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LOW ALTITUDE GLACIAL RELICTS IN THE ROMANIAN FLORA

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Abstract: Glacial relicts represent isolated populations of cold-adapted species, remnants of their past extensive distribution at southern latitudes that have survived *in situ* far from their current main areal since the Ice Age ended. We hereby aim to identify, based on a numerical evaluation that uses a scoring system applied for 14 ecological and biogeographic criteria, putative glacial relicts occurring in lowland wetlands from the Romanian part of the Carpathian Region. Our selection of (sub) species for evaluation includes mainly cold-adapted plants occurring in wetland areas of the intra-mountain depressions and peripheral lowland areas, while those occurring mostly in the high mountain areas of the Carpathians were excluded. As a result, of 171 evaluated taxa, 74 are considered to possess stronger lowland glacial relict features in the Romanian flora. Furthermore, based on the evaluation of their distribution in Romania, we highlight the hotspots of richness, rarity and range limit for these taxa. Both richness and rarity indices calculated for the 74 glacial relicts displayed the highest values in the Eastern Carpathians, probably linked to the wider development in this region of intra-mountain depressions harboring extensive wetlands. In addition, several potential refugia have been identified based on the distribution of very rare taxa in the north-eastern part of the Apuseni Mountains and the eastern part of the Southern Carpathians (Bucegi Mountains). The distribution of range limit populations of glacial relicts in Romania outlines two well-demarcated areas, one in the southern part of the Eastern Carpathians and the second in the western part of the Southern Carpathians, along deep intra-mountain valleys and depressions. Due to their limited, isolated distribution and the fragility of wetland habitats in which they occur, populations of glacial relicts are more prone to be affected by impacts generated by human activities and climate change. Therefore, our study can also serve as a useful tool for enhancing conservation efforts by highlighting the lowland wetland areas harboring a high number of cold-adapted relict populations that require careful monitoring and urgent protection measures.

Keywords: cold-adapted species, Carpathian Region, disjunct distribution, vascular plants, mires

Introduction

Distribution range dynamics of species across time has been strongly influenced by climatic oscillations [13, 35]. Both latitudinal and altitudinal range shifts have left traces of former distributions through the present-time existence of relict populations [1]. The term *relict* can have several meanings in biogeography, mainly referring to the distribution of species that were widespread and more adapted to the different climatic conditions from the past, and that currently survive in isolated populations outside their main areal, remnants of their former range [84]. More so, this is noticeable in cold-adapted plants, whose historical distribution imprints through remnant southern latitude or lower-altitude populations are evidence of their former areal during the colder climate, especially glacial periods [19]. The terms *glacial relict* or *arctic-alpine relict* are most often used for species adapted to cold climates from northern latitudes or high altitudes that were distributed in unglaciated areas from southern latitudes during the Glacial periods. Their survival was linked to areas with a more favorable climate than their surroundings [16]. Consequently, with species ranges shifting towards northern latitudes or higher altitudes during the post-glacial areal expansion and re-colonization of unglaciated land following the ice cap recession, cold-adapted plants have found harbor in a few remaining favorable habitat patches from their former distribution areal (mires, loess steppes and alpine habitats). Such habitat islands maintained marginal ecological conditions and offered refuge for scarce, isolated populations [107] and led to the currently observed highly fragmented and disjunct distribution of arctic-alpine or boreo-montane elements [9].

The current relict distribution of marginal populations in cold-adapted species, together with palaeobotanical evidence available mainly for peatland species that were common in the colder periods from the Last Glacial Maximum (LGM) represent the most relevant proof of the extent of their former distribution [31, 33]. The boreo-montane disjunction is similar to the arcto-alpine, being a biogeographical phenomenon documented mainly in Europe, but encountered also in Asia [90]. The former disjunction type includes species for which the Early Holocene is considered the period of maximum expansion, currently distributed in the Boreal region (taiga) and the European Alpine System [107]. In addition, cold-adapted relicts include not only species that were widely distributed during the LGM (glacial relicts), but also those widespread during the Early Holocene, the latter sometimes being referred to as postglacial relicts [84]. However, increasing evidence suggests that besides the arctic-alpine or peatland species from the cold and wet tundra, scrubs, fens and peatland forests, also steppic species (dry and meadow steppe, steppe-tundra), dark taiga and mesic forest-steppe (light-coniferous, mixed temperate forests and tall-herb vegetation) were thriving during the last glaciation [37, 10, 19].

In Europe, the first systematic attempts to evaluate and list arctic-alpine and boreal relict species date back to the early 20th century [53, 86, 109], then continued through the 1960s and 1970s [101, 108]. However, due to lack of consistent and direct evidence (i.e. macrofossil and palynological evidence, [37]) to support the classification of species as glacial relicts, such assessments were solely based on known distribution and thus quite speculative. Recently, the concept of glacial relicts has regained traction and raised even more interest, due to the support of novel, more accurate investigation tools, such as the development of phylogeographical methods [76, 106, 47], and the increasing number of radiocarbon-dated paleoecological records [31, 33, 28] that led to the emergence of multiple evidence. Consequently, with the advancement of these investigative methods, significant results for biogeographical history of glacial relicts have been obtained in Germany [110, 114], as well as the Czech Republic, Poland, and Slovakia [48, 68, 33, 37, 19].

