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REVIEW

Plant phylogeography of the Balkan Peninsula: spatiotemporal patterns and processes

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Abstract
The Balkan Peninsula is widely acknowledged as one of the centers of European biodiversity and a major glacial refugium for plant species. Its extensive geographic heterogeneity and diverse mosaic of habitats, coupled with relatively high environmental stability over long periods, have enabled the diversification of lineages and simultaneously fostered the long-term survival of diverse species. The increasing number of phylogeographically studied plant species in the region has substantially contributed to a better understanding of the relationships among closely related taxa and provides significant insights into intraspecific lineage differentiation. The present paper reviews the current knowledge on plant phylogeography in the Balkan Peninsula. By providing an updated overview of the most recent studies dealing with the diversity and evolution of Balkan plants, we explore the phylogeographic patterns and roles of refugia in structuring genetic diversity and highlight the crucial evolutionary processes that shaped the diversity of plants in the region. Molecular clock-based estimations highlight the importance of Pleistocene climatic fluctuations across taxonomic groups and lineage distribution patterns corroborate the persistence of multiple glacial refugia. Spatial congruence in phylogeographic splits is determined and discussed. An examination of phylogeographic connections with adjacent regions (i.e., the Alps, Apennine Peninsula, Asia Minor, Carpathians, and central Europe) uncovers several consistent patterns. Additionally, allopatric and ecological speciation, polyploidy, and hybridization are identified as crucial evolutionary mechanisms acting in the Balkan Peninsula and shaping species diversity. Furthermore, the existing research gaps are identified and future approaches with the potential to better understand the unique Balkan flora are highlighted.

Keywords Balkan Peninsula · Biogeographic links · Distribution patterns · Phylogeography · Refugia · Speciation

Introduction

The Balkan Peninsula comprises a region that extends from central Europe in the north to the southernmost part of Greece and is circumscribed by the Adriatic, Ionian, Cretan, Aegean, Marmara and Black Seas (Fig. 1). The adjacent Ionian and Saronic islands, Euboea, Sporades, Thasos, Cyclades, and Crete can also be assigned to the Balkans, while the easterly North Aegean and Dodecanese islands are considered part of Asia Minor (Turrill 1929). Although there is no consistent delineation of the Balkan Peninsula's continental boundaries the Soča-Sava-Danube river line is the most commonly used geographical border (Reed et al. 2004). Lying at the crossroads between Europe and Asia Minor, the Balkan Peninsula has long served as a meeting ground for species of varying origins. Its complex geological history, various environments, great species diversity, and high percentage of endemism make it one of the most

Stanislav Španiel and Ivana Rešetnik have contributed equally to this work.

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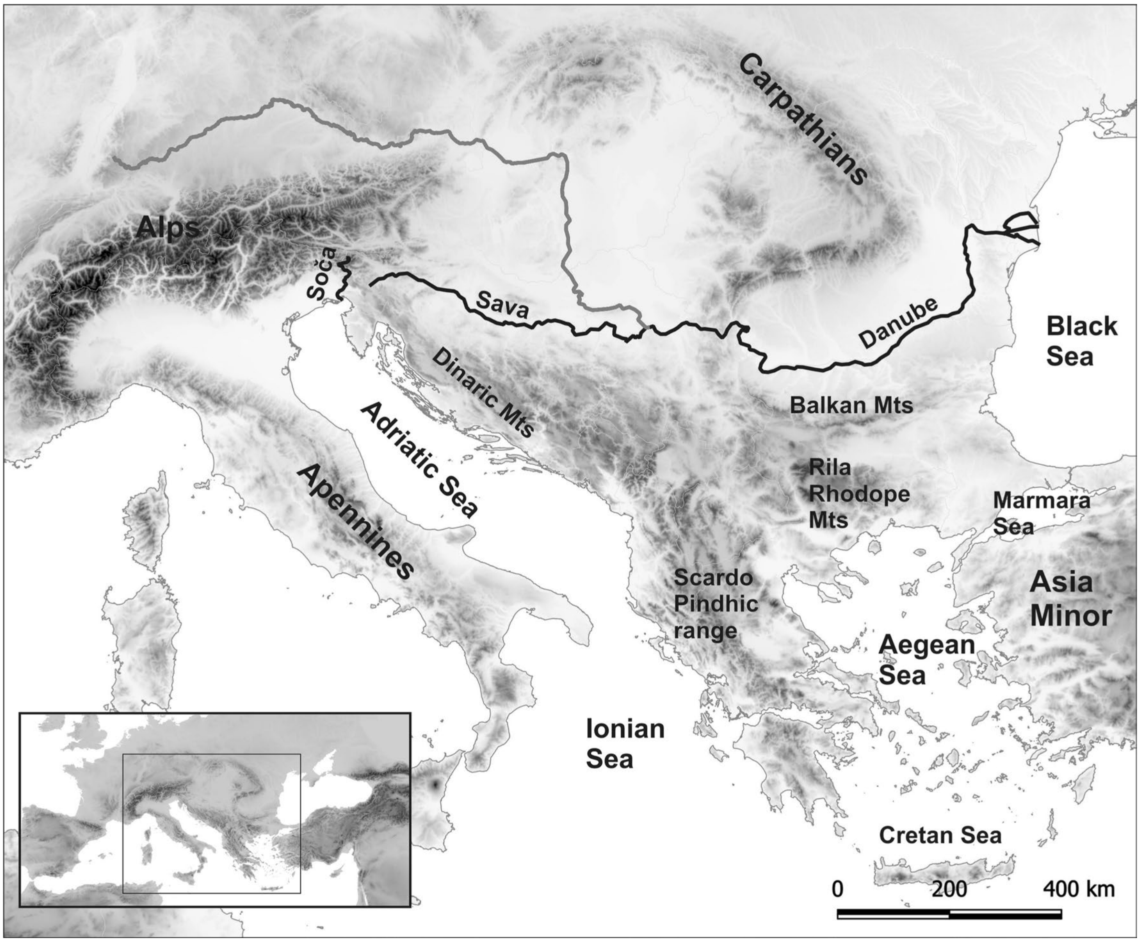

Fig. 1 Map of the Balkan Peninsula and adjacent regions with main geographic formations indicated. The Balkan Peninsula is circumscribed by the Adriatic, Ionian, Cretan, Aegean, Marmara and Black Seas, whereas its northern continental boundaries follow the Soča-Sava-Danube river line

interesting areas for biodiversity studies. The highly heterogeneous topography and diverse mosaic of habitats present an excellent natural laboratory for studying various evolutionary processes such as the effects of isolation on allopatric speciation, adaptive and non-adaptive radiation, and polyploid speciation. Therefore, it is no surprise that this area has increasingly become a hotspot for biogeographic research in recent decades.

Together with Iberia and the Apennines, the Balkans contain much genetic and species diversity and have played a significant role in European biogeography over the last million years (Hewitt 2011; Nieto Feliner 2014). The three southern peninsulas are known glacial refugia and considered major sources of the postglacial colonization of central and northern Europe (Taberlet et al. 1998; Hewitt 2011; Nieto Feliner 2014). The Balkans were an especially important source of lineage dispersal due to the lack of continuous large barriers to the north, whereas the Iberian and the Apennine Peninsulas were restricted by the Pyrenees and the Alps, respectively. Moreover, the Balkans are connected to Asia Minor (and thus to Asia) in the east, via the Bosporus and island chains, while the Mediterranean Sea separates it from northern Africa in the south.

The present paper reviews the current knowledge on plant phylogeography in the Balkan Peninsula. Our general goals are to (1) explore the phylogeographic patterns and roles of refugia in structuring genetic diversity in the region, (2) highlight the crucial evolutionary processes that shaped the diversity of plants in the region, and (3) provide an updated overview of the most recent studies dealing with Balkan plant diversity and evolution.

Topography

Almost 70% of the Balkan relief is formed by mountains (Reed et al. 2004), consisting of several main mountain chains, i.e., the Dinaric Mountains, Scardo-Pindhic range, Rila-Rhodope massif, and the Balkan Mountains (Stara

Planina). The highest peaks are located in Bulgaria (Rila: Musala Peak 2925 m and Pirin: Vihren 2915 m), Greece (Olympus: Mytikas 2917 m), and at the North Macedonia-Albania border (Korab 2764 m), while the most extensive lowlands are found in central Bulgaria (Thracian Plain) and European Turkey. Generally, the mountains of the Peninsula encompass two climatically and floristically distinct areas. The coastal western portion and a large southern portion belong to the Mediterranean (Hewitt 2011; Nieto Feliner 2014) but are also characterized by the deep incisions with summits reaching into the alpine belt and deep valleys with thermophilic sub-Mediterranean vegetation (Surina et al. 2011). The mountains of the northern portion (north of the Greek border with North Macedonia and Bulgaria) have a temperate-continental climatic influence and are similar to the central European mountains in terms of vegetation features (Horvat et al. 1974). However, throughout the Peninsula, its mountainous character confers extreme variability in the local climate with abrupt transitions and associated variability in vegetation types (Reed et al. 2004).

Geological and climatic history

The geological and climatic history of the Balkan Peninsula is a complex combination of tectonic events, orogenic processes, and sea level changes. All of these events have had a profound effect on the biota of the area (Thompson 2005). Below, we highlight the events that had the greatest impact on biogeographic patterns in the Balkans and thus represent potential drivers of diversification and current species distribution patterns in this region. The main land mass was formed during the Oligocene (33–23 Mya) when it arose from an archipelago within the Paratethys Sea and became connected to the southern part of Palaeo-Europe in the early Miocene (23–16 Mya) (Meulenkamp and Sissingh 2003). The collision of the Arabian plate with Eurasia closed the connection between the Paratethys and the Indian Ocean (Steininger and Rögl 1984; Krijgsman 2002), while the subsequent closure of the western part of the Palaeo-Balkan landmass with Palaeo-Europe formed the Pannonian Sea to the east during the late Miocene (Rögl 1999; Meulenkamp and Sissingh 2003). Simultaneously, the culmination of Alpine orogenic activity shaped the current topographic configuration of the Balkans, thereby giving rise to the Dinarides, Hellenides, and Balkanides, while the slow sea transgression in the south caused the emergence of the Aegean Sea and the formation of the Mid-Aegean Trench (MAT), which was accompanied by the fragmentation of the ancient Aegean landmass (Mai 1995). The Miocene ended with the Messinian phase when the Mediterranean Sea closed and became isolated from the Atlantic Ocean, which triggered a cycle of partial or almost complete desiccation in the Mediterranean Basin, an event known as the Messinian salinity crisis (MSC = 5.96–5.33 Mya; Krijgsman et al. 1999). This also included sea regressions in the Adriatic and Aegean regions, thus creating a land connection between the western Balkans and the middle/northern Apennines, along with some land bridges among the southern range of these two peninsulas and an overland passage between islands and the mainland of the Aegean (Popov et al. 2006; Rouchy and Caruso 2006). Simultaneously, the inner part of the Balkan Peninsula was covered with abundant lakes of various sizes that were the residual of the desiccated Pannonian Sea (Krstić et al. 2012). At the beginning of the Pliocene (5 Mya), the land-sea configuration was already similar to the present (Rögl 1999). More recent are the Pleistocene (2.6–0.012 Mya) climatic fluctuations, which mainly involved eustatic sea level changes and led to recurrent north–south shifts of the northern shore of the Adriatic Sea (Correggiari et al. 1996) and the formation and destruction of land connections in the Aegean region (Mai 1995).

The paleoclimatic history of the Balkan Peninsula followed the long-term global changes of the last few million years. Subtropical conditions persisted in the eastern Mediterranean through the early Miocene, with high summer rainfall and little seasonal temperature changes. A gradual decrease in summer rainfall and a trend toward increased aridification and clear seasonality with summer droughts and cold, humid winters began in the middle Miocene (9–8 Mya) and continued into the Pliocene, leading to the establishment of the current Mediterranean climate (3.4–2.8 Mya; Suc 1984; Hsü et al. 1977; Krijgsman et al. 1999; Meulenkamp and Sissingh 2003; Popov et al. 2006; Favre et al. 2007; Ivanov et al. 2011). During the glacial and interglacial periods of the Pleistocene, the sea level fluctuations also triggered changes in overall climate. Sea level reduction and the desiccation of large areas during glaciations increased aridification (Rapp 2012), in areas such as the northern Adriatic region (Horvat et al. 1974), while a warmer and more humid climate existed during interglacial periods.

Biological richness: species diversity and endemism

The uniqueness of the Balkan ecosystems is demonstrated by high species richness and a significant proportion of endemics, which renders it Europe's most floristically rich area (Kryštufek and Reed 2004; Stevanović et al. 2007; Hewitt 2011). Nonetheless, there is no consensus on the exact number of plant species. The extant literature contains assessments for approximately 6500 species, of which more than one-third (2600–2700) are endemic and about 400 are considered local endemics (Horvat et al. 1974; Kryštufek and Reed 2004; Stevanović et al. 2007). However, when considering the local floras and their numbers, these assessments are likely an underestimate. For example, the Greek flora includes 5752 species, of which 1278 are endemic to this country (Dimopoulos et al. 2013), while Croatia has 5147 taxa (including 393 endemics, Nikolić 2021), Serbia and Kosovo have 3662 taxa (including 492 endemics, Tomović et al. 2014) and Montenegro has approximately 3600 taxa (Stešević and Caković 2013). Moreover, numerous distinct intraspecific genetic lineages of various taxa have persisted in the Balkans through a series of late Tertiary and Quaternary climate fluctuations, thereby making it an important hotspot of genetic diversity (Hewitt 1999, 2011; Nieto Feliner 2014). This richness results from the combined effects of geographic position, and topographic, climatic and geological complexity. The Peninsula is located in the center of the Mediterranean and at the crossroads between Asia Minor and the rest of Europe, which has enabled the migration of Asian lineages and taxa since the Miocene (Hewitt 2011; Manafzadeh et al. 2014). Moreover, the high degree of spatial heterogeneity forms a system of diverse habitat islands separated by environmental barriers, such as mountain ranges of varying orientation or deep valleys and river canyons. This situation enables the diversification of lineages and acts as a trigger for allopatric speciation while simultaneously fostering the preservation of species in areas of relative ecological stability (Tzedakis et al. 2002) and in situ species radiations (Hellwig 2004; Boyer et al. 2005). For example, the endemics in continental Greece mostly occur at moderate to high elevations (above 600 m a.s.l.; Georghiou and Delipetrou 2010). In Serbia and Kosovo, endemics mostly occur on limestone at 1500–2000 m a.s.l. (Tomović et al. 2014). These examples can be regarded as a natural consequence of the role of mountains as centers of speciation (Tzedakis et al. 2002). Moreover, limestone mountains in areas such as the Alps or Iberia are richer in endemics than acidophilous areas (Essl et al. 2009; Domínguez Lozano et al. 2000) and the karst of the Dinaric Mountains represents the most extensive example of limestone mountains in Europe. Furthermore, the relatively weak and localized glaciation during Pleistocene climatic fluctuations (Bognar et al. 1991; Milivojević et al. 2008) provided suitable environmental conditions for the long-term survival of diverse species and lineages, thereby contributing to high species diversity and endemism.

