l., *Arundo plinii*; northern micro-locations as ecological sanctuaries: *Tanacetum cinerariifolium, Campanula fenestrellata, Helichrysum italicum*

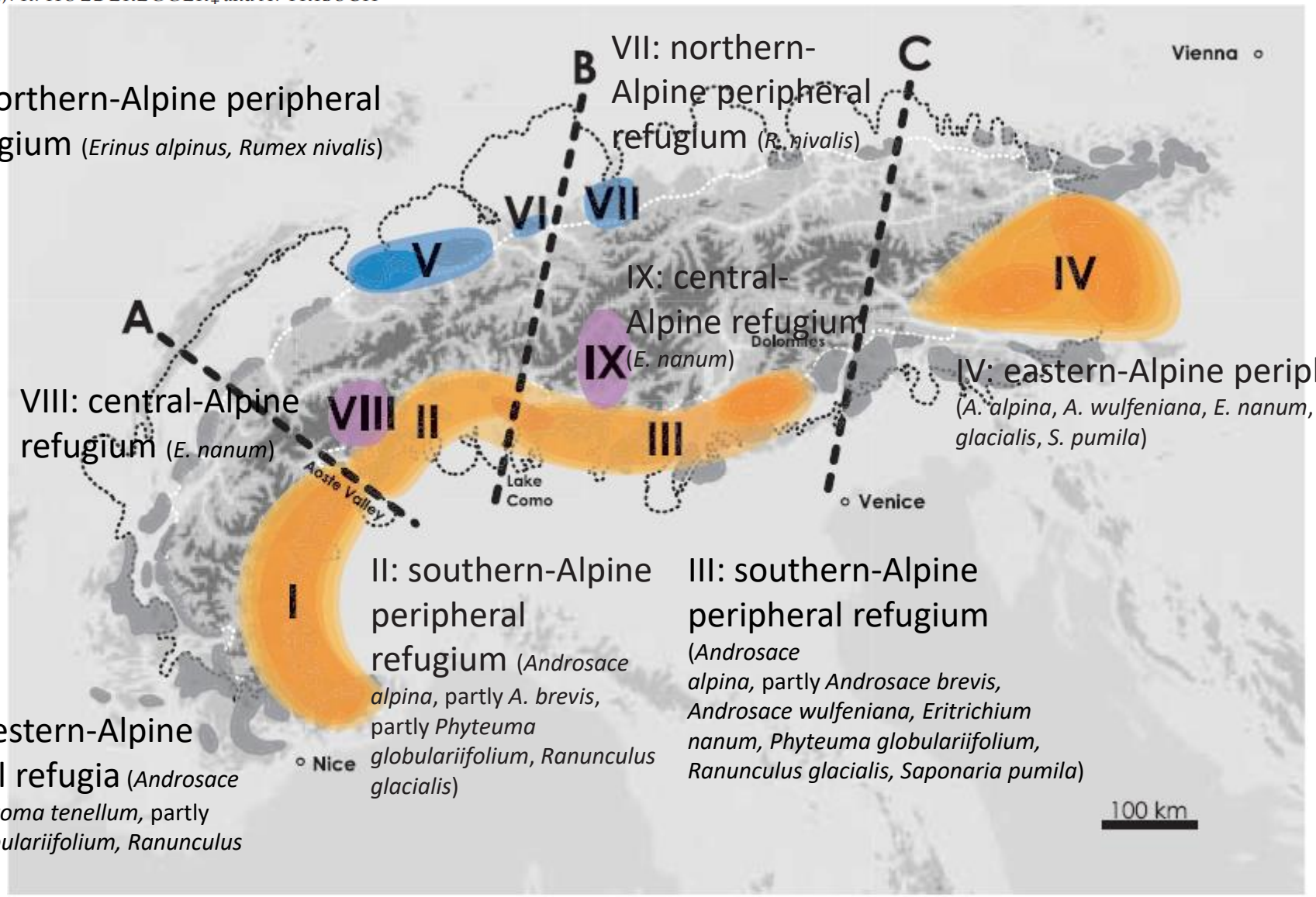
- **secondary contacts** - increased genetic diversity and admixed patterns: *Veronica chamaedrys, Tanacetum cinerariifolium, Campanula fenestrellata, Knautia drymeia*

Molecular Ecology (2005) 14, 3547–3555 doi: 10.1111/j.1365-294X.2005.02683.x

Molecular evidence for glacial refugia of mountain plants in the European Alps

P. SCHÖNSWETTER,* I. STEHLIK,† R. HOLDEREGGER‡ and A. TRIBSCH*

VI: northern-Alpine peripheral refugium (R. nivalis)



V: northern-Alpine peripheral refugium (*Erinus alpinus, Rumex nivalis*)

VII: northern-Alpine peripheral refugium (*R. nivalis*)

IX: central-Alpine refugium (*E. nanum*)

IV: eastern-Alpine peripheral refugium (*A. alpina*, *A. wulfeniana*, *E. nanum*, *P. globulariifolium*, *R. glacialis*, *S. pumila*)

VIII: central-Alpine refugium (*E. nanum*)

II: southern-Alpine peripheral refugium (*Androsace alpina*, partly *A. brevis*, partly *Phyteuma globulariifolium*, *Ranunculus glacialis*)

III: southern-Alpine peripheral refugium (*Androsace alpina,* partly *Androsace brevis, Androsace wulfeniana, Eritrichium nanum, Phyteuma globulariifolium, Ranunculus glacialis, Saponaria pumila*)

I: southwestern-Alpine peripheral refugia (*Androsace alpina, Comastoma tenellum,* partly *Phyteuma globulariifolium, Ranunculus glacialis*)

Alpine Botany (2022) 132:21–28
https://doi.org/10.1007/s00035-021-00259-6

REVIEW

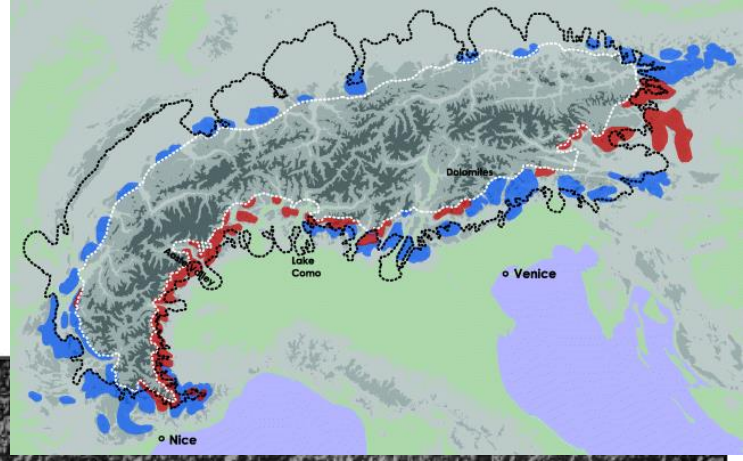
Plant speciation in the face of recurrent climate changes in the Alps