The Carpathian Mountains, spanning eight countries in the eastern part of Europe (Austria, Czechia, Slovakia, Poland, Ukraine, Hungary, Romania and Serbia), are an important part of the European mountains and still maintain extensive wetland habitats that harbour many cold-adapted species. Together with some of the Carpathian endemics, the glacial relicts represent one of the most ancient components of the Central European flora, the latter category most often including many of the boreal peatland flora and the arctic-alpine species [19]. The recently increasing number of pollen and macrofossil data in the region, corroborated with radiocarbon-dating, has offered a sharper image of the presence of these species in Central Europe and the Carpathians during the LGM [10, 7, 57, 58]. The presence of glacial relicts in the Romanian flora has long been debated among botanists and biogeographers, with several assessments being made [70, 73, 71, 60, 72, 12]. Among them, Emil Pop was the first scientist to discuss the presence of glacial relicts in the Romanian part of the South-Eastern Carpathians, with a special focus on peatland flora and vegetation [70], and later in analysing the Romanian flora [72]. However, previous studies have not used clear criteria for delimiting the glacial relicts, while in the past 45 years there have been no additional studies discussing the glacial relicts from Romania.

Our study focuses on lowland populations, mostly located in wetlands, namely peat bogs, fens, marshes, springs and forest swamps, remnants that we consider among the best present-day imprints of past widespread habitats [31]. Five major types of freshwater wetland habitats are more frequently encountered in the Carpathian Region [79, 115]. Extensive marshes are located in most intramontane depressions of the Eastern Carpathians and the Apuseni Mts, as well as in the north-western lowlands of Romania. The **eutrophic marsh**, the most common type in the region, is supplied by groundwater and rivers, and can host several vegetation types, the most encountered being reeds, high and low sedges, and the wet meadows [98]. It is occurring throughout the Carpathian Region, especially in lower outer montane areas, dominated by warmer climate. The **rich fens** (alkaline eutrophic marshes) receive nutrients and water mostly from mineral-rich springs and through groundwater movements and less from rainfall. Their pH usually exceeds 6, lack woody vegetation and form peat sediments, being typical of cold and humid climates. They are the most diverse and rich in species and also the most sensitive to environmental changes [29]. The most prominent rich fens in the region are encountered in the Bârsa Depression (border between the Southern and Eastern Carpathians) and Valea Morii Nature Reserve (north-eastern part of Apuseni Mountains). The **poor fens** (transitional marsh) are intermediate between the alkaline and oligotrophic fens, being hydrologically similar to the alkaline fens, but in terms of acidity and vegetation are closer to the ombrotrophic habitats like the oligotrophic peat bogs. However, species richness is much higher than in typical oligotrophic marshes [79]. Their distribution overlaps with most of the mountain depressions in the Eastern Carpathians, but can be encountered in the vicinity of peat bogs throughout the Carpathians. The **peat bog** (oligotrophic marsh) is fed exclusively by rainfall, its pH is highly acidic, and is poor in nutrients, leading to a low species diversity and a high proportion of ecologically specialised plants. It can be covered by tree vegetation (pine and spruce) [70]. In the South-Eastern Carpathians, these boglands are encountered within a narrow altitudinal range between 900-1200 m, in the lower part of the spruce or the upper part of the beech level, where most of the typical boglands with pine trees and large bogs have developed [70]. At higher or lower altitudes their development is interrupted. Even if some bogs are found at higher altitudes they lack characteristic bog species and pine trees. The fifth type of wetlands more frequently encountered in the investigated area includes the **alluvial forest and shrub swamps**, dominated by trees and shrubs that withstand flooding and prolonged stagnation of water. The compact canopy prevents light from penetrating, hence the lower number of species [98, 79]. These habitats are characterised by the more frequent occurrence of *Alnus glutinosa*, in the case of alluvial forests, and *Salix cinerea*, *Betula pendula*, and *B. pubescens* in the case of marshland thickets. The typical alluvial forests established with *Quercus robur, Fraxinus* spp. and *Ulmus* spp. have been excluded from this analysis. Consequently, we have first aimed to obtain a comprehensive list of putative glacial floristic elements from the Romanian flora, through more rigorous means than previously applied. Secondly, we aim to explore the patterns of distribution and hotspots of richness, rarity and range margin populations of glacial relicts occurring in low altitude wetlands from the Romanian part of the Carpathian Region. To the best of our knowledge, this is the first attempt in Romania to delimit relict elements through a numerical approach. In addition, we aim to highlight the hotspots of taxa richness, rarity and range limit for the glacial relicts across Romania.

Material and Methods

Study area

The study is focusing on the Romanian part of the South-Eastern Carpathians (Fig. 1), including also the Transylvanian Basin and the Apuseni Mts, which together constitute the Carpathian Region [40, 51], one of the major hotspots of biodiversity in Europe [61]. The Transylvanian Basin was already mentioned as a major glacial refugium [85], but also as one of the most important postglacial refugia for many cold-adapted plant species that have here their southern range limit [70]. Well-developed intra-mountain depressions, like those in the Eastern Carpathians, as well as rich precipitation characteristic for mountainous areas, favoured the establishment of extensive peatlands across the Carpathians [70]. In our study we analyse lower altitude to montane wetlands, especially mires, excluding the alpine region of the Carpathians. We do not discuss other types of habitats where glacial relicts can survive, namely alpine scrub, meadows and rocky ground. Consequently, the criteria for selecting the initial list of species to be evaluated for glacial relict traits took into account species adapted to cold environments occurring predominantly in low altitude wetlands.