Phylogeographic patterns within the Balkan Peninsula

Phylogeography explores the spatial distribution of genetic lineages that result from the evolutionary processes driving population expansion, population contraction, and gene movement, and are shaped by the impact of geological changes, geographic boundaries, and climate fluctuations (Avise et al. 1987). Phylogeographic studies encompass various temporal and spatial scales and their accumulation provides insights into the general drivers of biogeographical patterns. Here, we examine phylogeographic literature published over the last 20 years that has focused on the species level (within species or closely related species sensu Avise et al. 1987) of vascular and non-vascular plants. However, the phylogeographic patterns of tree species were assessed by Gömöry et al. (2020) in a separate review within the current topical journal collection "Plants of the Balkan Peninsula in Space and Time" and are thus not presented here in detail. To our knowledge, only a few phylogeographic studies have included samples from Balkan bryophytes (e.g., Natcheva and Cronberg 2003; Hedderson and Nowell 2006; Grundmann et al. 2008) and pteridophytes (Trewick et al. 2002) resulting in their limited presentation in this review.

Distribution of genetic lineages

The aforementioned geological and climatic history provided the conditions for diverse patterns of genetic architecture in Balkan taxa. The climatic alternations caused range shifts for many species, often resulting in disjunct distributions. However, the distribution histories and underlying evolutionary processes may vary in different phylogenetic and ecological groups.

For example, in the western Balkans, differentiation into two or three genetic units along the Dinaric Mountains appears to be the most common feature among thermophilic species (Fig. 2; *Edraianthus tenuifolius*, Surina et al. 2011; *Viola suavis*, Mereďa et al. 2011; *Tanacetum cinerariifolium*, Grdiša et al. 2014; *Salvia officinalis*, Rešetnik et al. 2016a; Jug-Dujaković et al. 2020; *Euphorbia myrsinites*, Falch et al. 2019; *Cerastium grandiflorum*, Đurović et al. 2021). These lineages are typically confined to northern, central, and southern groups, with the southern lineages more often being of higher genetic diversity than the northernmost.

A similar pattern is observed in species with a wider elevational tolerance and wider geographical distribution, i.e., *Veronica chamaedrys* (Bardy et al. 2010; Fig. 3j), *Silene saxifraga* (Đurović et al. 2017; Fig. 3i), and *Cerastium decalvans* (Đurović et al. 2021; Fig. 3d). However, northern lineages extend to the Alps, central lineages extend toward the Carpathians, and southern lineages are distributed in the Scardo-Pindhic range in the two latter examples. Lineage differentiation into four allopatric groups was recorded for the forest understory species *Cyclamen purpurascens* (Slovák et al. 2012; Fig. 3e) and *Knautia drymeia* (Rešetnik et al. 2016b; Fig. 3g), although with the rather limited distribution of southern groups in the central Balkans. Four genetic entities occurring in the central and eastern Balkan Peninsula and the Carpathians were found in *Sesleria rigida* s.l. (Kuzmanović et al. 2013; Fig. 3h). Similarly, at the north-eastern border of the Balkan Peninsula the two (out of four) genetic groups of

Astragalus onobrychis meet (Záveská et al. 2019; Figs. 3b, 5), as well as two (out of three) lineages of *Aurinia saxatilis* (Rešetnik et al. 2022, Fig. 5). In both cases one group is confined to the central Balkan Peninsula, while the eastern group extends across the Carpathians into central Europe.

The more restricted and disjunct distribution pattern of alpine species in the Balkans is also manifested in their

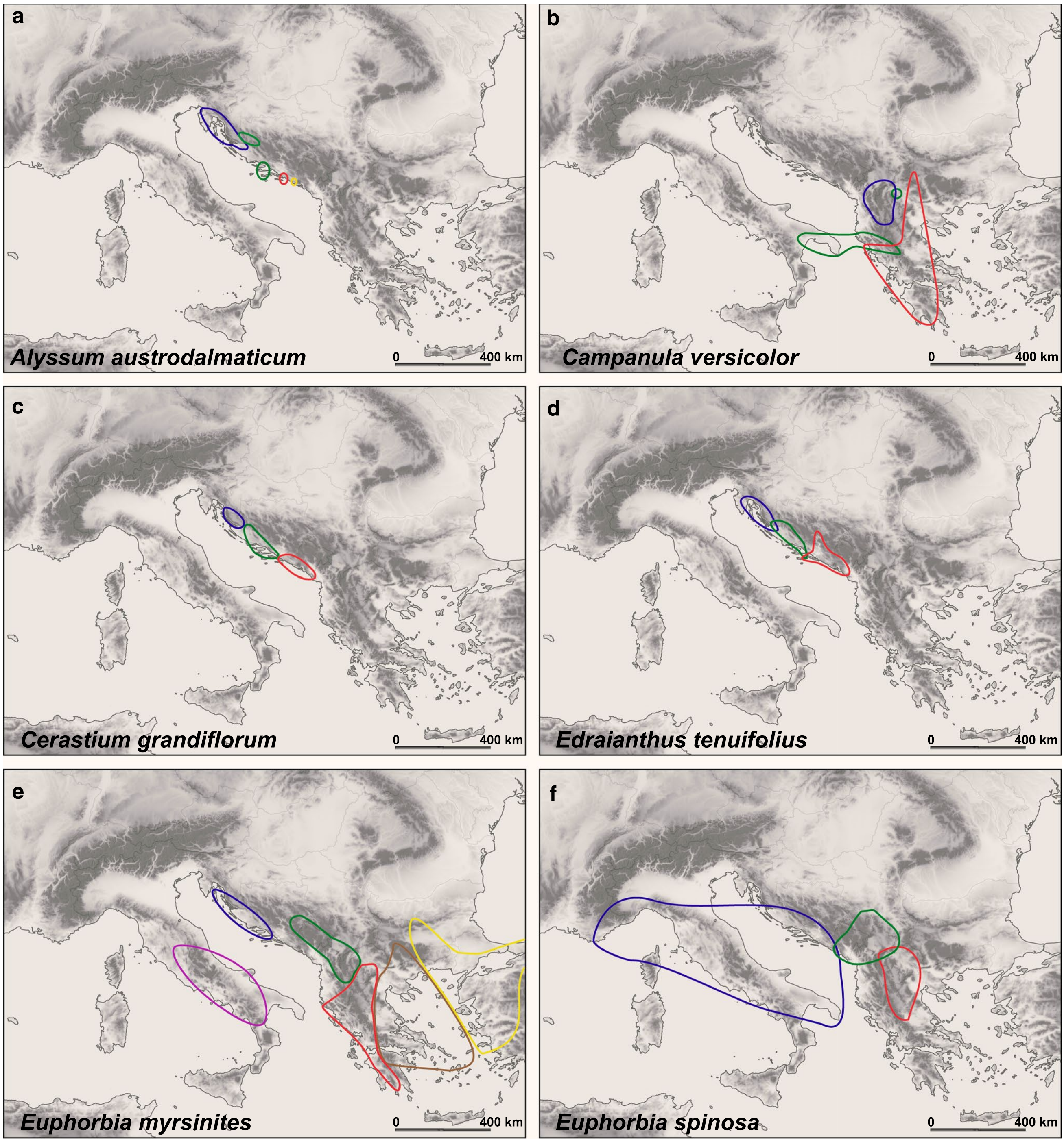

Fig. 2 Intraspecific genetic lineages observed in selected case studies of low-elevation plant species. **a** *Alyssum austrodalmaticum* (Zozomová-Lihová et al. 2020); **b** *Campanula versicolor* (Janković et al. 2019); **c** *Cerastium grandiflorum* (Đurović et al. 2021); **d** *Edraianthus tenuifolius* (Surina et al. 2011); **e** *Euphorbia myrsinites* (Falch et al. 2019); **f** *Euphorbia spinosa* (Stevanovski et al. 2020); **g** *Helichrysum italicum* (Ninčević et al. 2021); **h** *Salvia officinalis* (Rešetnik et al. 2016a); **i** *Tanacetum cinerariifolium* (Grdiša et al. 2014); **j** *Viola suavis* (Mereďa et al. 2011)

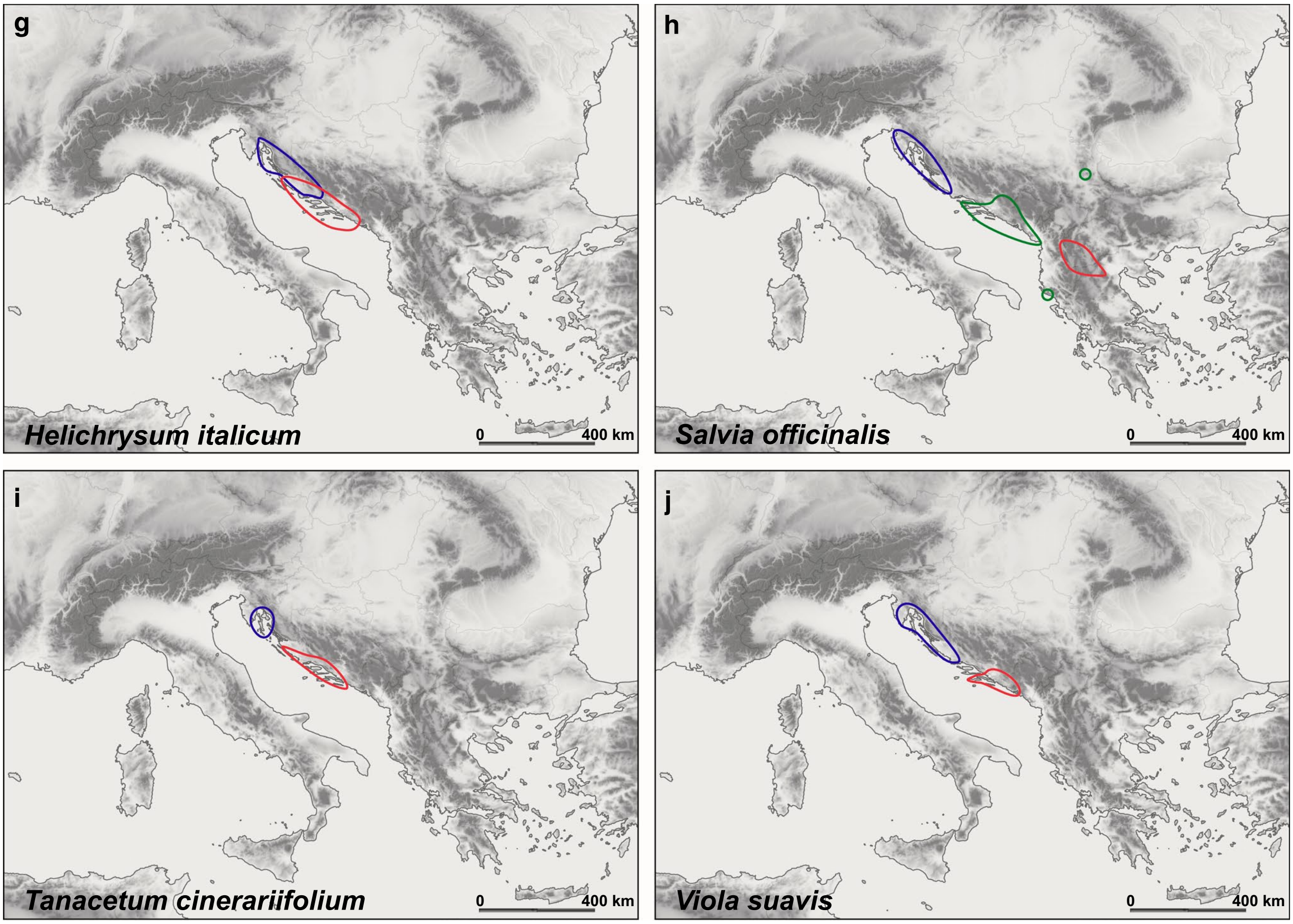

Fig. 2 (continued)

genetic structures (Fig. 4). The northern and southern disjunct populations of *Cerastium dinaricum* are clearly genetically divergent (Kutnjak et al. 2014; Đurović et al. 2021; Figs. 4a, 5), while the more continuously distributed *Edraianthus graminifolius* differentiated into three genetic units comparable to the pattern observed in thermophilic species (Surina et al. 2014b; Fig. 4b).

An intriguing area of spatially close but strongly differentiated genetic lineages is the borderline between the Dinaric Mountains and Scardo-Pindhic range. The three distinct genetic lineages of *Euphorbia myrsinites* (Falch et al. 2019; Fig. 2e) and *Amphoricarpos neumayerianus* (Caković et al. 2015; Fig. 3a) and two spatially intermingled lineages of *Silene saxifraga* were found in this area (Đurović et al. 2017; Fig. 3i).

Inference of major barriers

The patchy nature of the Balkan landscape fostered the aforementioned segmented distribution of genetic lineages. Thus, the phylogeographic breaks may be correlated with physiographical barriers that prevented species migration and/or gene flow. The barriers in main areas of co-distributed lineages from the previous chapter are discussed below. To date, the majority of studies have focused on taxa distributed in the Dinaric Mountains, and, to a lesser extent, the taxa distributed throughout the Scardo-Pindhic range (Fig. 5). Since the eastern part of the Balkan Peninsula has been less thoroughly explored through detailed phylogeographic studies, the knowledge of geographical barriers in this region remains very limited.