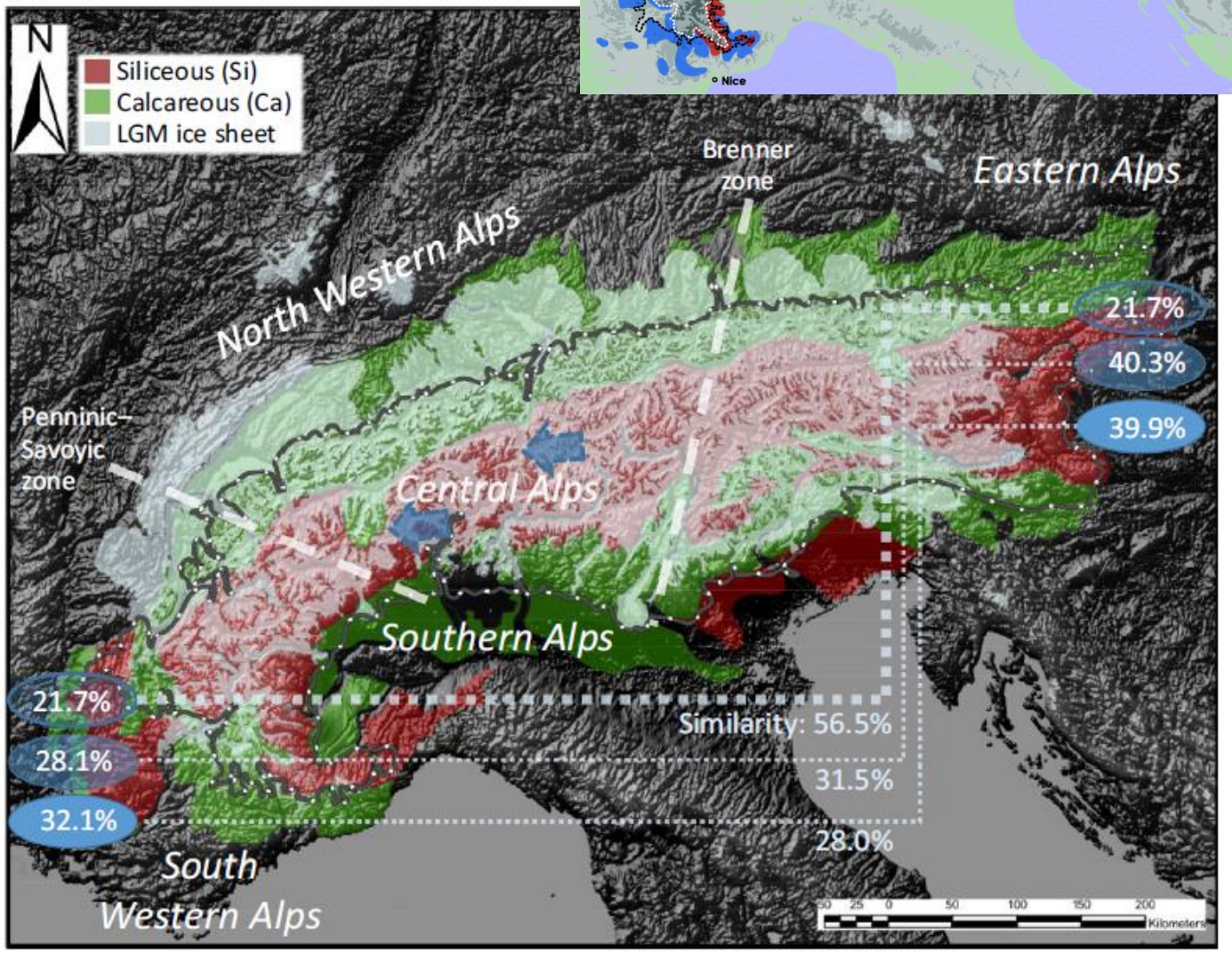
Christian Parisod[1]

- similar break zones in the distribution of alleles and supported secondary contact in suture zones away from the location of glacial refugia for both calcareous and siliceous species

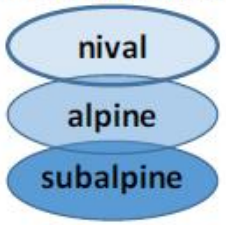
- similarity of endemic taxa between the South-western vs Eastern is increasing with elevation

- a substantial fraction of the lower-elevation endemics are restricted to the vicinity of refugia and likely originated there





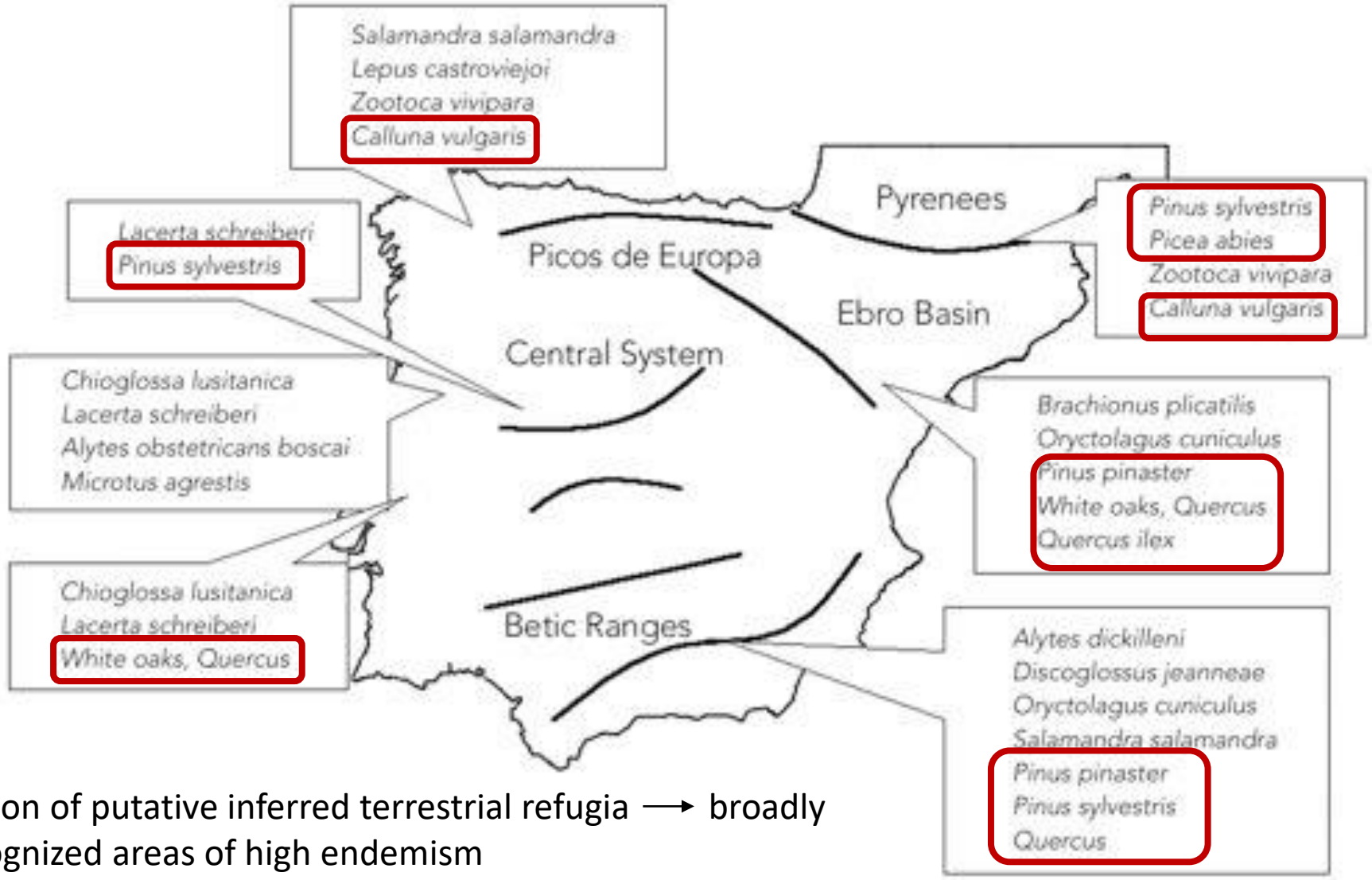
% endemic taxa



Refugia within refugia: patterns of phylogeographic concordance in the Iberian Peninsula