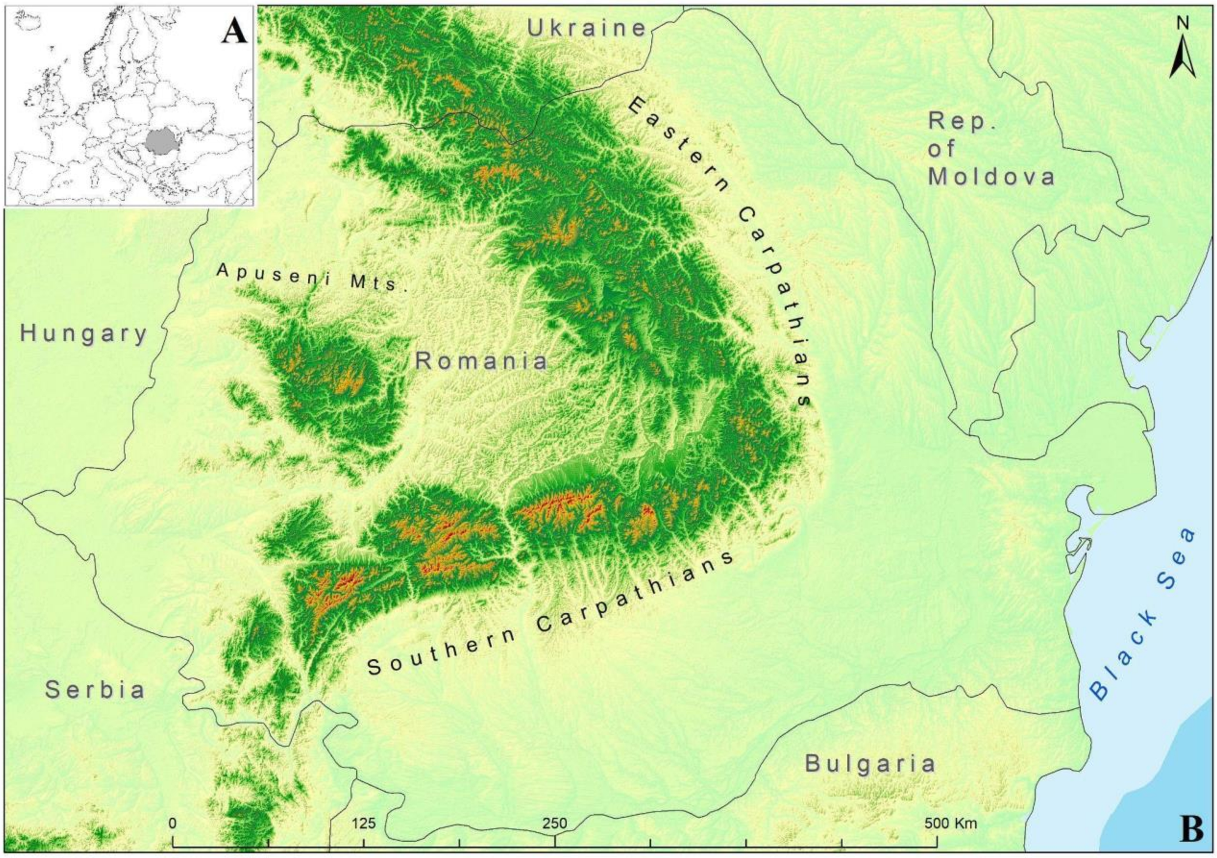

Fig. 1: A. Location of the study area (Romania) within Europe; and B. The spatial configuration of mountainous areas within Romania

Species selection

We initially took into account species previously considered as glacial relicts in the Romanian flora by various authors [70, 73, 72, 12]. In addition, for a thorough evaluation of taxa we included in our analysis all cold-adapted species mostly occurring in wetlands, following the main taxonomic [82, 12] and distribution knowledge [83, 70, 49, 21, 63] concerning the Romanian flora. However, we did not evaluate the arctic-alpine species occurring mostly in the high mountain areas of the Carpathians that are traditionally considered as glacial relicts (e.g., *Carex atrata, C. bicolor, C. bigelowii* subsp. *rigida, C. heleonastes, C. lachenalii, C. pediformis* subsp. *rhizodes, C. rupestris, Empetrum hermaphroditum, Juncus triglumis, Kobresia myosuroides, K. simpliciuscula, Loiseleuria procumbens, Saxifraga hieracifolia, Silene acaulis*) [111, 7, 90, 6].

Many of the (sub) species were selected according to their continental character, i.e. those with a wide distribution, spanning from Central Europe to Siberia. The list includes most of the circumpolar distributed peatland species (i.e. occurring in the arctic-alpine wet or dry tundra) and those growing in mineral-rich fens, but also several boreo-mountain species with unusual distribution in the lowlands, where they found a refugium in cold wetland environments. However, we did not include species from the steppes and saline marshes, considering that our study is focussed on freshwater wetlands. The complete list of evaluated taxa includes 171 species and subspecies. The nomenclature of species follows Tutin et al. [103].

Species evaluation

We evaluated each taxon by its distribution range and main ecological preferences. For assessing the biogeographical traits, including the distribution extent and areal disjunctivity, we used distribution maps (Atlas Florae Europaeae [43], the Euro+MedPlantbase [116], Plants of the World Online [118], Panarctic Flora [117]). Ecological traits of each (sub) species were retrieved from Sanda et al. [81] and Sârbu et al. [82].