Northern Dinaric Mountains

The western margin of the Dinaric Mountains represents the borderline between two genetic groups observed within *Cyclamen purpurascens* (Slovák et al. 2012; Figs. 3e, 5), while the northernmost split positioned within the northern Dinaric Mountains—between the Gorski Kotar region and the Velebit mountain range in Croatia—was found within the *Silene saxifraga* group (Đurović et al. 2017; Fig. 3i) and in *Knautia drymeia* (Rešetnik et al. 2014; Figs. 3g, 5). Within these species, the northern genetic clusters are extending toward the Alps and the observed splits are not linked to any specific distinct geographic barrier. However, the Dinaric Mountains have several pronounced deep and narrow canyons formed by karstic rivers that can likely represent a major barrier to the otherwise continuous distribution of species. On the southern edge of the Velebit mountains, the Paklenica, Zrmanja and Krka karst canyons likely promoted

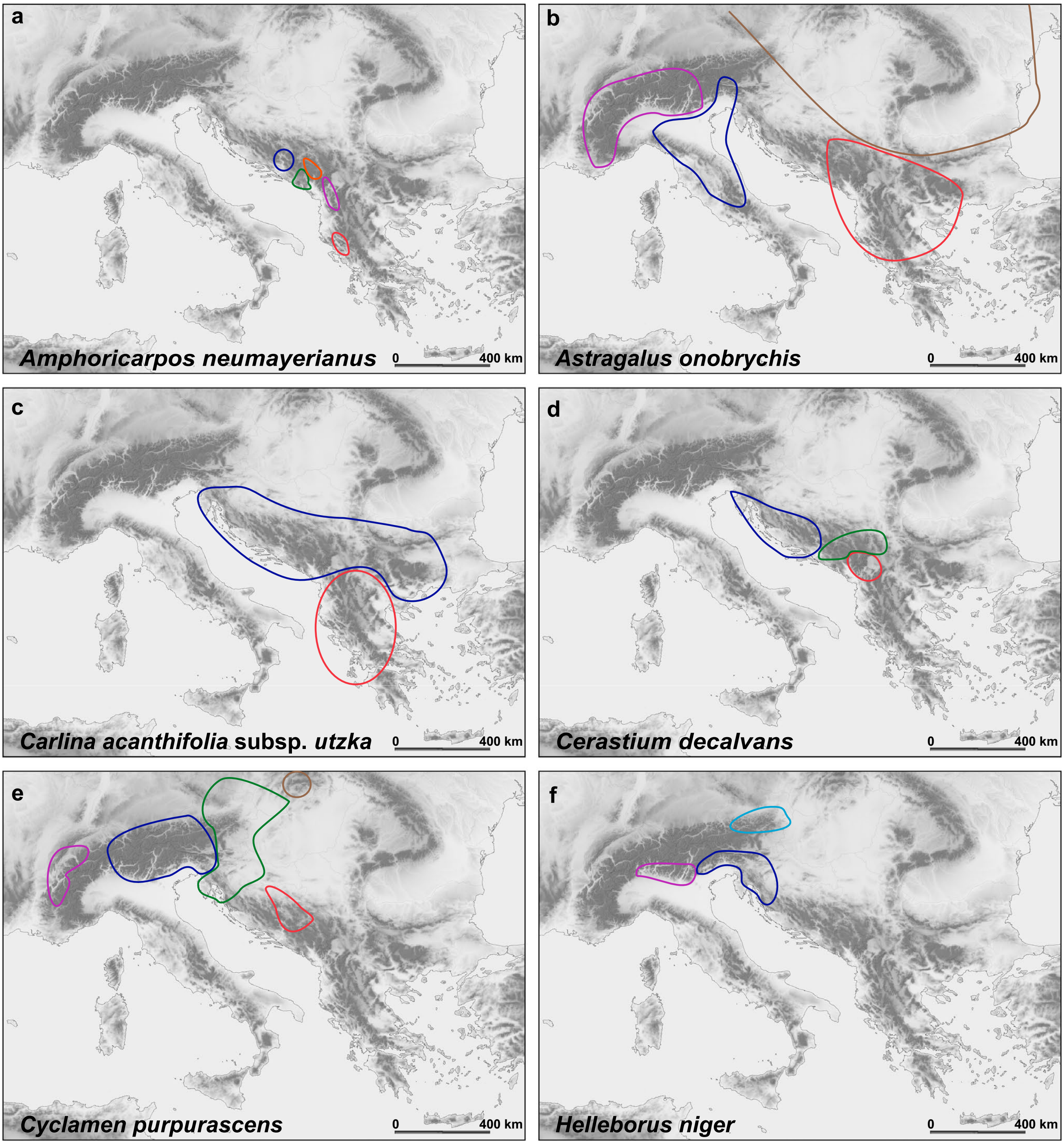

Fig. 3 Intraspecific genetic lineages observed in selected case studies of mid-elevation plant species. **a** *Amphoricarpos neumayerianus* (Caković et al. 2015); **b** *Astragalus onobrychis* (Záveská et al. 2019); **c** *Carlina acanthifolia* subsp. *utzka* (Cieślak and Drobniak 2019); **d** *Cerastium decalvans* (Đurović et al. 2021); **e** *Cyclamen purpurascens* (Slovák et al. 2012); **f** *Helleborus niger* (Záveská et al. 2021); **g** *Knautia drymeia* (Rešetnik et al. 2016b); **h** *Sesleria rigida* s.l. (Kuzmanović et al. 2013); **i** *Silene saxifraga* (Đurović et al. 2017); **j** *Veronica chamaedrys* (Bardy et al. 2010)

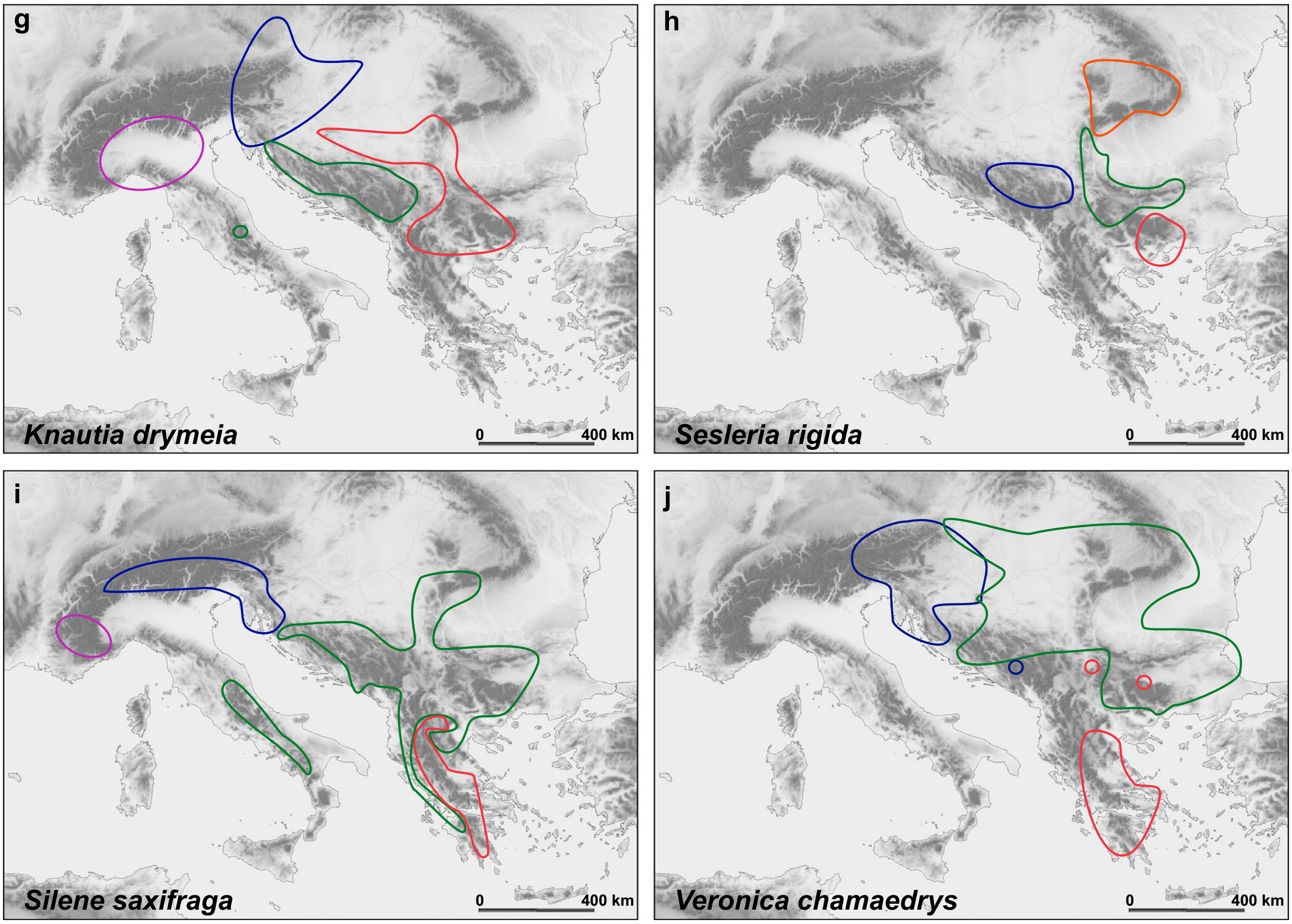

Fig. 3 (continued)

the genetic distinction of the southern populations of *Campanula fenestrellata*, while the distinction of its northernmost populations in Istria and the islands of Cres and Krk was facilitated by postglacial sea transgression (Rešetnik et al. 2020). Zrmanja canyon acted as a barrier within the continuous range of *Tanacetum cinerariifolium* and separated the northern and southern populations (Grdiša et al. 2014; Figs. 2i, 5). Moreover, roughly the same area represents the borderline between the two genetic groups within *Cerastium grandiflorum* (Đurović et al. 2021; Figs. 2c, 5), *Helichrysum italicum* (Ninčević et al. 2021; Fig. 2g), and the *Veronica chamaedrys* group (Bardy et al. 2010; Figs. 3j, 5).

Central Dinaric Mountains: Neretva

Multiple examples document the major biogeographical role of the border adjacent to the present Neretva river valley as an important barrier to gene flow and a trigger for allopatric lineage diversification. Accumulating evidence implies that the split was not caused by the river valley itself (but see Đurović et al. 2021), but that the position of the valley coincides with the break line between divergent environmental conditions that were formed in this area at the end of the Last Glacial Maximum (LGM; 18,000 years ago) (Lakušić et al. 2013; Španiel et al. 2017a). During the LGM, the northern coast of the Adriatic was shifted southward, close to the Neretva estuary, which then reached Sušac Island (Correggiari et al. 1996; Sikora et al. 2014). The proximity of the sea likely had a substantial influence on the distribution of vegetation types and general ecological conditions, which created changes in habitat conditions in the northern Dinaric Mountains distant from the sea and the southern Dinaric Mountains closer to the buffered environments. This phylogeographic break was mostly documented in thermophilous taxa such as *Alyssum austrodalmaticum* (Španiel et al. 2017a; Zozomová-Lihová et al. 2020; Figs. 2a, 5), *Cerastium decalvans* (Đurović et al. 2021; Figs. 3d, 5), *Edraianthus tenuifolius* (Surina et al. 2011; Glasnović et al. 2018; Figs. 2d, 5), *Euphorbia myrsinites* (Falch et al. 2019; Figs. 2e, 5), *Viola suavis* (Mereďa et al. 2011; Fig. 2j), and vicariant species pairs such as *Campanula pyramidalis* and *C. austroadriatica*

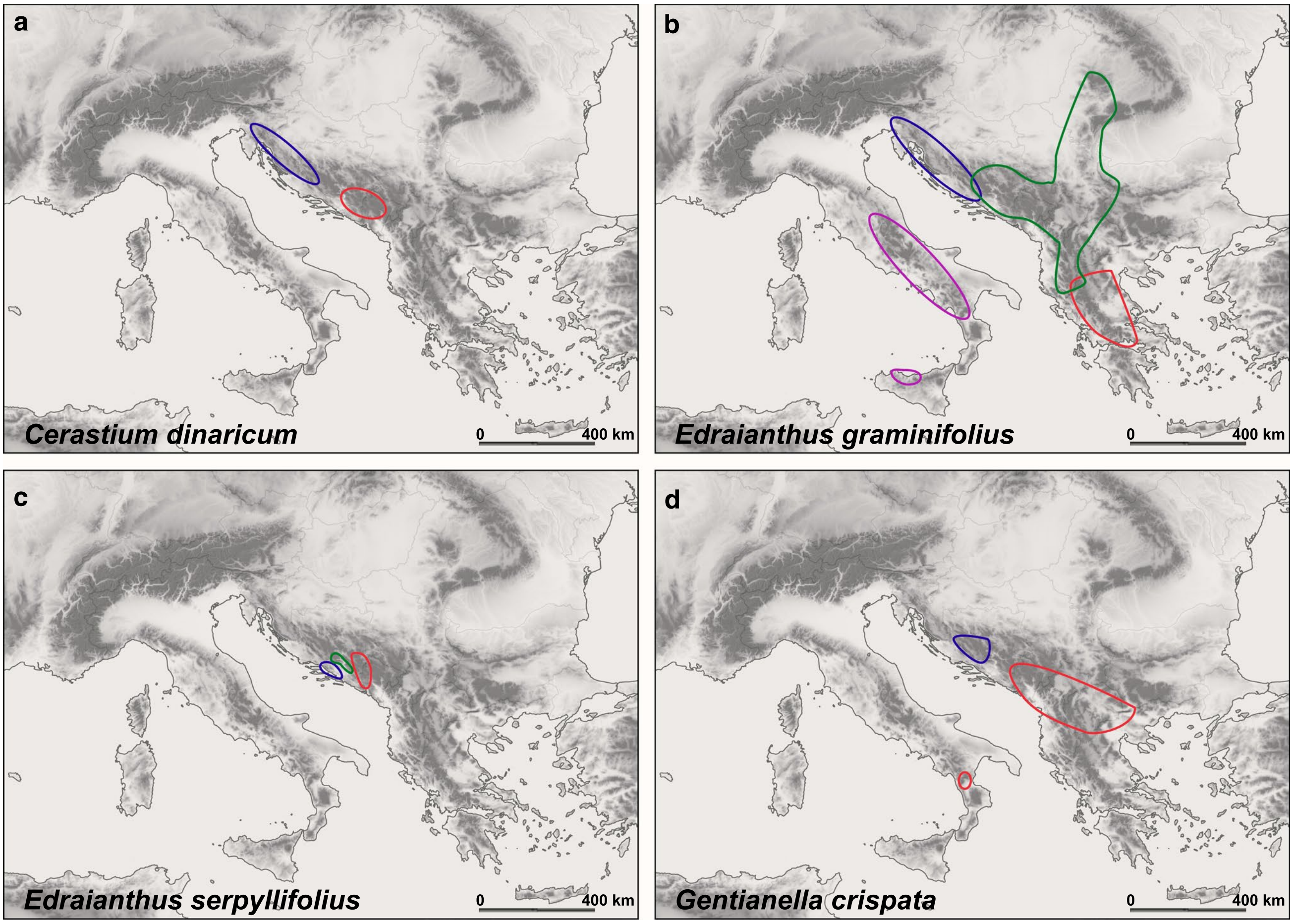

Fig. 4 Intraspecific genetic lineages observed in selected case studies of high-elevation plant species. **a** *Cerastium dinaricum* (Kutnjak et al. 2014; Đurović et al. 2021); **b** *Edraianthus graminifolius* (Surina et al. 2014b); **c** *Edraianthus serpyllifolius* (Surina et al. 2011); **d** *Gentianella crispata* (Reich et al. 2021)