2007

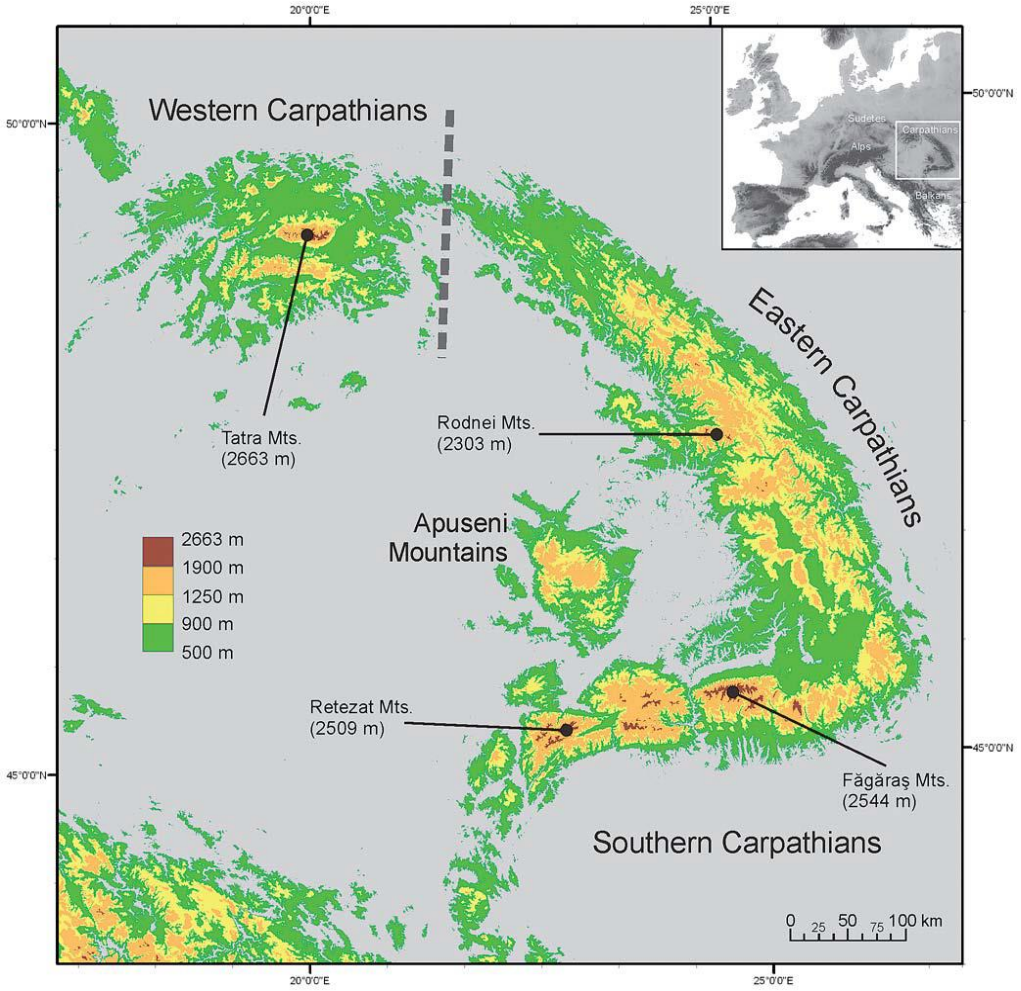
Africa Gómez and David H. Lunt



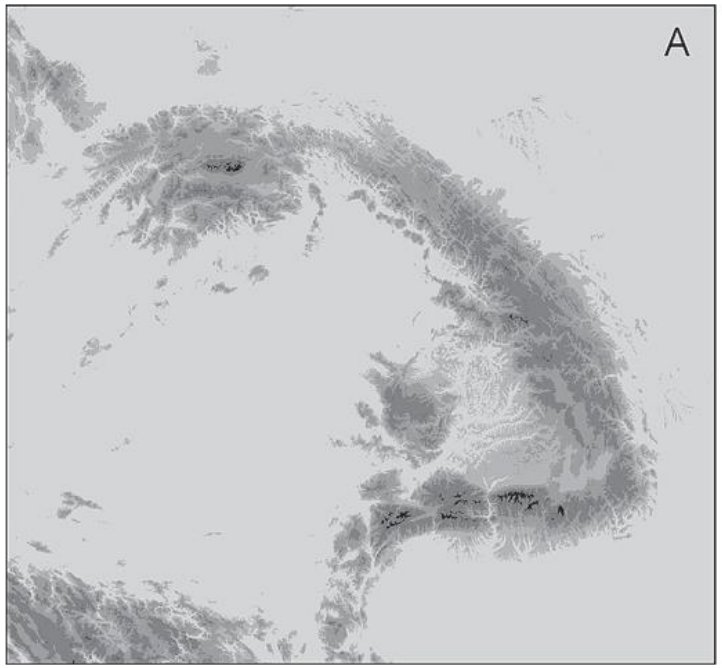
approximate location of putative inferred terrestrial refugia → broadly overlapp with recognized areas of high endemism

Biogeography of high-mountain plants in the Carpathians: An emerging phylogeographical perspective