We followed the evaluation criteria adopted by Dítě et al. [19], by using a four grade incremental scoring system (from zero to three) scaled similarly for each trait. The list of ecological and biogeographical traits include Continentality, Circumpolarity, Discontinuity of the distribution range, Conservatism of the regional distribution, Rarity, Affinity to dry or saline steppe vegetation, tundra vegetation, taiga vegetation, acidic peatlands (bogs) and non-calcareous arctic-alpine lakes, fens and springs, mesic forest-steppe habitats (light-coniferous temperate forests, meadow-steppe and tall-herb habitats), and Contraction of the realised ecological niche. In addition to these criteria, we added two more, namely the Presence in Romania of the southern limit of the species areal and the Temperature affinity. The final score for every taxon was obtained by adding individual scores for each ecological or biogeographical trait, with the total sum used as a proxy for a probability that a given species is a glacial relict. In our evaluation we follow the Last Glacial Maximum (LGM) vegetation types thoroughly described by Janská et al. [45].

1. Continentality

Glacial relicts are presumably more adapted to the continental climate specific during the glacial period in Central and Eastern Europe. Currently, this type of climate is characteristic for southern Siberia (for steppe species) and the mountains of Central Asia (tundra species). Despite not having exact current analogues in present climates [91], recent studies showed that past climate during the glacial period had characteristics resembling the current one experienced in the continental landscapes of South Siberian mountains [37].

Scale used for this trait:

0 - Species not occurring in the extreme continental regions of Siberia and Central Asia or in regions of Europe characterised by a continental climate;

1 - Species with a low degree of tolerance for continental climate in Europe (species that do not grow outside Europe or if they grow in Siberia then they are not found in the continental region);

2 - The distribution is largely in the continental region of Eurasia, but with many exceptions - these species do not occur in the steppe zone;

3 - The main distribution of the species is in Siberia, with only a few isolated populations in Europe.

2. Circumpolarity

Species with relict populations of glacial origin should tolerate the extreme climate of the Arctic and boreal regions, thus have a relatively uniform and wide distribution in the boreal hemisphere and not be restricted to southern latitudes of Europe [19]. Endemics have been excluded.

Scale used for this trait:

0 - The species does not occur in northern latitudes;

1 - The distribution is limited in the Arctic regions of Europe (Arctic-Alpine and Arctic-Boreal species);

2 - The species is distributed in the Arctic region of Asia and Europe;

3 - The species is distributed in the Arctic region of Asia, Europe and North America.

3. Discontinuity of the distribution range

Glacial relicts from Europe have been presumably widely distributed in the past in the southern latitudes. Consequently, the current distribution should display remnants of past distribution in the southern regions of the continent in a patchy pattern, being found only in refugia that still meet the former ecological conditions [19].

Scale used for this trait:

0 - The species has a continuous distribution in Europe;

1 - The species has a wide distribution but with small disjunctive populations in the immediate southern vicinity of its main distribution range;

2 - The species displays a very clear areal disjunction with a main distribution in the Arctic or in the continental steppe region (e.g. disjunction between Southern Siberia and Europe);

3 - The species has a highly discontinuous distribution in Europe, with few, isolated populations surviving in small favorable habitat patches (usually wetlands) at a great distance from its main areal (e.g. rare arctic-alpine species and northern tundra, Euro-Siberian species with disjunctive distribution in Europe and Siberia and relict species only with isolated populations).

4. Conservatism of the regional distribution

Glacial relicts should be highly conservative in terms of regional distribution and habitat affinity, suggesting low dispersal capacity and habitat permeability, and a high affinity (and habitat conservatism) for presumed glacial refugia [19].

Scale used for this trait:

0 - The species is widely distributed in the South-Eastern Carpathians, easily dispersing into secondary habitats or those severely disturbed mainly due to human activities;

1 - The species occurs in habitats that have been more common during the LGM, later spreading to similar man-made secondary habitats (e.g. artificial marshes);

2 - The species has a high affinity for relict habitats, but can occasionally also be found in secondary ones;

3 - The species has a clear affinity for and often is limited to relict habitats (peatlands, cold springs, etc.), surviving only in highly stable ecosystems and never in secondary ones.

5. Rarity

Habitat affinity of species would indicate their expected occurrence in all optimal habitats across their distribution range. However, the occurrences of glacial relicts are influenced by historical distributions and local processes like extinctions and, especially towards their range margins, such occurrences are not overlapping their potential distribution in optimal habitats. Consequently, this criterion evaluates the degree of consensus between expected and actual distribution of evaluated species in the studied region considering their optimal habitat requirements.

Scale used for this trait:

0 - The species occurs in almost all of the optimal habitats found across Romania, following its ecological requirements;

1 - The species does not occur in all places where it can find its preferred habitat, but can be found in more than 20 populations across Romania;

2 - The species is known from fewer than 20 sites across Romania and fewer than five geographical units;

3 - The species was recorded in only one to five sites and only one geographical unit across the Romanian part of the Carpathian Region, inhabiting only a small proportion of all the optimal habitats found in the study area, this being the strongest relictual symptom across the scale.

6. Affinity to dry or saline steppic vegetation

These habitats were much more widespread in our region during the Ice Age than they currently are. Since our analysis includes mainly species distributed in wetlands, most species will fall within the first category.

Scale used for this trait:

0 - The species never occurs in these types of habitats;

1 - The species has its ecological optimum linked with other types of habitats, but can rarely occur also dry or saline steppic vegetation, especially in refugia (old fens, alpine screes, etc.);

2 - The ecological requirements of the species include several habitat types, but it is more frequently encountered in this habitat type;

3 - The species is characteristic for this type of habitat.

7. Affinity to tundra vegetation

Tundra-type vegetation was more widespread during the last Ice Age than today in Central and Eastern Europe. The scale used for this symptom is the same as for the sixth criterion.