(Lakušić et al. 2013; Fig. 5), *Veronica dalmatica* and *V. orbiculata* (López-González et al. 2021; Fig. 5), and *Cardamine maritima s.l.* (Kučera et al. 2010; Fig. 5). This barrier is shifted further north in the case of the more cold-adapted *Edraianthus graminifolius* and supports both the aforementioned hypothesis (the role of the environmental break line formed in this area at the end of the LGM) as well as the existence of harsher environmental settings toward the north (Surina et al. 2014b; Figs. 4b, 5). An additional barrier for the cold-adapted taxa could be the existence of vast lower-elevation karst fields. Livno karst field, which separates the Čvrsnica and Dinara mountain ranges, could have acted as a barrier for *Cerastium dinaricum* (Kutnjak et al. 2014; Đurović et al. 2021; Figs. 4a, 5), while the karst fields Nevesinje and Gatačko polje—between the Neretva and Sutjeska rivers—could have presented an impediment for Balkan *Amphoricarpos* taxa (Caković et al. 2015; Figs. 3a, 5) and *Gentianella crispata* (Reich et al. 2021; Figs. 4d, 5).

Southern Dinaric Mountains

Within the southern Dinaric Mountains the inland karst rivers Drina and Sutjeska are postulated barriers for the genetic split in plastid data dated to the Pliocene within the *Heliosperma pusillum* group (Frajman and Oxelman 2007; Fig. 5). Likewise, the plastid data supported the Drina barrier within *Edraianthus graminifolius* lineages, although it was not supported by AFLP data, which indicated a more southern Morava Valley break (Surina et al. 2014b; Figs. 4b, 5). The canyons of the Tara and/or Lim rivers correspond to the genetic split observed between the sister species *Campanula secundiflora* and *C. montenegrina* (Lakušić et al. 2013; Janković et al. 2016; Fig. 5).

Scardo-Pindhic range

Within the Scardo-Pindhic range both north–south and west–east lineage divergences are found within taxa. The

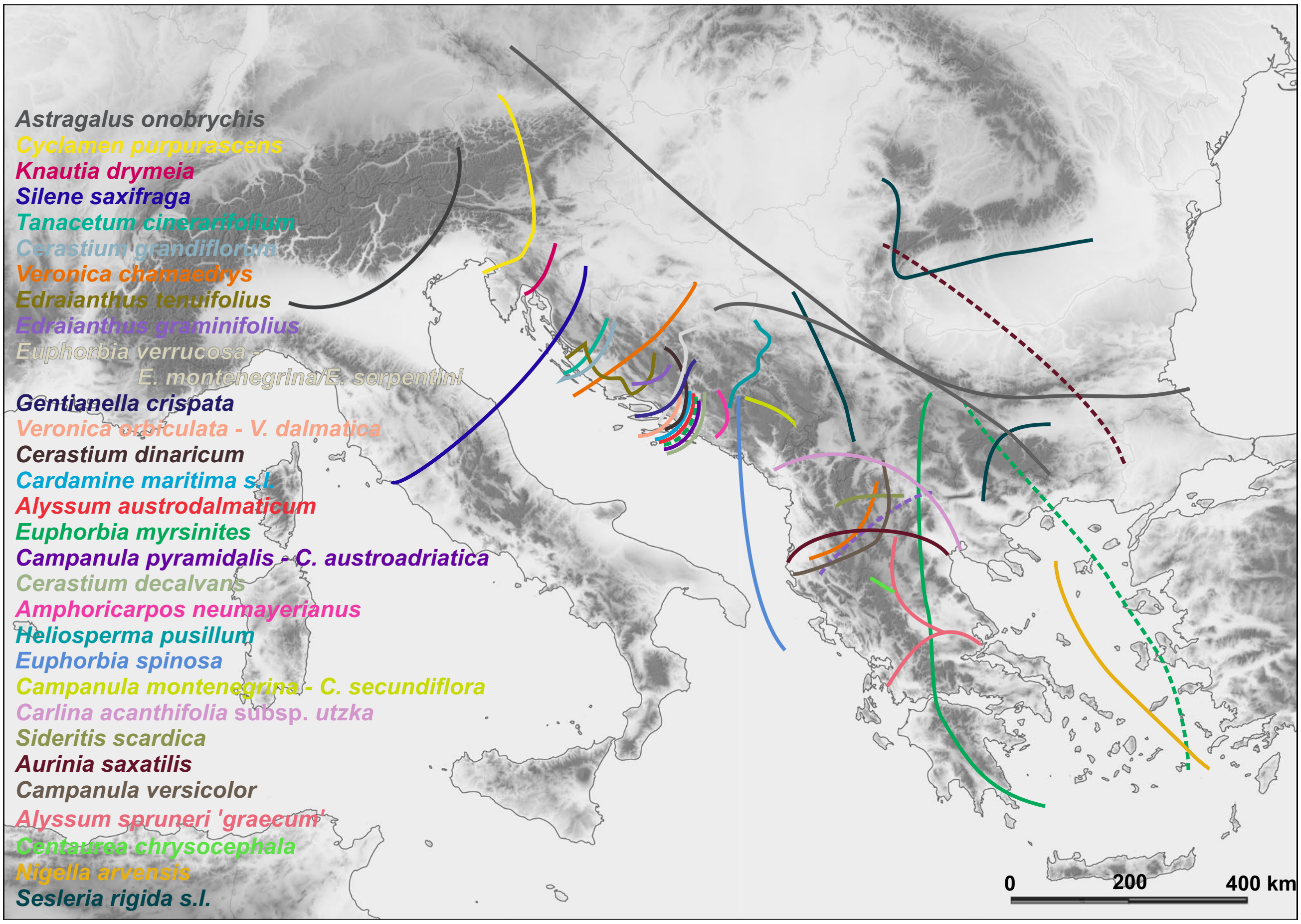

Fig. 5 Phylogeographic (intraspecific) genetic breaks observed in selected case studies. The coloring of the names of plant taxa on the left corresponds to their observed genetic breaks. The plant taxa are listed from north to south following the pattern of the breaks from north to south. The selected case studies include *Astragalus onobrychis* (Záveská et al. 2019), *Cyclamen purpurascens* (Slovák et al. 2012), *Knautia drymeia* (Rešetnik et al. 2016b), *Silene saxifraga* (Đurović et al. 2017), *Tanacetum cinerariifolium* (Grdiša et al. 2014), *Cerastium grandiflorum* (Đurović et al. 2021), *Veronica chamaedrys* (Bardy et al. 2010), *Edraianthus tenuifolius* (Surina et al. 2011), *Edraianthus graminifolius* (Surina et al. 2014b), *Euphorbia verrucosa—E. montenegrina/E. serpentini* (Cresti et al. 2019; Caković et al. 2021), *Gentianella crispata* (Reich et al. 2021), *Veronica orbiculata—V. dalmatica* (Rojas-Andrés et al. 2015), *Cerastium dinaricum* (Kutnjak et al. 2014; Đurović et al. 2021), *Cardamine maritima* s.l. (Kučera et al. 2010), *Alyssum austrodalmaticum* (Zozomová-Lihová et al. 2020), *Euphorbia myrsinites* (Falch et al. 2019), *Campanula pyramidalis—C. austroadriatica* (Lakušić et al. 2013), *Cerastium decalvans* (Đurović et al. 2021), *Amphoricarpos neumayerianus* (Caković et al. 2015), *Heliosperma pusillum* (Frajman and Oxelman 2007), *Euphorbia spinosa* (Stevanoski et al. 2020), *Campanula montenegrina—C. secundiflora* (Janković et al. 2016), *Carlina acanthifolia* subsp. *utzka* (Cieślak and Drobniak 2019), *Sideritis scardica* (Grdiša et al. 2019), *Aurinia saxatilis* (Rešetnik et al. 2022), *Campanula versicolor* (Janković et al. 2019), *Alyssum spruneri 'graecum'* (Španiel et al. 2017a), *Centaurea chrysocephala* (López-Vinyallonga et al. 2015), *Nigella arvensis* (Jaros et al. 2018), and *Sesleria rigida* s.l. (Kuzmanović et al. 2013)

northernmost genetic break is seen in subalpine/alpine *Sideritis scardica* separating the northern populations in the Šar Planina range from south-eastern populations (Grdiša et al. 2019; Fig. 5). A similar clear phylogeographic break, separating Scardo-Pindhic populations from Dinaric and Rhodope-Rila populations, was detected in *Carlina acanthifolia* subsp. *utzka* (Cieślak and Drobniak 2019; Figs. 3c, 5). *Campanula versicolor* revealed a more southern split occurring between the North Macedonian vs. Greek and south Albanian mountains (Janković et al. 2019; Figs. 2b, 5). A comparable genetic break between North Macedonian and Greek mountains has been recorded in *Edraianthus graminifolius* (Surina et al. 2014b; Figs. 4b, 5). The southern lineage was suggested to originate from a (re)colonization from the central Balkan lineage early in species diversification history. An early- to mid-Pleistocene differentiation between the southern cluster and other more northerly Balkan clusters was proposed for *Aurinia saxatilis* (Rešetnik et al. 2022; Fig. 5) and *Veronica chamaedrys* group (Bardy et al. 2010; Figs. 3j, 5). The glaciated mountain ranges of northern Greece were suggested to have acted as strong barriers between lineages and contributed to the genetic isolation of the southern populations, which exhibited distributional stasis and lack of expansion.

Geographic isolation might have also contributed to profound allopatric differentiation within adjacent regions of Greece. For example, two closely related but clearly genetically different species, *Cyanus epirotus* and *C. pindicola,* occupy separate areas within the northern Greek mountains, with the former species occurring in the southwestern part and the latter species occurring in the north-central part (Olšavská et al. 2016). The mountainous character of Greece likely fostered the occurrence of three allopatric clusters within the *Alyssum spruneri* subgroup *'graecum'* as a result of limited gene flow and previous isolation in regional refugia (Španiel et al. 2017a; Fig. 5). The genetic split occurring in central Greece separated western from eastern populations, while the second split on the northern side of Sterea Ellas separated the southern populations. A similar pattern caused by long-term geographic isolation was documented in *Cardamine acris,* which includes three allopatric subspecies: *C. acris* subsp. *acris* in northern and eastern Greece (and more northerly regions of the Balkans), *C. acris* subsp. *pindicola* in the northern Pindhos Mountains, and *C. acris* subsp. *vardousiae* in Sterea Ellas (Perný et al. 2004; Šlenker et al. 2021). The main genetic break running through central Greece and south-eastern North Macedonia is seen in the continuous distribution of *Euphorbia myrsinites* (Falch et al. 2019; Figs. 2e, 5). The spatial proximity of divergent lineages is also visible in *Centaurea chrysocephala,* with two genetic clusters being separated by the Pineios River gorge (López-Vinyallonga et al. 2015; Fig. 5). Overall, the local mountain ranges and adjacent valleys and gorges are postulated to have acted as dispersal barriers. However, the forest taxon *Helleborus odorus* subsp. *cyclophyllus*, despite being confined to fragmented and mountainous areas of mainland Greece, shows relatively low genetic differentiation between populations in the western part (Pindos range) of the area, indicating gene flow and more continuous distribution in the recent past (Fassou et al. 2021). The populations of eastern and southern Greece were more differentiated, which was likely due to more effective isolation by extensive plains. A fine geographic-genetic structure can also be found within the Peloponnese, coinciding with known centers of endemism (Kougioumoutzis et al. 2021). *Cymbalaria spetae* which is endemic to Taigetos is genetically and morphologically different from the closely related *C. microcalyx* sampled in other parts of the Peloponnese (Carnicero et al. 2021). Similarly, a population of *Juniperus drupacea* from Taigetos genetically differs from other populations in the nearby Parnon Mountain area (Sobierajska et al. 2016).