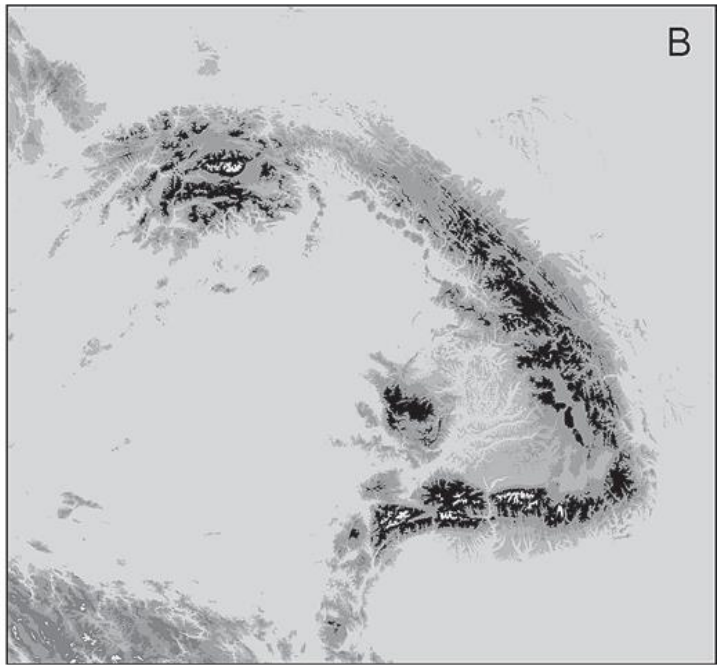
Michał Ronikier

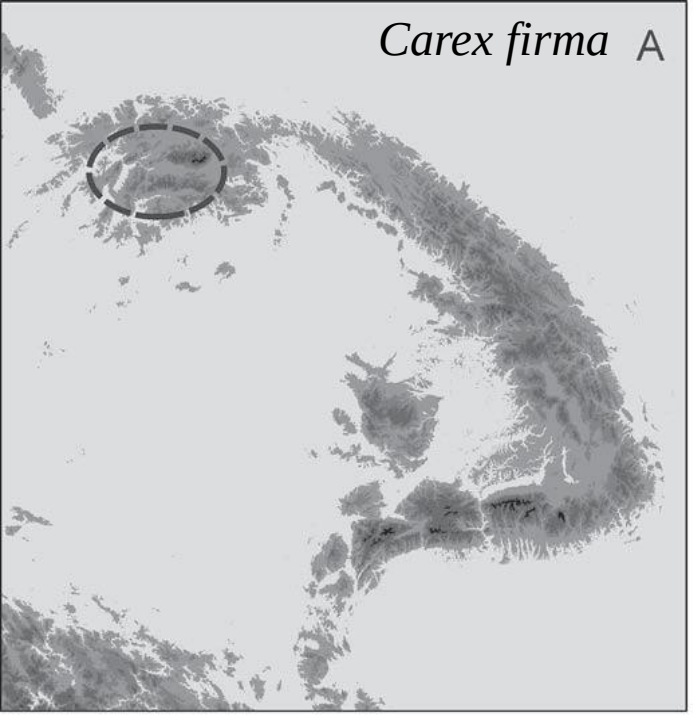


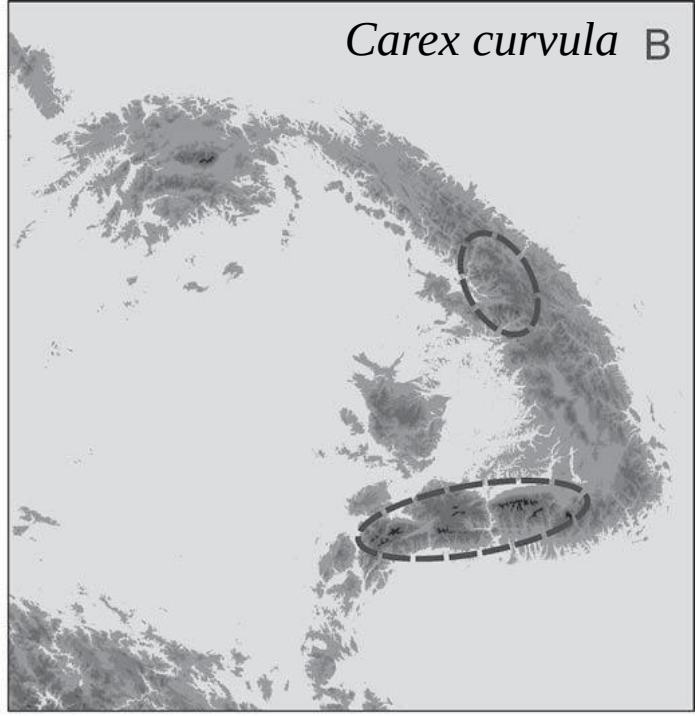
present

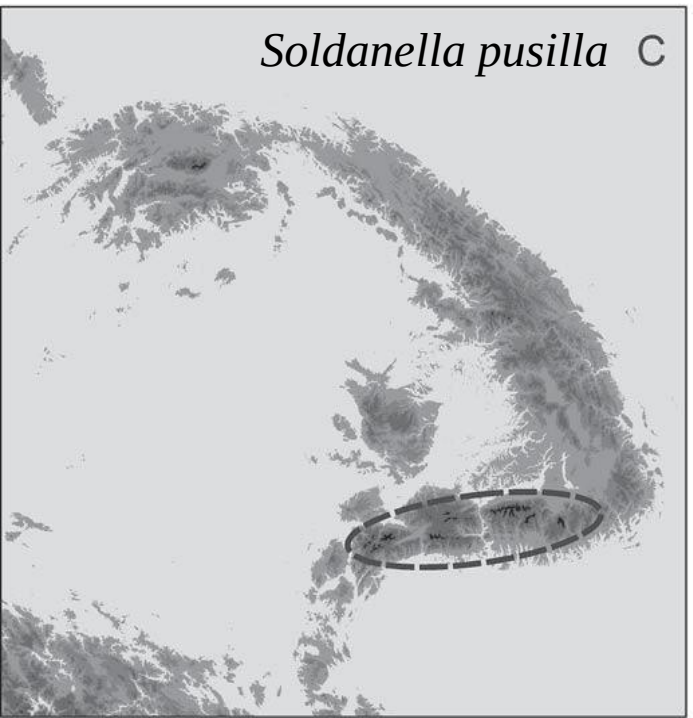


LGM

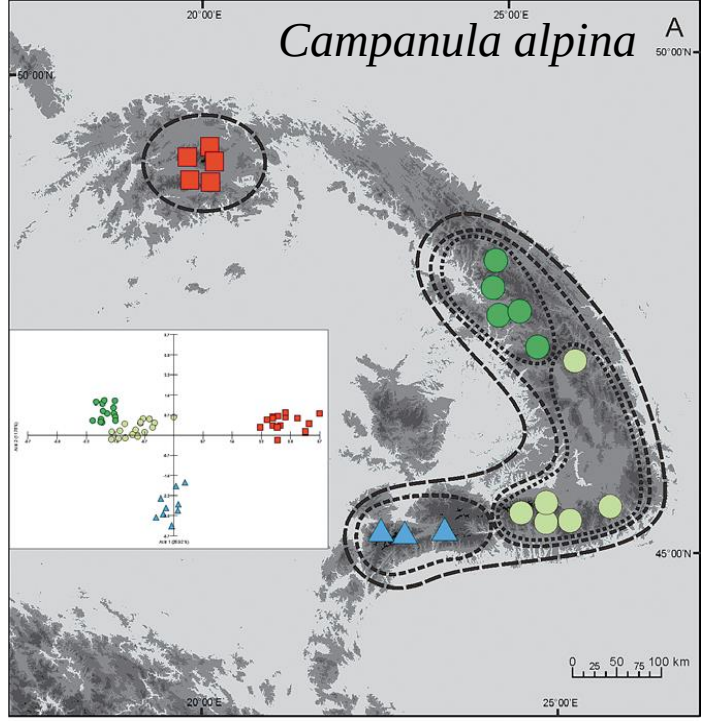


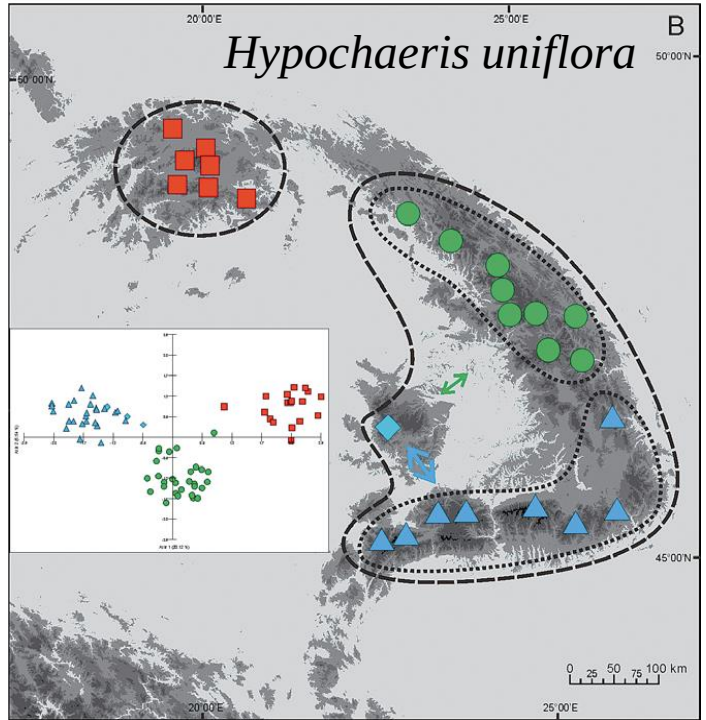

Carex firma A


Carex curvula B


Soldanella pusilla C


Silene (*Lychnis*) *nivalis* (dotted line) and *Silene zawadzkii* (dashed line). D