8. Affinity to taiga vegetation

This type of vegetation was also more widely distributed in the past compared to present day. However, it displayed a reduction in extent during the last Ice Age, being predominant during interglacial periods and especially towards the end of the LGM and the beginning of the Holocene. The scale used for this trait is the same as for the sixth criterion.

9. Affinity to acidic peatlands (bogs) and non-calcareous arctic-alpine lakes

Peatlands were much more widely distributed in the past than today, especially during wet periods such as the Early Holocene, but were more limitedly spread in the LGM. However, species characteristic to acidic peatlands (bogs) and non-calcareous arctic-alpine lakes are also able to survive in wet tundra and peatland forests. The scale adopted for this evaluation criterion is the same as for the sixth one.

10. Affinity to fens and springs

Unlike peat bogs, fens were more numerous and widespread during the LGM, a period characterised by a drier climate. The scale used for this trait is the same as for the sixth criterion.

11. Affinity to mesic forest-steppe habitats (light-coniferous temperate forests, meadow-steppe and tall-herb habitats)

These habitats (dominated by pine, larch, birch, and tall grasses) had a much wider distribution in Central and Eastern Europe in the past than today, being common in the Late Holocene and surviving in the wetlands of the LGM [44, 37]. The scale used for this trait is the same as for the sixth criterion.

12. Contraction of the ecological realized niche

Glacial relicts have a wider niche breadth in their main areal compared to their relict populations, where their adaptative capacity to various ecological requirements is drastically reduced. This might be due also to genetic depletion phenomenon manifested in these populations. In our case, the relict populations can occur in refugia represented by oligotrophic and eutrophic marshes. The scale used for this trait is the same as for the sixth criterion.

13. Southern areal limit of the species

The presence of cold adapted species at southern latitudes, especially in isolated populations found at their range limit, is a good indicator of their survival in refugia that still conserve favorable microclimate conditions.

Scale used for this trait:

0 - The species is uniformly distributed throughout Europe and Asia, in both northern and southern latitudes;

1 - The species is distributed mainly in Central and Northern Europe, Northern and Central Siberia, but spans to the southern parts of the Balkan Peninsula, Italy and Turkey, where it has several isolated populations;

2 – The populations from Romania are close to the species southern range limit, however several relict populations are found south of Romania, including here Bulgaria, North Macedonia, Croatia, or Serbia;

3 - The species southern or eastern range limit passes through Romania, where there are few isolated populations, distributed far from its areal core, usually located in northern Europe and/or Siberia.

14. Temperature affinity (T)

The cold-adapted species from northern latitudes and the high mountains of Europe were more widespread at the lower altitudes from the plains and hills of the Carpathian Region and surrounding areas in the past. Along with climate warming, many of these species migrated to higher altitudes and/or northern latitudes. However, some of them have survived in peat bogs and fens with favorable microclimates across the Carpathian lowlands. We differentiate between species with high ecological plasticity that are spread from the lower plains to the alpine area and those strictly adapted to cold climates that often survived in isolated populations from the lowlands, by using the following scale:

Index of species temperature optimum (T) across Romania, following the classification adopted by Sârbu et al. [82]:

0 - Tx, T6, T5 - plants that are widespread in lowland, hilly, and sub-montane areas, here including also the eurythermic species;

1 - T4 - plants occurring mostly in the montane belt;

2 - T3 - plants distributed predominantly in the subalpine belt;

3 - T2, T1 - plants from the cold climates, including boreal, arctic, and alpine species, as well as chionophiles.

Temperature preference of the species (T), following the scale adopted by Sanda et al. [81]:

0 - T0, T5, T4, T3 - amphitolerant, thermophilic, moderate-mezothermal and micromezothermal plants from warmer climates;

1 - T2.5 - microthermal plants from milder climates;

2 - T2 - microthermal plants from cold climates;

3 - T1, T1.5 - cryophilic plants from cold climates.

The final score for this criterion was averaged based on the individual scores obtained following the two scales, hence the appearance of decimal numbers.

A total of 171 taxa occurring in the marshy areas from the lower regions of the South-Eastern Carpathians that have circumpolarity, continentality, disjunct areal, have been considered as relicts in previous studies [70, 73, 72, 12], have an affinity for oligotrophic and eutrophic mires, as well as species from the high altitude mountains that managed to survive in the lowlands have been included in our initial list and have been evaluated. Two important varieties specific for wetland habitats (*Senecio papposus* var. *integerrimus* and *Juncus alpinoarticulatus* var. *fuscoater*) were included in the analyses, the latter being characteristic for lowland marshes. To see if any direct evidence of their *in situ* occurence exists, based on pollen or macrofossil information dating from the LGM or Early Holocene, we surveyed the published scientific literature covering the South-Eastern Carpathians. Due to the lack of paleontological analyses in Romania, we relied on evidence from the Western Carpathians using the Czech and Slovak Macrofossil Database [34].

Diversity analyses

In order to highlight the spatial distribution and hotspots of cold-adapted species considered as putative glacial relicts in Romania based on our evaluation, we recorded their distribution in two different UTM grid systems. For species richness and rarity we adopted the 10×10 km quadrat size, while for mapping the hotspots of range margin, we recorded the distribution of range margin populations on the 50×50 km UTM grid system. We opted for two differently sized quadrats and grid systems in order to adequately reflect the hotspots of richness, rarity and range margin at proper spatial scales. While for the former two, the distribution of wetlands requires a more detailed mapping of distribution, for the latter, a coarser scale would be adapted to the spatial amplitude of species total distribution range. The richness was calculated by summing the total number of species occurring in each grid cell, while the rarity values per quadrant was obtained by adding each species value down weighted by the total number of cells in which they occurred across Romania. A range limit population was included when it occurred along the main areal limit of the species; consequently for some taxa, several populations were recorded in Romania in different grid cells.