Eastern Balkan Peninsula

The eastern and south-eastern parts of the Balkan Peninsula are grossly understudied and usually represented by only a few sporadic populations, which hampers the inference of detailed phylogeographic patterns and processes in the area. A rare more detailed study identified four allopatrically distributed and genetically divergent entities within *Sesleria rigida* s.l. (Kuzmanović et al. 2013; Figs. 3h, 5). The borders between the lineages correspond to the lowland geographical borders between the mountain ranges, i.e., the central group is positioned on the Balkan mountain range (Stara Planina) and adjacent areas, while the northern group is on the Carpathians, the eastern is on the Rhodope massif, while the genetic split coincides with the Morava plain and separates populations on the Dinaric Mountains to the west. Distinct genetic lineages occupying adjacent—but mostly separate—geographical areas in the eastern and central Balkans were detected in the *Cyanus tuberosus* group (Skokanová et al. 2019a). The study revealed that the groups extensively radiated into nine nearly allopatric genetic lineages corresponding to separate species or subspecies. They are morphologically differentiated and their distribution ranges correspond to major mountain ranges in Bulgaria, northern Greece, North Macedonia and southern Serbia. Several populations in secondary contact zones of the taxa (the Rila Mountains, Babuna Mountains and Kožuf Mountains) showed traces of genetic admixture that also manifested in morphology and genome size (Olšavská et al. 2016). The eastern borders of the Rhodope Mountains also harbor highly admixed populations between the central Balkan and Carpathian-central European lineages of *Aurinia saxatilis* (Rešetnik et al. 2022; Fig. 5). Within a single mountain range the topology of the Rhodope massif was suggested to have acted as a barrier that separated the Bulgarian populations of *Haberlea rhodopensis* situated on the northern flanks from the Greek populations on the southern flanks (Petrova et al. 2015). The two groups were likely separated during the LGM after having migrated downslope from the mountains on opposite sites in valleys belonging to different river catchment areas.

Glacial refugia and their genetic imprints

An examination of available dated phylogenies reveals that the majority of genera in the area have diversified in the Miocene and Pliocene, which were characterized by intense tectonism and major climate shifts (e.g., Oberprieler 2005; Mansion et al. 2008; Frajman et al. 2009; Roquet et al. 2009; Vargas et al. 2017). However, the differentiation within species and closely related species groups most likely occurred in response to Pleistocene glacial oscillations (e.g., Bardy et al. 2010; Caković et al. 2015; Frajman and Schönswetter 2017; Rešetnik et al. 2022).

The Balkan Peninsula was only partially affected by glaciation during the cold stages. Only the highest peaks were glaciated, with data indicating that the mean temperature in July during the LGM was approximately 5 °C lower than today, while the snow line was approximately 1000 m lower (Bognar and Prugovečki 1997). During the cold cycles, the climate was drier. At lower elevations, *Artemisa*-steppes elements thrived, while the highest diversity existed at middle elevations due to the higher air humidity (Willis 1994). The warmer interglacial periods were shorter and characterized by higher temperatures than at present (Kukla et al. 2002). Mild and more stable environment in the Balkan Peninsula during glacial cycles provided favorable conditions and refugia for many species that could not thrive in more northerly regions of Europe.

Multiple data confirm the "refugia-within-refugia" model (Gómez and Lunt 2007), i.e., the existence of multiple refugia in the Balkan Peninsula. The smaller, distinct, and isolated refugia mutually differed in their ecological variables and encompassed specific conditions that were important to the survival of diverse species. Within these refugia, the populations did not only survive and maintain genetic diversity but also became genetically differentiated. The Pleistocene climatic cycles caused repeated retreat-recolonization events that, coupled with periods of secondary contact between previously isolated lineages, had a marked impact on genetic diversity.

Species responded to such environmental changes individually with respect to their ecological features. Specifically, both high and low-elevation species encountered range fragmentation. The former encountered range fragmentation during the warmer but shorter interglacial periods, while the latter encountered it during the colder and longer glacial periods. As a result, low-elevation species are expected to show stronger phylogeographic signals and higher genetic differentiation than high-elevation species, as postulated by the "displacement refugia model" (Kropf et al. 2003). This hypothesis was investigated by Surina et al. (2011) for two Balkan species with different elevational preferences, growing in the same region and having similar reproductive and dispersal features. The authors proposed that cold-adapted species (*Edraianthus serpyllifolius*; Fig. 4c) experienced elevational range shifts, while the thermophilic species (*E. tenuifolius*) underwent latitudinal range shifts. However, in contrast to the displacement refugia hypothesis, the two elevationally differentiated species did not differ in their genetic diversity. Cold-adapted species likely had a more continuous distribution during cold stages, which was sufficient for gene flow to occur between different mountain ranges, which also enabled their retreat into disjunct, higher elevations during periods with a warmer climate. This scenario was confirmed for *Cerastium dinaricum* (Kutnjak et al. 2014; Đurović et al. 2021) and *Sideritis scardica* (Grdiša et al. 2019), while higher levels of genetic diversity were observed in the northern populations (Balkan Mountains) of *Haberlea rhodopensis*, with a decrease toward the southern populations (Greece) (Petrova et al. 2015). Glacial-induced small-scale migrations in neighboring mountains fostered the in situ survival of populations in habitats with refugial character, such as screes or rocky slopes facing the sea, deep sheltered valleys and river gorges (Thompson 2005) that remain occupied today in some cases (Caković et al. 2015). Seven taxa of the *Centaurea* subsect. *Phalolepis* in Greece have relatively low levels of genetic differentiation, which is likely the result of a recent postglacial fragmentation process; however, the taxa have meanwhile morphologically differentiated (López-Vinyallonga et al. 2015).

The latitudinal movements of more thermophilic groups are manifested through two main patterns of genetic differentiation. The first pattern presents the traditional southern richness-northern purity hypothesis (Hewitt 2000), which implies higher demographic stability and diversity in southern populations and a corresponding reduction of genetic variation in a clinical fashion toward the north (leading edge colonization pattern; Hewitt 2000). For example, Falch et al. (2019) suggested that the divergence in *Euphorbia myrsinites* is a result of postglacial northward colonization accompanied by strong genetic drift. Comparable genetic architecture was observed in *Edraianthus tenuifolius* (Surina et al. 2011) and Adriatic populations of *Salvia officinalis* (Rešetnik et al. 2016a). Similarly, the southern populations of *Onosma heterophylla* s.l. in southwestern Bulgaria displayed the highest diversity and divergence with decreased values toward the northern and eastern populations (Kolarčik et al. 2010). From their southern refugia some groups experienced rapid range expansion (i.e., *Silene saxifraga* group; Đurović et al. 2017 and genus *Knautia*; Frajman et al. 2016). On the contrary, within some lineages, distributional stasis and a lack of southern population expansion are evident (the southern lineages of *Aurinia saxatilis;* Rešetnik et al. 2022 and *Veronica chamaedrys;* Bardy et al. 2010). Comparably, the *Alyssum montanum*-*A. repens* complex shows high genetic and species diversity in the Balkans, but lacks expansion from this region to the north (Španiel et al. 2017a, b).

The second pattern of latitudinal differentiation of populations, but with equivalent and relatively high genetic diversity, confirms that glacial persistence in both the north-western and southern Balkans was documented in the phylogeographic studies of several taxa; for example, in the *Veronica chamaedrys* group (Bardy et al. 2010), *Viola suavis* s.l. (Mereďa et al. 2011) and *Arundo plinii* (Hardion et al. 2014). The two areas likely acted differently as refugia. While environmental conditions in the southern areas were more stable and more or less widespread, the favorable conditions in the north-western part were limited to geographically confined micro-locations that acted as ecological sanctuaries. The existence of the northerly located microrefugia in the western Balkans for the thermophilic *Tanacetum cinerariifolium* (Grdiša et al. 2014) was postulated to be the consequence of expansion from the southern parts of the Adriatic basin during the warmer last interglacial period (approximately 130,000 to 116,000 years ago). Especially Northern Adriatic populations are characterized by highest level of gene diversity, the number of private alleles and the frequency down-weighted marker values (DW; Schönswetter and Tribsch 2005) which decrease toward the southern boundary of the species range. The low genetic variability of these southern populations could be attributed to human-related activities, such as overexploitation and cultivation practices. Similar microrefugia along the northern Adriatic coast were proposed for *Campanula fenestrellata* (Rešetnik et al. 2020) and *Helichrysum italicum* (Ninčević et al. 2021).

The repeated alternations of climatic conditions facilitated lineage expansions from their refugia and enabled secondary contact among previously isolated populations. The mixing of different gene pools often resulted in increased genetic diversity and admixed patterns; for example, in *Veronica chamaedrys* (Bardy et al. 2010), *Tanacetum cinerariifolium* (Grdiša et al. 2014), and *Campanula fenestrellata* (Rešetnik et al. 2020). Within *Veronica chamaedrys* (Bardy et al. 2010) and *Knautia drymeia* (Rešetnik et al. 2016b), secondary contact and hybridization triggered polyploidization events (see below). Coupled with rapid range expansion the genetic legacy of secondary contact is also visible in the sharing of plastid haplotypes across widely distributed taxa, polymorphism observed in the ITS sequences and contemporary weak genetic differentiation (Frajman et al. 2016; Đurović et al. 2017).

Phylogeographic patterns in the Balkan Peninsula and adjacent areas

The Balkans as a source for the colonization of northerly regions

There are various phylogeographic studies in which genetic diversity patterns support the hypothesis that the Balkans served as a glacial refugium for many taxa and served as a source for the postglacial colonization of central and northern Europe. A retreat of biota to the south and their postglacial migration from the Balkan Peninsula toward the north (or even repeated migration during Pleistocene climatic cycles) could have been affected by the presence of mountain ranges representing topographic obstacles at least for some species. However, for other taxa—especially trees—lowlands such as the Pannonian and Lower Danubian plain also could have served as barriers to migration (Magri et al. 2006). The role of particular parts of the Balkans as refugia for trees and a source for their postglacial colonization of more northerly regions was recently reviewed and discussed by Gömöry et al. (2020). Therefore, the details will not be repeated here. However, similarities and connections with the biogeographic history of understory herbs are worth noting. For instance, the north-western Dinaric Mountains served as one of the major refugia for beech (*Fagus sylvatica*; Magri et al. 2006) and hornbeam (*Carpinus betulus*; Postolache et al. 2017). A similar pattern was detected in the forest understory herb *Cyclamen purpurascens* (Slovák et al. 2012). The refugia of the west Pannonian, Moravian (a region in the east of the Czech Republic) and easternmost Alpine populations of the latter species were likely placed in the north-western Dinaric Mountains, from where they also postglacially spread to the eastern Dinaric Mountains in Bosnia and Herzegovina and Serbia (Slovák et al. 2012). Northern Dinaric glacial refugia were suggested for many other forest herbs (Willner et al. 2009), as evidenced specifically in *Cerastium sylvaticum* (Skubic et al. 2018), *Euphorbia amygdaloides* (Caković and Frajman 2020), *Helleborus niger* (Záveská et al. 2021; Fig. 3f), *Knautia drymeia* (Rešetnik et al. 2016b; Fig. 3g), *Polygonatum verticillatum* (Kramp et al. 2009), *Ranunculus auricomus* (Paule et al. 2018), *Veronica chamaedrys* (Bardy et al. 2010), but also a temperate grassland species *Euphorbia verrucosa* (Caković et al. 2021) and *Tephroseris longifolia* subsp. *longifolia* and *T. longifolia* subsp. *moravica*, both growing in forest margins and mesotrophic grasslands (Skokanová et al. 2019b).

The Balkan origin of non-Balkan populations was detected in several other taxa. In the *Heliosperma pusillum* complex, Alpine populations showed an expected genetic affinity to adjacent northern Dinaric populations in Slovenia, while the Carpathians were likely colonized from refugia in the eastern margins of the Dinaric Mountains (Frajman and Oxelman 2007). *Cherleria garckeana*, the sister species of the Alpine calcifuge *Ch. laricifolia* subsp. *laricifolia*, is confined to the southern part of the Balkan Peninsula where it grows on serpentine, calcareous, and siliceous substrates; however, its exact colonization route is uncertain (Moore and Kadereit 2013; Moore et al. 2021). Interestingly, the Apennine serpentine *Ch. laricifolia* subsp. *ophiolitica* neither came directly from the Balkans nor contributed to the colonization of the Alps. Instead, it originated from calcifuge *Ch. laricifolia* populations of the Maritime Alps. Two other *Cherleria species*, both calcicole, likely colonized the Alps via two different routes: *Ch. capillacea* first colonized the southern Alps and then the western Alps from the western part of the Balkan Peninsula, whereas *Ch. langii* likely colonized the northern Alps from the Carpathians (Moore and Kadereit 2013). In *Wulfenia carinthiaca*, the Alpine-Dinaric disjunction can be explained either as a result of fragmentation of the previously larger species range or as a consequence of long-distance dispersal, which seems to be more probable based on genetic patterns (Surina et al. 2014a). Notably, the eastern Alpine *Ranunculus crenatus* originated from immigration from populations in the Bosnian mountains (Kuzmanović et al. 2021). Another example of the biogeographic relationship between the Bosnian mountains and eastern Alps is seen in geographic range of *Cirsium greimleri* (Bureš et al. 2018). Relatively recent (Pleistocene) long-distance dispersal from the Balkan Peninsula was suggested for the western Alpine endemic *Alyssum cognense* (Španiel et al., 2022). A biogeographic relationship between the Balkans and the Alps was also documented by eastern Alpine *Alyssum neglectum* and central Dinaric *A. bosniacum* (Magauer et al. 2014; Zozomová-Lihová et al. 2014; Španiel et al. 2017a, b) or eastern Alpine *Androsace hausmanni* and Montenegrian *A. komovensis* (Schönswetter and Schneeweiss 2009). However, the biogeographic pattern in *Androsace* seems to be the result of an ancestral range expansion from the center of diversity in the European Alps into the Balkan Peninsula rather than the consequence of colonization in the opposite direction (Schönswetter and Schneeweiss 2009).