Campanula alpina A
20°00'E
25°00'E
50°00'N
45°00'N
0 25 50 75 100 km


Hypochaeris uniflora B
20°00'E
25°00'E
50°00'N
45°00'N
0 25 50 75 100 km

The Linnean Society of London
BIOLOGICAL Journal of the Linnean Society

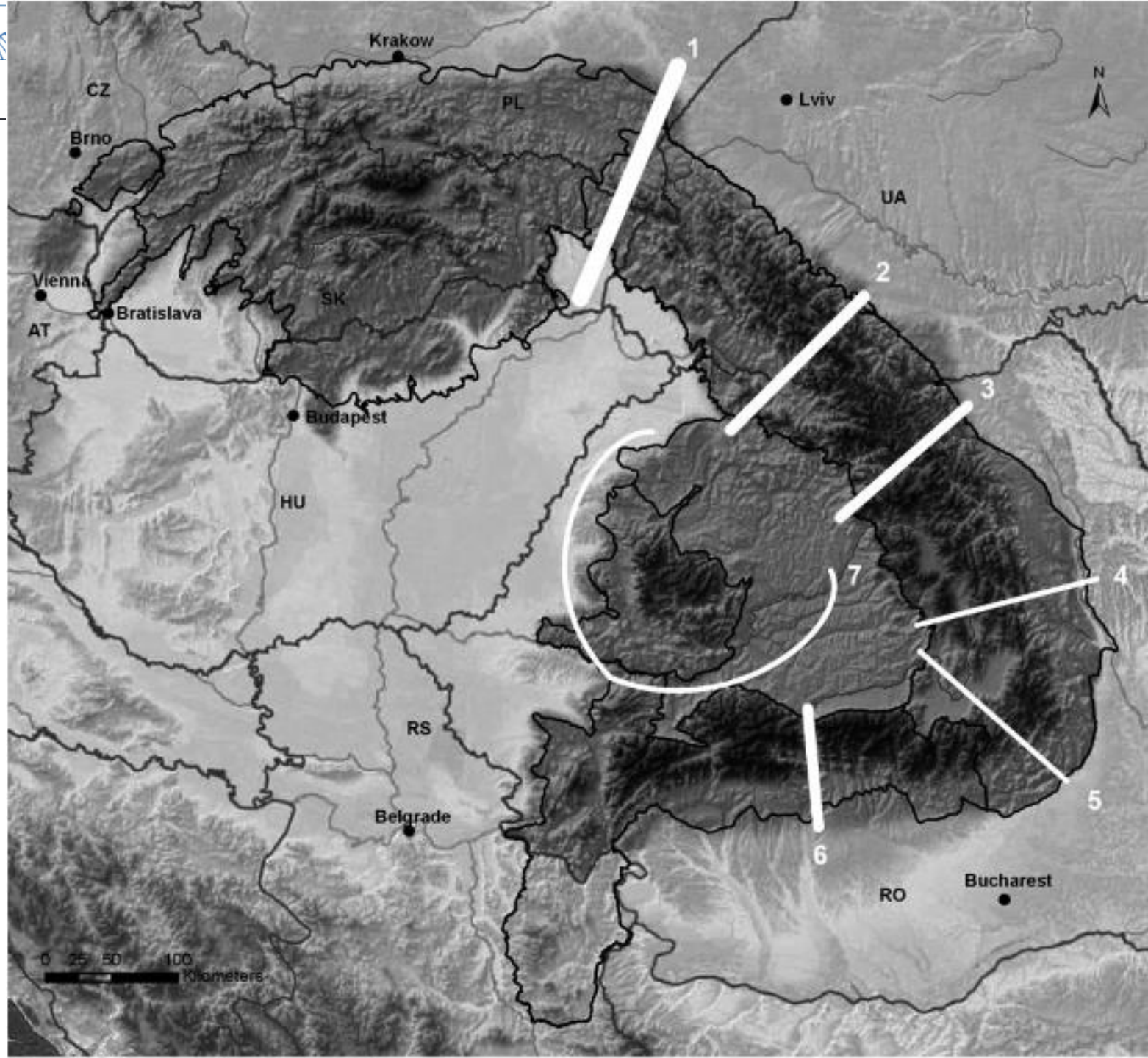
Biological Journal of the Linnean Society, 2016, **119**, 528–559. With 5 figures.

REVIEW ARTICLE

Biogeography of the Carpathians: evolutionary and spatial facets of biodiversity

PATRIK MRÁZ[1†] and MICHAŁ RONIKIER[2*,†]

Phylogeographical (intraspecific) boundaries observed in selected case studies based on dense population sampling



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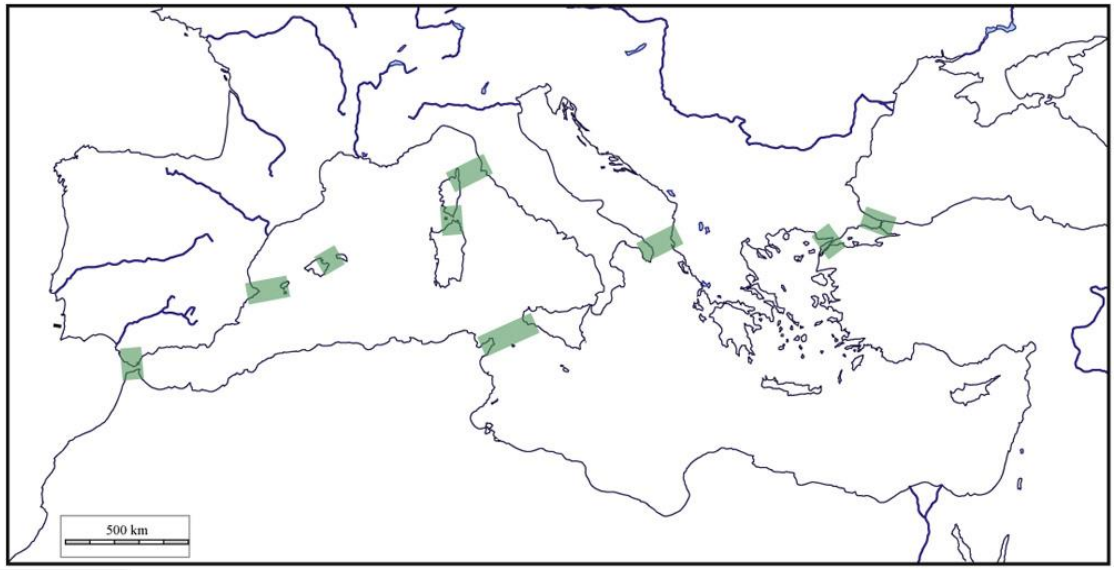
journal homepage: www.elsevier.com/locate/ppees