Results

Following our evaluation criteria, the lowest final score obtained by a taxon was 3.5, while the maximum value was 27. We set an arbitrary threshold of 15, considering the taxa reaching the final score ≥ 15 as displaying sufficient characteristics to be considered as glacial relicts in the Romanian flora. Consequently, out of the 171 evaluated taxa, we retained 74 vascular plants that have obtained a score equal or higher than 15, hereby considered as putative glacial relicts occurring in lowland refugia across Romania (Table 1). These include 46 species that acquired a score higher than 20, 25 species had a score ranging between 16 and 19.5, while three species obtained 15 points. The species with the highest scores (≥ 20) are the most likely to be remnants of the LGM, Late Glacial and Early Holocene distribution, here including: *Betula nana*, *Carex chordorrhiza*, and *Carex loliacea* (27 points), *Carex vaginata*, *Ledum palustre*, *Salix myrtilloides*, and *Saxifraga hirculus* (26.5), and *Andromeda polifolia*, *Betula humilis* and *Carex magellanica* subsp. *irrigua* (26).

Considering that our evaluation accounted mainly for wetland-occurring taxa, most (sub) species display a high affinity to humid habitats. Following the habitat preferences (multiple habitats can be preferred by certain taxa), there are no typical taxa for steppic habitats (sixth criterion), 28 display a higher affinity (a score of two or three for the criterion) for tundra habitats (seventh criterion), five (sub) species occur mostly in the taiga (eighth criterion), 17 (sub) species usually grow in peatlands (ninth criterion), 49 taxa are linked more frequently to fens and springs (10^{th} criterion), while only seven taxa display a higher affinity for light-coniferous temperate forests, meadow-steppe and tall-herb habitats (11^{th} criterion). Thus, for the tundra habitat, the species with the highest scores are: *Betula nana*, *Carex chordorrhiza*, and *Carex loliacea* (27 total score), followed by *Carex vaginata*, *Ledum palustre*, *Salix myrtilloides* and *Saxifraga hirculus* (26.5). The highest ranked taiga species in this study are *Betula humilis* (26), followed by

Trientalis europaea (22.5) and *Chimaphila umbellata* (19.5). For peat bogs the highest affinity is represented by *Ledum palustre* (26.5), *Andromeda polifolia* (26) and *Vaccinium uliginosum* subsp. *uliginosum* (25), and for marshes and streams *Carex chordorrhiza* and *Carex loliacea* (27), followed by *Saxifraga hirculus* (26.5). The best adapted species to the light-coniferous temperate forests, meadow-steppe and tall-herb habitats are *Spiraea salicifolia* (21.5) (Fig. 2E), *Crepis sibirica* (21), *Ligularia glauca* (20.5), followed by *Polemonium caeruleum* (18) (Fig. 2A) and *Adenophora liliifolia* (15). Regarding the discontinuity of the areal (the third criterion), 11 (sub) species have a highly disjunct areal (a score of three for the criterion). In terms of rarity (fifth criterion) there are 37 taxa found in a maximum of five sites across Romania and 26 species in a maximum of 20 sites (5b). Finally, regarding the presence of the southern range limit across Romania (the 13th criterion), there are 24 taxa that have their areal boundary within the studied region, while 19 (sub) species are found here close to their range limit, having only few isolated populations south of the Carpathian Region.

Table 1: List of the putative glacial relicts from Romania. The **Highest ecological affinity** for each (sub) species is shown, where the highest score obtained for a type of habitat is three (multiple habitats preferred by certain taxa), while an asterisk adjacent to the habitat name indicates a lower preference score for that habitat, but still the highest habitat specificity of that taxon (e.g., a score of two out of three). **The (sub) species biogeographical characteristics** highlights three main distribution traits for each taxon: Discontinuity of the distribution range (third criterion), Rarity of occurrences in Romania (fifth criterion), and the Southern areal limit of the species (13th criterion). For each of the latter two criteria, we indicated the maximum score value (three) by adding the letter ”a” after the criterion number, while for those species where the maximum value was two we added the letter ”b”. The taxa currently considered Extinct (EX) from the Romanian flora according to the latest distribution knowledge are highlighted. Furthermore, we reference the **oldest palynological and/or macrofossil information recorded in the Carpathian Region** for each (sub) species. The references for each source previously considering the taxon a glacial relict in the Carpathian Region are also shown. Finally, column **(I)** is showing the total score for each evaluated taxon, **(II)** the number of grid cells (10 $\times$ 10 Km) in which the taxon was recorded across Romania and, **(III)** indicating if the taxon is found in Romania at the limit of its areal

No.	Species	Highest ecological affinity	(Sub) species biogeographic characteristics	The first palynological records and macrofossils recorded in the Carpathian Region	Cited as glacial relict species in:	I	II	III
1.	*Betula nana*	Tundra	3, 5a, 13a	Würm-Glacial Maximum [34, 93, 58]	[72, 111, 19]	27	3	YES
2.	*Carex chordorrhiza*	Tundra, Marshes	5a, 13a	Preboreal [34]	[111, 19]	27	5	YES
3.	*Carex loliacea*	Tundra, Marshes	3, 5a, 13a	-	[72]	27	3	YES
4.	*Carex vaginata*	Tundra	3, 5a, 13a	-	[20, 19]	26.5	1	YES
5.	*Ledum palustre*	Tundra, Peat bog	5a, 13a, EX	Subboreal [34]	[72, 111, 19]	26.5	2	YES