Some taxa that presently occur in both northern and southern European regions, survived glacial periods in the Balkans and more northerly non-Balkan refugia. In such cases, Balkan populations might not have contributed to the postglacial colonization of adjacent northern regions that were occupied by populations persisting during the glacial cycles in situ. For example, *Atriplex tatarica* survived the LGM in an eastern Balkan refugium and a more northerly refugium in the Pannonian Basin (Hodková et al. 2019). While it expanded from these refugia approximately 7000 years ago, the massive colonization of central Europe only occurred hundreds of years ago with the unintentional contribution of humans. In *Carlina acanthifolia* subsp. *utzka*, the populations from the southern Balkans (Scardo-Pindhic range) obviously did not contribute to the colonization of central Europe, whereas the populations from the northern Balkans (Dinaric) and Rhodope-Rila populations share genetic variation with central and eastern European populations. It is hypothesized that they survived the glacial periods not only in the northern Balkans but also in local central and eastern European refugia (Cieślak and Drobniak 2019). The three main geographically distinct lineages of *Aurinia saxatilis* diverged in early to middle Pleistocene and likely survived glaciations in different Balkan and non-Balkan refugia (Rešetnik et al. 2022). While the southern Balkan lineage stably persisted in situ over time without expansion to the north, the central Balkan lineage gave rise to east Balkan-Carpathian populations through an old founder event. Subsequently, the east Balkan-Carpathian populations contributed as ancestral populations to establishment of central European populations. All these central Balkan to central European populations likely survived glacial cycles in separate small refugia in the central and eastern Balkans and southern margins of the Carpathians. It is assumed that five out of six detected genetic lineages of *Eryngium alpinum* survived glaciations in a southwestern Alpine refugium and repeatedly colonized the entire Alpine arc at different periods. The sixth lineage—highly divergent from the other ones—was found in the Dinaric Mountains, where it likely persisted during the last glaciations but did not postglacially influence the genetic variation of the populations in the Alpine part of its distribution area (Naciri and Gaudeul 2007). Populations of *Doronicum austriacum* from Bulgaria and North Macedonia form a separate genetic lineage that is strongly divergent from populations in the Carpathians where the species survived at least the most recent climatic oscillations of the Quaternary (Stachurska-Swakoń et al. 2020). Similarly, the previously hypothesized postglacial influence of the Balkan gene pool on the more northerly lineages of *Campanula alpina* s.l., including the not so-distant Southern Carpathian populations, was rejected (Ronikier and Zalewska-Gałosz 2014). The subalpine *Cardamine rivularis* currently occurs in the Southern Carpathians and mountains of Bulgaria. Although the origin of this disjunction is unknown (more recent dispersal or ancient range fragmentation), the recently discovered genome size divergence between the Romanian and Bulgarian populations indicates their long-term evolution in allopatry (Melichárková et al. 2020). A common pattern detected in many herbs is the genetic similarity between populations from the northern Balkans and the southern and eastern Carpathians, whereas the western Carpathian populations are usually genetically distinct. Such a phylogeographic structure was detected in *Arabidopsis arenosa*, *Cicerbita alpina,* and *Ranunculus platanifolius* (Stachurska-Swakoń et al. 2012, 2013; Kolář et al. 2016). In *A. arenosa*, two different central European lineages (Pannonian and west Carpathian) show elevated genetic diversity in present-day populations, which suggests their glacial persistence within the area of their current distribution. A lineage of *A. arenosa* from the Dinaric Mountains is genetically distinct and did not contribute to the postglacial colonization of more northern regions, whereas eastern Balkan populations form a common lineage with populations from the southern and eastern Carpathians. Additionally, there is an indication that the latter lineage and the western Carpathian lineage together (after hybridization) colonized disjunct localities on the Baltic coast (Kolář et al. 2016). The combined role of Balkan and more northerly (Alpine and Western Carpathian) refugia in the postglacial colonization of central Europe was inferred also for *Rosa pendulina* (Daneck et al. 2016).

In some species groups, the Balkan populations did not postglacially colonize central Europe but influenced the genetic diversity of the present-day northern populations and taxa via hybridization during glacial or postglacial periods. For example, it is assumed that the Alpine *Pilosella alpicola* s.str. is a result of hybridization between Alpine *P. glacialis* and Balkan *P. rhodopea*. The latter taxon likely underwent range expansion from its core area in the Balkans during favorable cold periods and hybridized with *P. glacialis* in the Alpine periglacial refugia or the area between the Alps and the Balkan mountains (Šingliarová et al. 2011). Similarly, a more complex evolutionary history was suggested for the current populations of the Carpathian-Alpine species *Alyssum repens*. Although this species does not occur in the Balkans at present, Carpathian allotetraploids show genetic affinities to the Balkan species *A. vernale*. This may be due to hybridization or a common ancestor (Melichárková et al. 2019).

Studies dealing with the Balkan glacial refugia of bryophytes and pteridophytes are rare and were mostly published two decades ago. For instance, the unique study of Trewick et al. (2002) focused on the rock fern *Asplenium ceterach* and suggested the colonization of more northern regions from the common Pannonian-Balkan refugium and an extensive refugium in Greece. In bryophytes, several studies have shown higher genetic variation in southern populations compared to northern, indicating their survival during the LGM in the south and postglacial colonization of the north (reviewed by Kyrkjeeide et al. 2012, 2014). Notably, only a handful of such studies pointed to Balkan refugia. For example, Cronberg (2000) indicated the existence of Greek glacial refugia for Scandinavian populations of the epiphytic moss *Leucodon sciuroides*. Hedderson and Nowell (2006) hypothesized that the bryophyte *Homalothecium sericeum* may have postglacially colonized northern Europe from refugia in the Apennine Peninsula and the Balkans. Similarly, the moss *Pleurochaete squarrosa* seems to have survived the LGM in the Balkan and Iberian Peninsulas and colonized central Europe from both regions (Grundmann et al. 2008). Natcheva and Cronberg (2003) did not find evidence of the peat moss *Sphagnum capillifolium* colonizing northern Europe from Balkan glacial refugia. Simulations based on the phylogeographic patterns of 15 bryophyte species by Ledent et al. (2019) challenged the general role of southern refugia in the postglacial colonization of more northerly regions and suggested a complex postglacial history involving a substantial contribution from populations of diverse geographic origin (not excepting their extra-European ranges). In contrast to the results of the aforementioned single-species studies, Ledent et al. (2019) concluded that the latter scenario is consistent with the globally balanced genetic diversities and extremely low divergence observed among biogeographic regions.

Balkan-Apennine connections

The distribution of the same or closely related taxa on both the western and eastern coasts of the Adriatic Sea can indicate the common evolutionary history of plants in the Apennine and Balkan Peninsulas. Based on chorological data, amphi-Adriatic disjunctions have been studied since the beginning of the twentieth century (Trotter 1912; Turrill 1929). Moreover, due to a number of molecular-based studies published over the last two decades, several biogeographical patterns have emerged.

First, some—if not majority—of trans-Adriatic disjunctions could be explained by a previous land connection between the two peninsulas during the MSC (5.96–5.33 Mya; Krijgsman et al. 1999) or by Pleistocene climatic fluctuations when the Adriatic Sea repeatedly retreated southwards (Correggiari et al. 1996). Nevertheless, some cases of amphi-Adriatic distribution could be attributed to long-distance dispersals across the sea at any period (Surina et al. 2014b; Rešetnik et al. 2016b; Cetlová et al. 2021). Only a few phylogeographic studies employed dating analyses to estimate the approximate timing of trans-Adriatic dispersals. For instance, the trans-Adriatic spread of closely related *Goniolimon* species (Buzurović et al. 2020) was hypothesized to have occurred during MSC. The late Messinian origin of a Balkan-Apennine disjunction was also hypothesized (but not inspected by dating analyses) for *Orchis palustris* (Musacchio et al. 2006). The phylogenetic split between two closely related endemic species, the Balkan *Campanula poscharskyana* and the Apennine *C. garganica* (Park et al. 2006), was estimated to have occurred during the early Pliocene (Frajman and Schneeweiss 2009). However, the vast majority of traceable cases (with dating analyses available) can be placed into the Pleistocene (see review in Frajman and Schönswetter 2017).

Second, an asymmetry in migration is observed since most trans-Adriatic dispersals are postulated to have occurred from the Balkan to the Apennine Peninsula. The reason could be the younger age of the Apennine Peninsula whose largest part was either an island or a peninsula of the Alps for a long period in the Tertiary (Meulenkamp et al. 2003; Frajman and Schönswetter 2017). Moreover, the Balkan Peninsula is larger and better connected to the rest of the continent and is thus expected to have higher species richness according to the classical island biogeography theory (MacArthur and Wilson 1967). Notably, the majority of available studies are based on species that have larger distributions in the Balkan Peninsula than in the Apennine Peninsula. Nevertheless, for *Euphorbia spinosa*—a species with a distribution of similar size on both peninsulas—dispersal from the Balkans to the Apennine Peninsula was also suggested (Stevanoski et al. 2020).

Third, in most cases, evidence for dispersal from the Balkans is supported by the higher genetic diversity of the Balkan populations. In a number of cases, the genetic differentiation of the Balkan populations is more pronounced, with the Adriatic Sea representing a weaker genetic barrier and the main genetic splits occurring among Balkan populations (Surina et al. 2014b; Rešetnik et al. 2016b; Falch et al. 2019; Stevanoski et al. 2020).

Fourth, independent dispersals within the same species and species groups have been inferred. For example, two separate trans-Adriatic dispersals were identified within the *Campanula garganica* group (Park et al. 2006; Frajman and Schneeweiss 2009), *Edraianthus graminifolius* (Surina et al. 2014b), and *Silene saxifraga* group (Đurović et al. 2017).

Finally, several geographically based patterns can be observed among the available phylogenies. The majority of Balkan–Apennine connections are restricted to their southern parts and display close relationships between southern Balkan lineages and southern to central Apennine populations as seen in *Abies alba* (Piotti et al. 2017), *Alyssum siculum* (Cetlová et al. 2021), *Aurinia saxatilis* (Rešetnik et al. 2022), *Campanula versicolor* (Janković et al. 2019; Fig. 2b), *Centaurea solstitialis* (Barker et al. 2017), *Euphorbia myrsinites* (Falch et al. 2019), *Genista sericea* (Vižintin et al. 2012), *Gymnospermium scipetarum* (Rosati et al. 2019), *Orchis palustris* (Musacchio et al. 2006), and the *Silene saxifraga* group (Đurović et al. 2017; Fig. 3i). Some connections encompass the central Dinaric and/or central Balkan populations and the central to the southern part of the Apennines; for example the *Cardamine maritima* group (Kučera et al. 2008, 2010), *Centaurea deusta* (Garcia-Jacas et al. 2019), *Euphorbia barrelieri* (Frajman and Schönswetter 2017), *Euphorbia spinosa* (Stevanovski et al. 2020; Fig. 2f), *Gentianella crispata* (Reich et al. 2021; Fig. 4d), *Silene ciliata* (Kyrkou et al. 2015), and the *Silene saxifraga* group (Đurović et al. 2017; Fig. 3i). The associations of the north Adriatic lineages to the central Apennines are seen in *Astragalus onobrychis* (Záveská et al. 2019; Fig. 3b), *Knautia drymeia* (Rešetnik et al. 2014; Fig. 3g), and *Onosma echioides* (Kolarčik et al. 2010), while connections to the northern Apennines are found in *Euphorbia verrucosa* (Cresti et al. 2019; Caković et al. 2021) and *Genista sericea* (Vižintin et al. 2012).

Pairs of closely related taxa revealed by molecular markers and separated by the Adriatic Sea also include the Sicilian *Cymbalaria pubescens* and Balkan *C. ebelii* (Carnicero et al. 2021), Apennine *Phyllolepidum rupestre* and Balkan-Anatolian *P. cyclocarpum* (Cecchi 2011), Apennine *Ranunculus magellensis* and Balkan *R. bertisceus* and *R. crenatus* (Kuzmanović et al. 2021) and Balkan *Veronica orbiculata* and Italian *V. orsiniana* (Rojas-Andrés et al. 2015).

Other examples of amphi-Adriatic disjunct distributions have not been studied using molecular markers to date, including those listed by Turrill (1929) and later authors, such as *Aegilops uniaristata* (Perrino 2011; Bogdanović et al. 2015), *Asyneuma limoniifolium* (Castroviejo et al. 2010), *Bromus parvispiculatus* (Karl and Scholz 2009), *Centaurea pumilio* (Greuter 2006), *Ephedra campylopoda* (Bianco et al. 1988), *Erica manipuliflora* (Valdés and Scholz 2009), *Helictotrichon convolutum* (Valdés and Scholz 2009), *Hellenocarum multiflorum* (Hand 2011), *Inula verbascifolia* (Greuter 2006), *Phlomis fruticosa* (Fanelli et al. 2015), *Ranunculus asiaticus* (Hörandl and Raab-Straube 2015), *Scrophularia lucida* (Marhold 2011b), *Sesleria juncifolia* (Di Pietro et al. 2005; Di Pietro and Wagensommer 2014), and *Umbilicus chloranthus* (Marhold 2011a). Gottschlich et al. (2017) listed five amphi-Adriatic species or pairs of geographically vicariant species in the genus *Hieracium*. Additionally, recent findings of Balkan (or eastern Mediterranean) taxa in Italy that were new to the known Italian flora, also contribute to the list of amphi-Adriatic distributions; for example *Alyssum doerfleri* (Bernardo et al. 2018), *Cerinthe retorta* (Wagensommer et al. 2014), *Gagea peduncularis* (Peruzzi and Caparelli 2007), *Hieracium umbrosum* subsp. *abietinum* (Gottschlich et al. 2017), *Linum elegans* (Wagensommer et al. 2017), *Poa jubata* (Brullo et al. 2019), and *Stipa crassiculmis* subsp. *picentina* (Kabaš et al. 2019). The opposite cases are rare, such as that of *Echinops siculus* Strobl (Conti et al. 2020), which was newly discovered in Corfu, Greece. However, in the absence of independent evidence from molecular data, the aforementioned examples must be interpreted with caution. For example, the phylogeographic study of the central Apennine species *Androsace mathildae* rejected the previous hypothesis about its amphi-Adriatic distribution and revealed that its single Balkan population belongs to another species with a biogeographical connection to the eastern Alps (Schönswetter and Schneeweiss 2009).

Balkans, Aegean region, and Asia Minor connections

The Balkan Peninsula borders one of the richest Asian regions in terms of biodiversity—the peninsular region of Anatolia, also known as Asia Minor. It is separated from the Balkans by the Black Sea, the narrow Marmara Sea and the Aegean Sea which is covered by a dense chain of islands. The current distribution of evolutionary lineages across the Aegean Sea and floristic similarities and differences between the Balkan Peninsula and Asia Minor were affected by the complex climatic and geological history of the Aegean Archipelago (Kougioumoutzis et al. 2017; Hammoud et al. 2021). Geological and paleoclimatic events promoted species divergence during the periods of range fragmentation, while plant migrations and colonization processes occurred during the periods of land connections (Simaiakis et al. 2017; Panitsa et al. 2018). The long history of human presence and influence in these regions could have been another important factor forming the species ranges (Hammoud et al., 2021). Although this phenomenon has not yet been sufficiently evaluated, humans had well-established seafaring between the Greek mainland and Aegean islands approximately 15,000 years before present (Laskaris et al. 2011).