2014

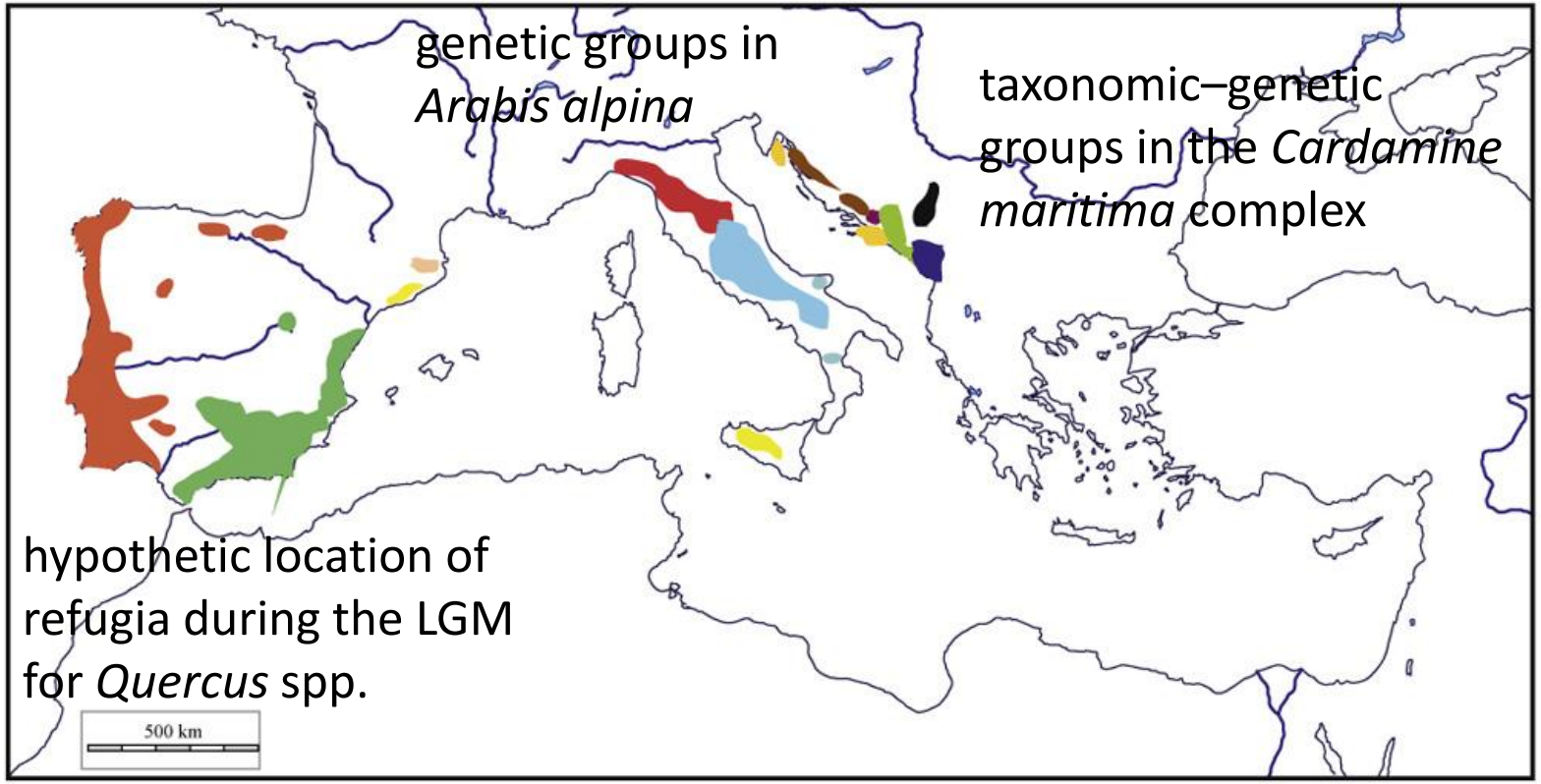
Review

Patterns and processes in plant phylogeography in the Mediterranean Basin. A review

Gonzalo Nieto Feliner*



Sea straits whose biogeographic role as barriers or corridors has been addressed in phylogeographic studies around the Mediterranean Basin



Examples of the refugia-within-refugia model

Balkan Peninsula and adjacent areas → Balkans as a source for postglacial colonisation of northerly regions

- **north-western Dinaric Mountains major refugia** for *Fagus sylvatica* and *Carpinus betulus* - similar pattern in understory herbs: *Cyclamen purpurascens*, *Helleborus niger*, *Knautia drymeia*, *Polygonatum verticillatum*, *Veronica chamaedrys*, *Cerastium sylvaticum*, *Ranunculus auricomus*,…
- **Balkan origin of non-Balkan populations/species**:

a) genetic affinity of Alpine populations: *Heliosperma pusillum* complex, *Wulfenia carinthiaca*, *Ranunculus crenatus*, *Alyssum neglectum, A. cognense, Cirsium greimleri,…*

b) genetic similarity of southern and eastern Carpathian populations: *Arabidopsis arenosa, Cicerbita alpina, Ranunculus platanifolius*

- **both Balkan and northerly non-Balkan refugia:**

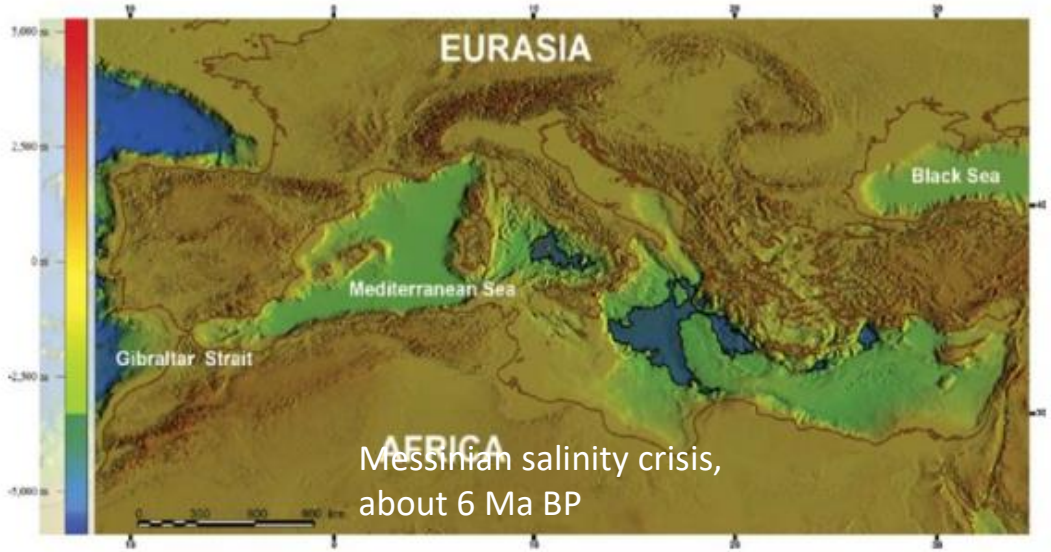
a) no contribution of Balkan populations to postglacial colonization: *Atriplex tatarica, Eryngium alpinum, Doronicum austriacum*

b) no contribution of the southern Balkan lineages and some contribution of northern/central Balkan lineages: *Carlina acanthifolia subsp. utzka, Aurinia saxatilis, Veronica chamaedrys*

- influence to genetic diversity of the present-day northern populations and taxa via hybridization during glacial or postglacial periods: *Pilosella alpicola* ← Alpine *P. glacialis* and Balkan *P. rhodopea, Alyssum repens* ← Balkan *Alyssum vernale*

Balkan Peninsula and adjacent areas → Balkan-Apennine connections

1. a part (if not majority) of trans-Adriatic disjunctions could be explained by **previous land connection** between two peninsulas during the Messinian Salinity Crisis or during the Pleistocene climatic fluctuations: *Campanula poscharskyana - C. garganica* (Pliocene), *Goniolimon* ssp. and *Orchis palustris* (MSC), all others → Pleistocene



M. Anzidei, F. Antonioli, A. Benini, K. Lambeck, D. Sivan, E. Serpelloni, P. Stocchi (2011) Sea level change and vertical land movements since the last two millennia along the coasts of southwestern Turkey and Israel. https://doi.org/10.1016/j.quaint.2010.05.005.