6.	*Salix myrtilloides*	Tundra	3, 5a, 13a	Dryas III [34]	[72, 111, 19]	26.5	1	YES
7.	*Saxifraga hirculus*	Tundra, Marshes	3, 5a, 13b	Glacial Maximum [58]	[72, 111, 19]	26.5	3	NO
8.	*Andromeda polifolia*	Tundra, Peat bog	5b, 13a	Preboreal [34]	[72, 111, 19]	26	28	YES
9.	*Betula humilis*	Taiga	3, 5a, 13a	Würm-Dryas III [34]	[72, 111]	26	12	YES
10.	*Carex magellanica* subsp. *irrigua*	Tundra, Marshes	5b, 13b	-	[72, 19]	26	16	NO
11.	*Stellaria longifolia*	Taiga, Marshes	5a, 13a	-	[72, 111, 19]	25	21	YES
12.	*Vaccinium uliginosum* subsp. *uliginosum*	Tundra, Peat bog	5a, 13a	Preboreal [34]	[70, 19]	25	17	YES
13.	*Achillea impatiens*	Marshes	3, 5a, 13a	-	[72, 111]	24.5	2	YES
14.	*Hammarbya paludosa*	Peat bog, Marshes	5a, 13b	-	[111]	24.5	6	NO
15.	*Vaccinium microcarpum*	Tundra, Peat bog	5b, 13a	-	[72, 111, 19]	24.5	30	YES
16.	*Vaccinium oxycoccos*	Tundra, Peat bog	5b, 13a	Preboreal [34]	[72, 111, 19]	24.5	46	YES
17.	*Calamagrostis purpurea*	Marshes	5a, 13a	-	[52]	24	4	YES
18.	*Carex pauciflora*	Tundra, Marshes	13a	Subatlantic [34]	[72, 19]	24	52	YES
19.	*Drosera anglica*	Tundra, Peat bog	5a	-	[72, 111, 19]	24	7	NO
20.	*Calamagrostis stricta*	Tundra, Marshes	5b, 13b	-	[72, 111]	23.5	27	NO
21.	*Carex dioica*	Tundra, Fens	5b, 13b	Allerød [34]	[72, 111, 19]	23.5	20	NO
22.	*Trichophorum alpinum*	Tundra*, Peat bog*, Marshes*	5a, 13a, EX	Subatlantic [34]	[19]	23.5	1	YES
23.	*Potamogeton alpinus*	Tundra, Marshes and watercourses	5a	Dryas I [26, 34]	[72, 19]	23	4	NO

24.	*Primula farinosa*	Tundra, Fens	5a	Preboreal [32]	[72, 19]	23	10	NO
25.	*Empetrum nigrum* subsp. *nigrum*	Tundra, Peat bog	5a	Dryas III [34]	[72, 19]	22.5	20	NO
26.	*Pedicularis sceptrum-carolinum*	Marshes	5a, 13a	-	[72, 111, 19]	22.5	23	YES
27.	*Trientalis europaea*	Tundra, Taiga	5b, 13a	Dryas III [55]	[72]	22.5	16	YES
28.	*Angelica palustris*	Marshes	5a, 13b	-	[72, 111]	21.5	23	NO
29.	*Carex limosa*	Tundra, Marshes		Glacial Maximum [34]	[72, 111, 19]	21.5	38	NO
30.	*Drosera intermedia*	Peat bog	5a	-	[72]	21.5	3	NO
31.	*Salix starkeana*	Marshes*, Tall-herbs/Continental shrubs*	3, 5a, 13a	-	[72, 111, 19]	21.5	11	YES
32.	*Scheuchzeria palustris*	Peat bog	5b, 13b	Dryas I [96]	[72, 111, 19]	21.5	33	NO
33.	*Spiraea salicifolia*	Marshes, Tall-herbs/Continental shrubs	3, 5b, 13b	-	[72]	21.5	29	NO
34.	*Calla palustris*	Marshes	5b, 13b	Atlantic [34]	[72, 19]	21	23	NO
35.	*Carex capillaris*	Tundra	5b	Subatlantic [34]	[10, 19]	21	15	NO
36.	*Crepis sibirica*	Tall-herbs/Continental shrubs	5a, 13a	-	[73, 111, 19]	21	9	YES
37.	*Ligularia sibirica*	Marshes	5b, 13b	Late Glacial [92]	[72, 111, 19]	21	60	NO
38.	*Lycopodiella inundata*	Peat bog, Marshes	5a	Dryas III [97]	[72, 111]	21	20	NO
39.	*Viola epipsila*	Marshes	5b, 13a	-	[72, 111, 19]	21	15	YES
40.	*Ligularia glauca*	Tall-herbs /Continental shrubs	3, 5a, 13a	-	[111, 38, 19]	20.5	4	YES