The geographic distribution of taxa and genetic lineages in the Balkans, Aegean Archipelago, and Anatolia document their historic range dynamics. The Aegean Sea poses an effective barrier to Balkan-Anatolian (European-Asiatic) dispersal for many plant species (e.g., Greuter 1979; Runemark 1980; Strid 1996). This is manifested as the phytogeographical 'Rechinger's line' (cf. Strid 1996), which mostly corresponds to the MAT. This line intersects the Aegean Sea from northwest to southeast and is located between islands in the west (Cyclades, Levitha, Astypalea, Syrna, Karpathos, etc.) and east (Chios, Ikaria, Patmos, Leros, Kalymnos, Kos, Nisyros, Tilos, Rhodes, etc.), thereby constituting the phytogeographical borderline between Europe and Asia (Strid 1996).

The genetic break coinciding with Rechinger's line and the entire MAT has been found in the Aegean *Nigella arvensis* complex (Bittkau and Comes 2005; Jaros et al. 2018; Fig. 5). The sea barrier-induced vicariant speciation and bi-regional colonizations, as well as subsequent allopatric divergences occurring at different time scales throughout the Pleistocene, were proposed to have shaped genetic differentiation within the complex. The phylogeographic split following the MAT was also detected within the *Roucela* complex of the *Campanula* subgenus *Roucela* (Crowl et al. 2015). The separation of the western Aegean and eastern Aegean-Pontic populations of *Euphorbia myrsinites* similarly follows Rechinger's line with the continental extension going through the Rila-Rhodope mountain range (Falch et al. 2019; Figs. 2e, 5). The genetic differentiation between Balkan and Asian populations isolated by the Aegean Sea was evidenced in *Centaurea solstitialis* (Barker et al. 2017) and *Juniperus drupacea* (Sobierajska et al. 2016). The latter study also showed that Asian populations are characterized by a higher level of genetic diversity than Balkan populations. Some taxa occur on both sides of Rechinger's line because they were able to cross it in the past or more recently. A good example is the circum-Aegean genetic lineage in *Cymbalaria* and especially the case of *C. acutiloba* subsp. *dodekanesi* which occurs in both the western and eastern Aegean islands (Carnicero et al. 2017, 2021). The origin of the circum-Aegean distribution of *Alyssum smyrnaeum*, which occurs in the southern Greek mainland, Aegean Archipelago, and Anatolia (but also Crimea), is also worthy of a more detailed future investigation (Ilyinska et al. 2021).

However, land bridges formed—especially in the north—across the Marmara Sea, which allowed gene flow during different periods. Some studies based on phylogenetic inferences and floristic similarities have suggested a scenario of older migrations of Irano-Turanian elements into the Balkans during the late Tertiary (Thompson 2005; Manafzadeh et al. 2014). The biogeographic patterns revealed in *Bormuellera* (Özüdoğru and Mummenhoff 2020) indicate that this genus, which is disjunctly distributed in the Balkans and Anatolia, originated in the Asian portion of its range. The same study also suggested that the divergence between one particular Anatolian clade (comprising *B. cappadocica* and *B. kiyakii*) and the clade that includes all Balkan representatives occurred during the Plio-Pleistocene transition.

Based on paleobotanical evidence, Magyari et al. (2008) hypothesized that many plant taxa could have reached the Balkan Peninsula from Anatolia via the Thracian Plain during the Quarternary glacial period. A study of the arctic-alpine herb *Arabis alpina*, showed that related haplotypes, are distributed in both Anatolia and the southern Balkans with only negligible genetic differentiation (Ansell et al. 2011). It was inferred that the gene flow between the two regions was predominantly unidirectional (i.e., from Asia to Europe) and likely occurred during the Pleistocene glaciation periods, when the alpine habitats were presumably at lower elevations. The phylogeographic connection between the Balkans and Anatolia has been also recently documented in two annual Brassicaceae species *Microthlaspi erraticum* and *M. perfoliatum* (Ali et al. 2016, 2019), while the distribution of intraspecific genetic diversity of some plant and animal species between Anatolia and the Balkans was reviewed by Bilgin (2011).

Throughout the Aegean Archipelago, the genetic affinity between taxa and genetic lineages from the Greek mainland and western Aegean islands or Asia Minor and eastern Aegean can be documented by several examples. For instance, Carnicero et al. (2021) confirmed close relationships between populations of *Cymbalaria microcalyx* on Peloponnese (*C. m.* subsp. *microcalyx*) and Crete (*C. m.* subsp. *heterosepala*). They hypothesized that the Cretic populations came from Peloponnese during Pleistocene sea level oscillations. Similarly, *Alyssum siculum* occurs (besides in Sicily) on the Greek mainland and Crete and is missing eastwards. In contrast *Alyssum fulvescens* is known only from Anatolia and four eastern Aegean islands and does not occur in western Aegean islands or Balkan mainland (Strid 2016; Cetlová et al. 2021).

Processes driving the evolution and diversity of Balkan plants

Allopatric and ecological diversification

The high species and genetic richness of the Balkan Peninsula can be attributed to a variety of factors stemming from the complex paleoclimatic and geological history of this area. The most obvious and fundamental evolutionary process acting in topographically structured regions such as the Balkans is allopatric diversification. Spatial barriers to gene flow changed over time along with species ranges, which underwent periods of expansion and retreat as well as migration to new areas. Traces of these processes are visible as gaps in current species ranges, the geographic distributions of genetic lineages and phylogeographic links within the Balkans and between the Balkans and adjacent regions (Figs. 2, 3, 4, 5).

Besides allopatric diversification, spatiotemporal changes in species ranges may often be connected with ecological adaptations and environmental niche shifts. During allopatric diversification (and speciation) the genetic incompatibilities between geographically isolated populations may develop purely by genetic drift or founder effects, but also by other processes including adaptation to different niches (Mayr 1942, 1947). The adaptation to different environmental niches is even more important in sympatric or parapatric models of diversification. In these models, a continuous population that is distributed in an area with wide range of environmental conditions (e.g., along an altitudinal gradient) is divided in subpopulations that locally adapt to different niches and the original subpopulations become ecologically differentiated due to non-random mating and the formation of reproductive barriers (Schluter 2000; Simpson 1953). Scientific research focused on the ecological niches of Balkan plant taxa and their evolutionary significance remains scarce. Here, we summarize examples of various studies focusing on Balkan taxa in which ecological niche conservatism or shift, habitat differences, and ecological adaptations can be considered as possible causes of observed genetic variation, the diversification of lineages, and speciation.

A study of the genetic diversity and structure of *Tanacetum cinerariifolium* in Croatia revealed that genetic differentiation among populations was more strongly shaped by the environmental (bioclimatic) conditions of the sampling sites than by geographic distance (Grdiša et al. 2014). A study of the genetic diversity and structure of *Helichrysum italicum* along the eastern Adriatic environmental gradient revealed a certain association between genetic variation and bioclimatic variables, which suggests ongoing local adaptation and divergence (Ninčević et al. 2021). A study of the genetic variation and its ecological correlates in populations of *Fraxinus angustifolia* from environmentally divergent habitats in Croatia suggested that environmental differences between regions may have led to a subdivision into two ecotypes: continental and Mediterranean (Temunović et al. 2012). Additionally, the pronounced environmental heterogeneity in the Mediterranean region promoted the further genetic differentiation of coastal populations. In contrast, a study of the Mediterranean *Astragalus* section *Tragacantha* demonstrated that—contrary to what was widely claimed by previous authors—range fragmentation and geographic isolation were the main drivers of diversification in the group rather than a coastal-to-mountain ecological shift (Hardion et al 2016).

Habitat-related adaptations may affect the overall distribution and range limits of species. Grdiša et al. (2019) studied the association between genetic markers and bioclimatic variables in populations of *Sideritis scardica* in northern Greece and North Macedonia. They concluded that variables related to precipitation might have a key role in the adaptive genetic variation of this taxon. A comparison of habitat preferences among the closely related species *Euphorbia montenegrina*, *E. serpentini,* and *E. verrucosa* also inspired speculations regarding the association between ecological niches and the spatiotemporal dynamics of species ranges (Caković et al. 2021). The authors of the latter study hypothesized that the adaptation of *E. verrucosa* to mesic grasslands might be the reason why the species expanded its range from Balkan Pleistocene refugia, which was likely in connection with the human-mediated deforestation occurring over the last several thousand years. This is in contrast with the limited geographic distributions of *E. montenegrina* restricted to alpine grasslands and *E. serpentini* inhabiting naturally forest-free areas or open forest serpentine outcrops. It seems that such habitat specificity might have represented a constraint that hampered the substantial range expansion of these taxa during Pleistocene oscillations, and they remained in their current areas over longer periods while isolated by forests (Caković et al. 2021). In some cases, the ecological divergence between closely related and interbreeding taxa can be one of a few factors preventing their complete genetic homogenization, as hypothesized for the three species *Veronica barrelieri*, *V. orchidea,* and *V. spicata*, which are connected by numerous gradual genotypic transitions, but differ in their ecological preferences (Bardy et al. 2011; Buono et al. 2021). Certain differences in ecological niches were recently detected between *Campanula fenestrellata* subsp. *istriaca* and *C. f.* subsp. *fenestrellata*, two parapatric taxa that are clearly differentiated morphologically, but do not differ genetically (Rešetnik et al. 2020). Two allopatric but genetically and morphologically close taxa of the *Edrianthus tenuifolius* complex clearly differ in their ecology: *E. dalmaticus* frequently occurs in the flooded karst meadows of the central Dinaric Mountains, whereas *E.*

serbicus inhabits rocky limestone grounds and crevices in eastern Serbia and western Bulgaria (Stefanović et al. 2008). Although the current data are not conclusive with respect to the role of ecological adaptation, the evolutionary context of their different ecological preferences seems worthy of future research. Climatic niche analyses of the closely related *Euphorbia niciciana* and *E. seguieriana* revealed that they occupy different niches (Frajman et al. 2019). However, these differences are negligible when compared to the climatic differences between the regions over which they are distributed, thereby indicating the lack of ecological contribution to their speciation.

An important environmental factor shaping Balkan species diversity and evolution is bedrock type. For instance, many species are adapted to serpentine rocks and ultramafic soils, with as many as 335 Balkan taxa being considered serpentine endemics (Stevanović et al. 2003). These numbers might be partly overestimated given the rarity of studies that provide unambiguous genetic or morphometric evidence of differentiation between serpentine taxa and their non-serpentine counterparts, especially in more complicated and widespread species groups. A study of Greek populations of the *Alyssum montanum-repens* complex disproved the separate taxonomic status of the putative serpentine endemics *A. densistellatum* and *A. vourinonese,* which instead fell within the genetic variation of *A. spruneri* growing on both serpentine and calcareous substrates (Španiel et al. 2017a, b). Similarly, populations of *Arabidopsis arenosa* from neutral/siliceous sites did not genetically differ from populations growing on calcareous sites, thereby indicating that different substrates did not play a substantial role in the diversification of this group within the Balkan Peninsula and other parts of Europe (Kolář et al. 2016). On the other hand, *Sesleria serbica* (Kuzmanović et al. 2013) and *Euphorbia serpentini* (Caković et al. 2021) were confirmed as obligate serpentinophytes that were clearly genetically differentiated from their closest Balkan relatives. Similar conclusions were made based on genetic analyses of the Balkan serpentine endemics *Minuartia dirphya* and *M. baldaccii* and the facultative serpentinophyte *M. garckeana* which is primarily found on serpentine but can also grow on other substrate types (Moore and Kadereit 2013). Separate taxonomic status was also recently advocated for the serpentine endemics *Odontarrhena baldaccii* and *O. stridii* (Cecchi et al. 2020).

Some studies have forecasted future distribution of Balkan species based on examination of their ecological niches. Such studies are especially timely during this period of global warming, when climate conditions in vast regions of Europe, including the Balkan Peninsula, are changing at an unprecedented pace and could affect species ranges or even lead to extinctions in the near future (Thomas et al. 2006; Hoffmann and Sgro 2011; Duffy and Jacquemyn 2019). Global warming could notably influence high-elevation species in mountains of northern hemisphere via rise in air temperature, occurrence of drought and heat wave episodes, changes in water vapor content, duration of snowpack, and atmospheric nitrogen deposition (Kosonen et al. 2019; Körner and Hiltbrunner 2021). Although the alpine flora appears relatively resilient against global warming due to the range of thermal niches that the alpine environment provides, certain habitat types will shrink considerably (Körner and Hiltbrunner 2021). Indeed, as isotherms will move upslope, the possibilities for upward elevational migrations of some species (and in some mountains) will be very limited. One of the few studies that attempted to anticipate the consequences of current climate warming on Balkan flora predicted that cold-adapted high-alpine species such as *Cerastium dinaricum* will likely face a substantial decrease in suitable habitats followed by range-wide extinction within the next several decades (Kutnjak et al. 2014; Đurović et al. 2021). A decrease in habitat suitability and large range contractions were also indicated for mesophilous *C. decalvans* (Đurović et al. 2021). On the other hand, a small decrease in habitat suitability coupled with the shifting and expansion of favorable habitat toward the northwest was forecasted for thermophilous *C. grandiflorum* (Đurović et al. 2021).

Polyploidy and hybridization

Polyploidy, whole-genome duplication, or the presence of more than two complete sets of chromosomes in the cell nucleus, has a crucial role in the evolution of flowering plants (Otto 2007; Soltis et al. 2015). It enriches cytotype variation within a species, creates an immediate reproductive isolation and acts as an effective mechanism of sympatric speciation (Otto and Whitton 2000; Wood et al. 2009). Autopolyploids, originating from genetically identical or very similar individuals of the same species, were considered less common than allopolyploids, whose origin is accompanied by hybridization between different species or conspecific divergent populations (Ramsey and Schemske 1998; Harlan and De Wet 1975; Tate et al. 2005; Soltis et al. 2014).