2. **asymmetry** in migration - from the Balkan to the Apennine Peninsula; higher genetic diversity of the Balkan populations, genetic differentiation of the Balkan populations is more pronounced and repeatedly the Adriatic Sea represents a weaker genetic barrier

3. **independent dispersals** within the same species and species groups: *Campanula garganica* group, *Edraianthus graminifolius*, *Silene saxifraga* group

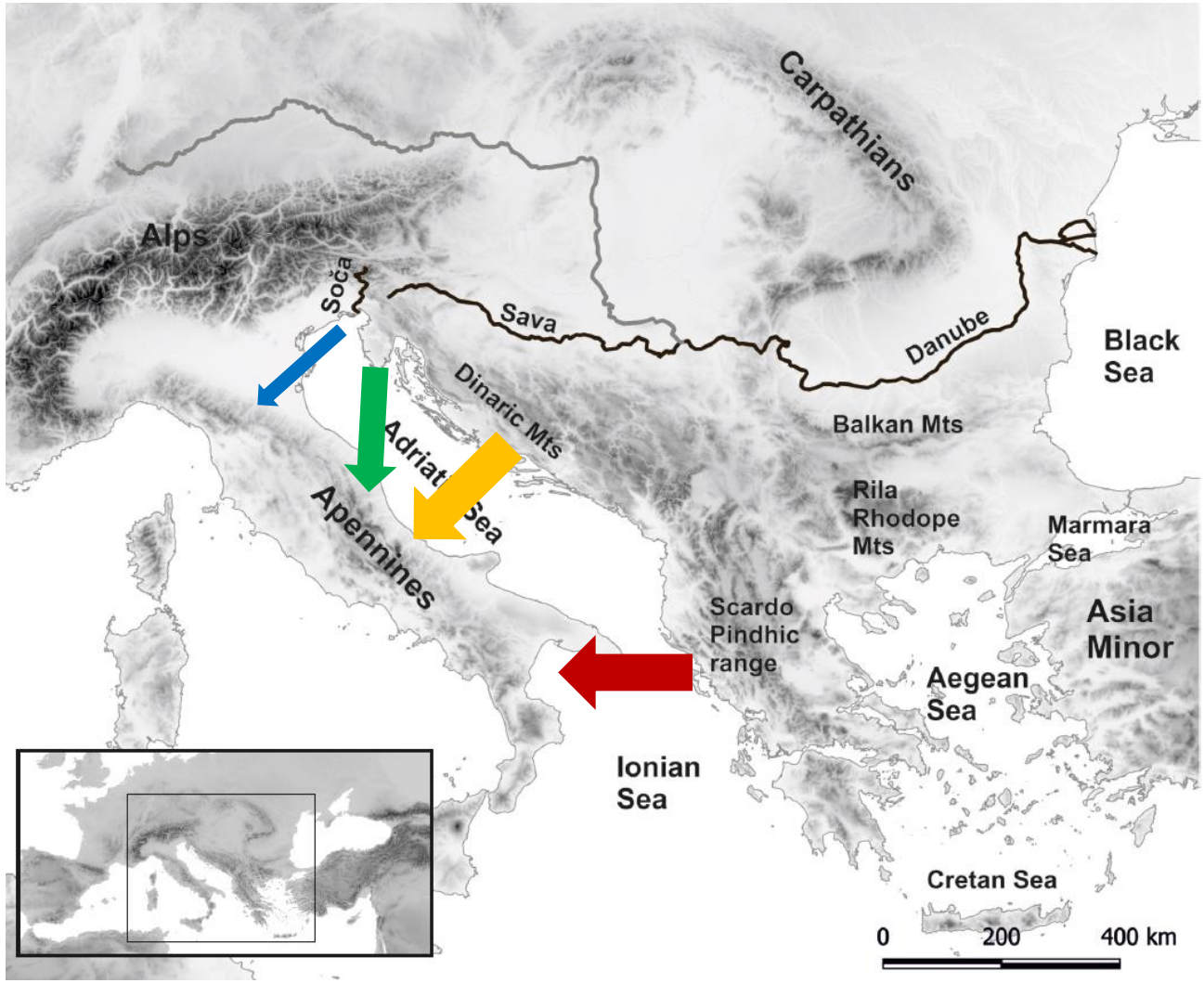
4. geographically based patterns:

a) southern Balkan lineages and southern to central Apennine populations: *Alyssum siculum, Aurinia saxatilis, Campanula versicolor, Centaurea solstitialis, Euphorbia myrsinites, Genista sericea, Gymnospermium scipetarum, Orchis palustris, Silene saxifraga* group

b) central Dinaric and/or central Balkan populations and central to southern part of the Apennines: *Cardamine maritima* group, *Centaurea deusta, Euphorbia barrelieri, Euphorbia spinosa, Gentianella crispata, Silene ciliata, Silene saxifraga* group

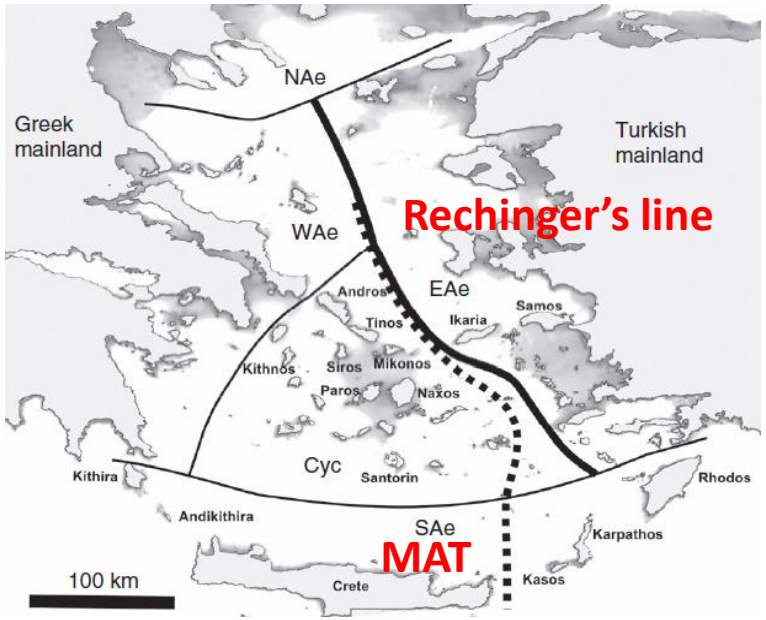
c) north Adriatic lineages to central Apennines: *Astragalus onobrychis, Knautia drymeia, Onosma echioides*

d) north Adriatic lineages to northern Apennines: *Euphorbia verrucosa, Genista sericea*



Balkan Peninsula and adjacent areas → Balkans, Aegean region and Asia Minor connections

- phytogeographical **'Rechinger's line'** (cf. Strid 1996) - mostly corresponds to Mid-Aegean Trench (MAT) - an effective barrier to Balkan-Anatolian (European-Asiatic) dispersal: *Nigella arvensis* complex, *Campanula* subgenus *Roucela, Euphorbia myrsinites, Centaurea solstitialis, Juniperus drupacea, …*



- **colonisaton and/or gene flow from Asia Minor to the Balkans**: *Bormuellera, Arabis alpina, Microthlaspi erraticum, M. perfoliatum*

a) via land bridges (Marmara Sea)

b) via the Thracian Plain

- genetic affinity between taxa and genetic lineages from the **Greek mainland and Aegean islands**: *Cymbalaria microcalyx*

Processes driving the evolution and diversity of Balkan plants → Allopatric and ecological speciation

- **allopatric diversification** - the most obvious and fundamental evolutionary process acting in topographically structured regions such as the Balkans

- **environmental niche shifts** i.e. adaptation to different environmental niches – studies revealing association between genetic variation and bioclimatic variables: *Helichrysum italicum, Tanacetum cinerariifolium, Fraxinus angustifolia, Sideritis scardica, Euphorbia montenegrina*, *E. serpentini, E. verrucosa, …*

- **bedrock type** - serpentine endemics: *Sesleria serbica, Euphorbia serpentini, Minuartia dirphya, M. baldaccii, Odontarrhena baldaccii, O. stridii*

  - or not?: *Alyssum densistellatum* and *A. vourinonese → A. spruneri*; *Arabidopsis arenosa*

- **SDMs future projections** - substantial decrease in suitable habitats for cold-adapted high-alpine species *Cerastium dinaricum* and mesophilous *C. decalvans,* shifting and expansion of favorable habitat toward the northwest for thermophilous *C. grandiflorum*

Processes driving the evolution and diversity of Balkan plants → Polyploidy and hybridization

- **autopolyploidy**: *Veronica chamaedrys* (4x), *Euphorbia spinosa* subsp. *glabriflora* (4x), *Astragalus onobrychis* (4x), *Cyanus pindicola* (4x), *Dianthus sylvestris* (4x), *Euphorbia verrucosa* (4x), *Knautia drymeia* (4x), polyploids of *Pilosella rhodopea, Cerastium grandiflorum* (8x), *Sesleria filifolia* (8x)
- **both** auto- and allopolyploid origins: *Veronica*, *Bellevalia, Knautia* sect. *Trichera*
- **allopolyploidy**: *Cardamine barbaraeoides, Campanula erinus, Alyssum spruneri, Alyssum austrodalmaticum, Veronica austriaca* subsp. *jacquinii, …*

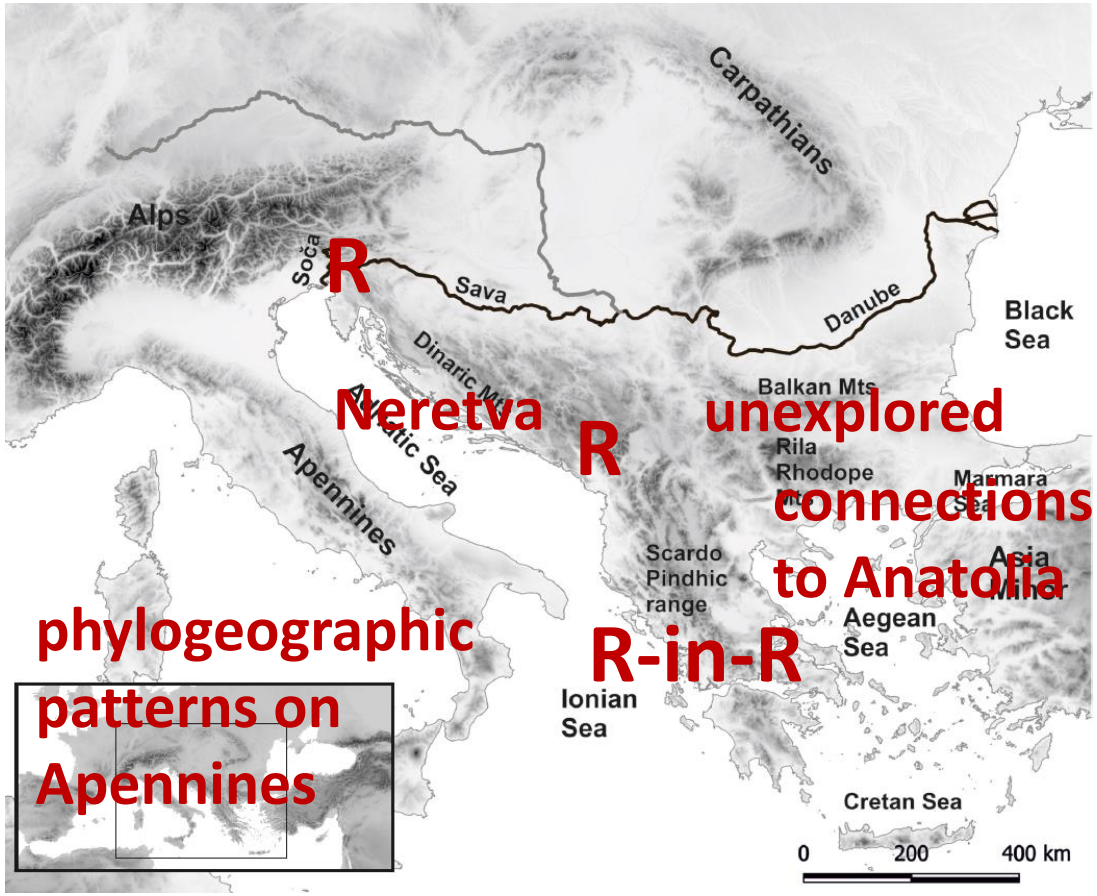
- (allo)polyploids harbor more genetic variation and can become successful colonizers with larger distribution areas or even wider ecological niches than diploids - Greek endemics: 10 % polyploids among the single-mountain endemics, 15% among the single-area endemics, and 40–48% among widespread species

- **homoploid interspecific hybridization** - blurs species boundaries and hinders taxonomic treatments: *Knautia,* hybrid swarms between *Veronica barrelieri*, *V. orchidea* and *V. spicata, Cyanus napulifer* group

2012 → 2022 Some thoughts… 2022

- there is still much to be discovered in the Balkans, most probably more than anywhere else in Europe
- a good balance of field work and molecular-based work is needed
- cooperative efforts on a larger scale should be preferred over regional/national approaches
- what is needed most urgently is a good representation of Balkan taxa in sound phylogenies
- we are ”standing on the shoulders of giants”, but this should not mean that traditional hypotheses on taxonomy, biogeography etc. should not be tested and – if necessary – rejected and abondoned
- gaps in even geographic coverage → eastern part still largely undersampled and unexplored
- phylogeographic connections between the Balkans and Anatolia
- high-throughput next-generation sequencing (NGS)
- **integrative approach** (molecular methods, morphometry, genome size, SDM, ENM…)

Take home message



Thank you!

Theth National Park, Albania