Recently, many cases of both auto- and allopolyploid formation in Balkan species have been revealed. Some authors argued that the rate of autopolyploid formation could be higher than previously anticipated (Soltis et al. 2007), but currently available data do not allow definite conclusions on the relative abundance of auto- and allopolyploids (Barker et al. 2016). Balkan tetraploids of *Veronica chamaedrys* were mostly formed by autopolyploidy and independently emerged several times in each of the detected genetic groups (Bardy et al. 2010). Although the latter study detected the genetically admixed state of many tetraploid individuals, this could not be conclusively explained by allopolyploidy because it may also have resulted from crosses at the tetraploid level. A single detected tetraploid population of another Balkan taxon *Euphorbia spinosa* subsp. *glabriflora* was genetically very similar to the geographically close diploids, which confirms its autopolyploid origin (Stevanoski et al. 2020). Within the taxa distributed in the Balkan Peninsula, an autopolyploid origin was also recently suggested for tetraploids of *Astragalus onobrychis* (Záveská et al. 2019), *Cyanus pindicola* (Olšavská et al. 2016), *Dianthus sylvestris* (Terlević et al. 2022), *Euphorbia verrucosa* (Cresti et al. 2019), *Knautia drymeia* (Rešetnik et al. 2016b), polyploids of *Pilosella rhodopea* (Šingliarová et al. 2011), octoploids of *Cerastium grandiflorum* (Đurović et al. 2021) and *Sesleria filifolia* (Kuzmanović et al. 2013). Both auto- and allopolyploid origins were detected in *Veronica*. Autopolyploid origin was inferred for Balkan tetraploids of *Veronica longifolia* (Buono et al. 2021), *V. orbiculata* (Rojas-Andrés et al. 2015) and *V. spicata* (Bardy et al. 2011). This was in contrast to tetraploids of *V. barrelieri* and *V. orchidea* which most likely originated via allopolyploidization involving distinct diploid lineages (Bardy et al. 2011). Allopolyploidization events were also recently confirmed in the *Veronica* subsection *Pentasepalae* (López-González et al. 2021). Taxonomically uncertain tetraploids of this group originated via allopolyploidization from diploid *V. orbiculata* and *V. dalmatica* as putative parents and these tetraploids likely hybridized with *V. dalmatica* to form the allohexaploid taxon *V. austriaca* subsp. *jacquinii* (López-González et al. 2021). Both auto- and allopolyploid origins were detected in a molecular-cytogenetic study of eight taxa of the genus *Bellevalia* occurring in Greece (Bareka et al. 2012). An allopolyploid origin was also recently inferred for Greek stenoendemic *Cardamine barbaraeoides* whose parental species include (1) common ancestors of the widespread European *C. amara* and Anatolian *C. lazica* and (2) ancestors of Balkan *C. acris* and a western Anatolian taxon provisionally assigned to *C. uliginosa* (Šlenker et al. 2021). The Balkan taxon *Pilosella rhodopea* contributed to the polytopic allopolyploid formation of the Alpine *P. alpicola* s.str. by hybridization with the Alpine *P. glacialis* as the second parent (Šingliarová et al. 2011). Crowl et al. (2017) suggested the allopolyploid origin of the octoploid lineage of *Campanula erinus* derived from hybridization between tetraploid *C. erinus* and tetraploid *C. creutzburgii,* with the latter species likely being the maternal parent. The octoploid represents an example of cryptic diversity since it is morphologically unrecognizable from tetraploid *C. erinus*. Additionally, the authors of the study hypothesized that the *C. erinus*-*C. creutzburgii* hybridization event may have occurred during the MSC when species ranges may have been different from now, thereby enabling contact between the two currently allopatric progenitors (Crowl et al. 2017). Hybridization events associated with allopolyploidization were also detected in the Balkan polymorphic species *Alyssum spruneri* (Španiel et al. 2017a, b), which is in agreement with the prevailing allopolyploidy of the *A. montanum*-*A. repens* group in other parts of Europe (Melichárková et al. 2017, 2019). Balkan diploid representatives ($2n = 48$) of the genus *Ramonda* (*R. nathaliae* and *R. myconi*) are considered diploidized paleotetraploids since the basic chromosome number ($x = 24$) in the genus is quite high (Rakić et al. 2014). Hexaploid *Ramonda serbica* ($2n = 144$) hybridizes with diploid *R. nathaliae* in a sympatric contact zone to form hybrid tetraploid individuals ($2n = 96$; Siljak-Yakovlev et al. 2008). In the case of *Cymbalaria microcalyx* and related taxa, further research is required to reveal the origin of tetraploids, differentiate between auto- and allopolyploidy and identify the parental taxa involved (Carnicero et al. 2017, 2021). Similarly, in *Knautia* sect. *Trichera*, weak genetic differentiation among taxa hampers the identification of the auto- or allopolyploidization events involved in the origin of polyploids (Frajman et al. 2016). Tetraploids occurring in the central part of the distribution area of *Alyssum austrodalmaticum* originated by allopolyploidization following the secondary contact of two groups of diploids previously isolated in north-western and south-eastern Adriatic areas (Zozomová-Lihová et al. 2020; Fig. 2a). The origin of tetraploids in the southern part of this species range is less clear. It involved southern diploids, the aforementioned central tetraploids (directly or through later introgression) or even other Balkan relatives. Allopolyploidization events were also involved in the origin of three tetraploid and two hexaploid annual species of *Alyssum* occurring in the Balkans and the Aegean (Cetlová et al. 2021).

The distribution patterns of several of these species tentatively corroborate the hypothesis that (allo)polyploids, which harbor more genetic variation, can become successful colonizers with larger distribution areas or even wider ecological niches than diploids (Ramsey 2011; Soltis et al. 2014; Arrigo et al. 2016; Maguilla et al. 2021). Indeed, this hypothesis is also indirectly supported by estimates of the frequency of polyploids among Greek endemics: 10% polyploids among the single-mountain endemics, 15% among the single-area endemics, and 40–48% among widespread species (Strid 1993; Strid et al. 2003). Arrigo et al. (2016) suggested that the assumption of higher colonization success among polyploids can be narrowed down to allopolyploids. They inferred that hybridization accompanying the formation of allopolyploids can increase the ability to colonize new environmental niches since allopolyploids show higher rates of niche evolution than autopolyploids and can occupy different climatic conditions than those of their diploid congeners. Enhanced dispersal abilities or increased ecological tolerances have also been hypothesized for allohexaploid *Veronica austriaca* subsp. *jacquinii* which has a wider distribution range in the Balkan Peninsula and Carpathians, while closely related diploid-tetraploid lineages of the *V.*

austriaca-*V. orbiculata* complex are mostly restricted to the west coast of the Balkans and adjacent mountains (López-González et al. 2021). Kuzmanović et al. (2013) observed that geographically and genetically close tetraploids and octoploids of *Sesleria filifolia* differed in elevation (ca 200 m a.s.l. versus 700 m a.s.l respectively) and habitat preferences (rock crevices in a gorge versus rocky grasslands on wind-exposed ridges respectively), indicating the higher tolerance of octoploids to habitats with stronger competition. The ecological differentiation of cytotypes, with high polyploids appearing better adapted to colder and wetter regions, has been recently detected in the *Veronica* subsection *Pentasepalae* (Rojas-Andrés et al. 2020). It is expected that future fine-scale analyses of detected coexisting cytotypes—especially in the western Balkans—could shed more light on the connection between polyploidy and ecological niche shifts (Rojas-Andrés et al. 2020). The niche expansion of tetraploids in comparison to conspecific diploids was detected in *Festuca amethystina*, with tetraploids occurring at lower elevations and in more diverse climates and having a larger potential range than diploids, and polyploidy was identified as a major driver of ecological and adaptive variation in this species (Kiedrzyński et al. 2021).

Apart from hybridizations directly associated with allopolyploidization events, homoploid hybridization also has a substantial effect on plant diversity (Yakimowski and Rieseberg 2014). Hybridization per se largely contributes to biological diversity and plays an important role in the evolution of plants (Abbott et al. 2013). Hybridization can increase biological diversity through heterosis (Chen 2013), the reinforcement of reproductive isolation (Hopkins 2013), adaptive introgression (Whitney et al. 2010; Suarez-Gonzalez et al. 2018), or even homoploid hybrid speciation (Abbott and Rieseberg 2012). On the other hand, it may have a damaging effect on existing species, genetic lineages, and populations through outbreeding depression (Lynch 1991), genetic swamping, and even the extinction of rare taxa and genotypes (Buerkle et al. 2003; Todesco et al. 2016). A recent study of *Cherleria* species revealed many hybridization events between lineages and species that came into contact on the Balkan Peninsula, including cases where the contemporary ranges of these species do not overlap (Moore et al. 2021). This study also suggested a positive effect of hybridization on the colonization abilities of the lineages and expansion of their niches to new substrates and areas. Interspecific hybridization is also quite common in *Knautia* where it largely blurs species boundaries and hinders efforts to find satisfactory taxonomic treatments (Rešetnik et al. 2014). Intermediate phenotypes were even detected between ecologically differentiated and morphologically distinct *Knautia* species, which suggests substantial rate of gene flow between taxa (Rešetnik et al. 2014). Similarly, hybrid swarms between *Veronica barrelieri*, *V. orchidea* and *V. spicata* were often previously misinterpreted as separate taxa (Bardy et al. 2011). Genetic data and crossing experiments detected the directional introgression from *V. spicata* to *V. longifolia* in areas where the distribution ranges of both species overlap (Buono et al. 2021). Nevertheless, it is hypothesized that the two species remain distinct due to their adaptations to different habitats (riparian habitats versus dry grasslands), partial spatial isolation, and the assumed decreased competitive ability of hybrids. Morphometric and molecular analyses detected natural hybridization between *Edraianthus tenuifolius* and *E. wettsteinii* subsp. *lovcenicus*, which has resulted in the morphologically intermediate intersectional hybrid *Edraianthus* × *lakusicii* known from a single locality in Montenegro (Lakušić et al. 2009). A previously reported assumed hybrid (Kuzmanović et al. 2017) resulting from hybridization between two octoploid taxa, *Sesleria kalnikensis* × *S. sadleriana*, was not confirmed by a recent investigation since only tetraploid individuals were discovered at presumed localities (Lazarević et al. 2015; Hodálová et al. 2020). An ancient hybrid origin was hypothesized for the recently described species *Cyanus vichrenensis* which displays genetic admixture with respect to *C. adamovicii* and *C. orbelicus* (Skokanová et al. 2019a). Traces of more recent hybridization supported by genome size, morphology and genetic data, were detected in several Balkan populations and taxa of the *Cyanus napulifer* group (Olšavská et al. 2016). Hybridization also played a role in some Balkan populations and taxa of the genus *Rubus* (Sochor et al. 2019). Moreover, hybridization was also implicated in the origin of the Greek *Onosma malkarmayorum* which displayed genetic affinity to *O. heterophylla* s.l. and *O. thracica*, as potential ancestors (Kolarčik et al. 2010).

Conclusions and future prospects

The studies summarized in this review demonstrate that the Balkan Peninsula, with its topographic complexity and diverse environmental conditions, can be considered a source for the diversification of lineages in situ and for other areas while also providing grounds for more intricate evolutionary phenomena (e.g., hybridization and polyploidization). Thus, the Balkan Peninsula provides an opportunity to explore the historic and ongoing evolutionary processes responsible for the complex phylogeographic patterns of plant species.

Despite a recent increase in the number of botanical studies (especially phylogeographic) dealing with Balkan plants, many scientific challenges remain. A good balance of thorough field work and molecular-based approaches appears essential for further progress in botanical research in this area. There are still obvious gaps in even geographic coverage of this region in phylogeographic studies. While much attention has been paid to the western half of the Balkans and the Dinaric Mountains, the eastern part of the region and the Balkan Mountains remain largely undersampled and unexplored. New data on phylogeographic patterns from this area could help to replace the patchy taxonomic knowledge and evolutionary history of many plant species. As shown in the reviewed studies, the in-depth investigation of genetic, morphological and ploidy level variation of species usually leads to substantial changes in taxonomic treatments. Given the high biodiversity of the Balkans, attaining a good representation of Balkan taxa in European-wide phylogenies is a highly advisable way to achieve sound and sustainable taxonomic concepts. Cooperative efforts on a larger geographical scale should be preferred over regional or national approaches. The major knowledge gap involves our lack of understanding of the phylogeographic connections between the Balkans and Anatolia, which is mostly due to insufficient sampling in the Asian part of the distribution area of taxa (Bilgin 2011). Studies focusing on species complexes sampled in both regions could help us better understand how the taxa and lineages from Asia Minor contributed to European biodiversity.

Current advances in molecular methods based on high-throughput next-generation sequencing (NGS) also largely extend the possibilities for further and more thorough scientific investigation of the evolutionary processes and patterns of Balkan flora. These methods allow researchers to obtain hundreds to thousands of single and low-copy nuclear loci and single-nucleotide polymorphisms, and represent powerful tools for addressing a wide range of evolutionary questions. NGS can be particularly useful when dealing with cases of low genetic divergence in rapidly evolving groups, hybridization, incomplete lineage sorting and intricate reticulate evolution (e.g., Schmickl et al. 2016; Rothfels et al. 2017; Karbstein et al. 2020; Larridon et al. 2020) which have been witnessed in many Balkan species complexes. These methods can bring new and deeper insights into the evolutionary history of Balkan plants and improve phylogenetic inferences, as already demonstrated by the recent studies (e.g., Crowl et al. 2017; Frajman et al. 2019; Buono et al. 2021; Moore et al. 2021; Šlenker et al. 2021; Rešetnik et al. 2022). Continuing and deepening the research of evolutionary patterns and processes and their taxonomic consequences has the potential to help us better understand why the Balkan Peninsula has become a biodiversity hotspot and how its unique flora can be conserved more effectively.

Overall, the discovery and description of Balkan biodiversity have been proceeding at a fluctuating pace for over 200 years (Strid 2020; Lack and Barina 2002). We are "standing on the shoulders of giants," but new sources of information will allow us to test (and if deem necessary, to reject and abandon) traditional hypotheses on taxonomy, biogeography and evolutionary trajectories. Current methodological and analytical advancements provide exciting possibilities for the transfer of traditional ideas over time while allowing scientific theories to be built, questioned, and refined.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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