41.	*Dactylorhiza lapponica*	Fens	5a, 13b	-	[50]	20	2	NO
42.	*Dactylorhiza traunsteineri*	Fens	5a, 13b	-	[50]	20	3	NO
43.	*Drosera rotundifolia*	Tundra, Peat bog		Preboreal [96]	[72, 19]	20	77	NO
44.	*Liparis loeselii*	Fens	5a	-	[73]	20	18	NO
45.	*Swertia perennis*	Fens	5b	-	[72, 19]	20	19	NO
46.	*Tephroseris palustris*	Marshes	5a, 13b, EX	-	[111]	20	7	NO
47.	*Chimaphila umbellata*	Taiga	5a, 13a	-	[111]	19.5	24	YES
48.	*Dryopteris cristata*	Marshes	5b, 13b	-	[72]	19.5	24	NO
49.	*Lysimachia thyrsiflora*	Marshes	5b, 13b	Atlantic [34]	[72, 111, 19]	19.5	29	NO
50.	*Rhynchospora alba*	Peat bog	5b	Glacial Maximum [58]	[72, 19]	19.5	22	NO
51.	*Carex hartmanii*	Marshes	5b	Subboreal [34]	[70, 111, 19]	19	42	NO
52.	*Cnidium dubium*	Marshes	5b, 13a	-	[72]	19	29	YES
53.	*Comarum palustre*	Tundra, Marshes		Würm-Dryas II [34]	[111, 19]	19	66	NO
54.	*Betula pubescens*	Tundra, Peat bog		Würm-Glacial Maximum [34, 44]	[70, 19]	18.5	59	NO
55.	*Eriophorum vaginatum*	Tundra, Peat bog		Allerød-Dryas III [34]	[72, 19]	18.5	66	NO
56.	*Tofieldia calyculata*	Alpine Tundra*, Fens*	5a	Postglacial [21]	[72]	18.5	3	NO
57.	*Euonymus nanus*	Tall-herbs /Continental shrubs*	3, 5a, 13b	-	[70, 111]	18	22	NO
58.	*Polemonium caeruleum*	Marshes, Tall-herbs /Continental shrubs	5b	Glacial Maximum [44]	[72, 19]	18	37	NO

59.	*Sparganium minimum*	Marshes	5b	Glacial Maximum [105]	[72]	18	16	NO
60.	*Viola palustris*	Marshes	5a	Dryas III [34]	[72]	18	9	NO
61.	*Carex lasiocarpa*	Marshes	5b	Würm-Glacial Maximum [34]	[19]	17.5	32	NO
62.	*Malaxis monophyllos*	Taiga*, Peat bog*	5b	-	-	17.5	18	NO
63.	*Salix pentandra*	Marshes		Subatlantic [34]	[23, 112]	17.5	53	NO
64.	*Carex diandra*	Marshes		Allerød-Dryas III [34]	[72, 111, 19]	17	33	NO
65.	*Carex hostiana*	Marshes	5b, 13b	Subboreal [34]	[31]	17	17	NO
66.	*Eriophorum gracile*	Marshes	5b	-	[70, 19]	17	26	NO
67.	*Juncus alpinoarticulatus* var. *fuscoater*	Fens		-	[19]	17	21	NO
68.	*Schoenus ferrugineus*	Fens	5a, 13b	Subatlantic [34]	[10, 19]	17	4	NO
69.	*Calamagrostis canescens*	Marshes		Subatlantic [34]	[72, 19]	16	52	NO
70.	*Pedicularis palustris*	Marshes	5b	Preboreal [34]	[31]	16	64	NO
71.	*Sesleria uliginosa*	Fens	5a	-	[72]	16	6	NO
72.	*Adenophora liliifolia*	Tall-herbs /Continental shrubs	5a, 13b	-	[70, 19]	15	44	NO
73.	*Carex elongata*	Marshes		Atlantic [34]	[72]	15	69	NO
74.	*Cladium mariscus* subsp. *mariscus*	Fens	5a	Dryas I-Dryas III [34]	[10, 62, 15, 69]	15	12	NO

The (sub) species with a total evaluation score below 15: *Saxifraga mutata* subsp. *mutata* (14.5), *Carex appropinquata* (14), *Carex davalliana* (14), *Menyanthes trifoliata* (14), *Ribes nigrum* (14), *Schoenus nigricans* (14), *Valeriana simplicifolia* (13.5), *Carex canescens* (13), *Eleocharis mamillata* (13), *Eriophorum angustifolium* (13), *Eriophorum latifolium* (13), *Scirpus radicans* (13), *Utricularia minor* (13), *Carex paniculata* (13), *Equisetum fluviatile* (13), *Silene multiflora* (13), *Triglochin maritima* (13), *Triglochin palustris* (13), *Pedicularis sylvatica* (12.5), *Angelica archangelica* (12), *Betula pendula* (12), *Carex nigra* (12), *Cirsium heterophyllum* (12), *Equisetum variegatum* (12), *Galium boreale* (12), *Lycopodium annotinum* (12), *Pinguicula vulgaris* (12), *Equisetum sylvaticum* (12), *Carex* *cespitosa* (12), *Carex echinata* (11.5), *Carex rostrata* (11.5), *Polygala amarella* (11.5), *Senecio papposus* var. *integerrimus* (11.5), *Trollius europaeus* (11.5), *Luzula multiflora* (11.5), *Dianthus superbus* (11.5), *Equisetum palustre* (11), *Parnassia palustris* (11), *Polygonum bistorta* (11), *Geum rivale* (11), *Herminium monorchis* (11), *Epilobium palustre* (11), *Lathyrus pannonicus* (11), *Molinia caerulea* (11), *Peucedanum palustre* (11), *Pyrola minor* (10.5), *Ribes petraeum* (10), *Hieracium aurantiacum* (10), *Lycopodium complanatum* (10), *Vaccinium myrtillus* (10), *Vaccinium vitis-idaea* (10), *Veratrum album* (10), *Cirsium palustre* (10), *Oreopteris limbosperma* (10), *Carex flava* (10), *Dryopteris carthusiana* (10), *Euphorbia palustris* (10), *Lathyrus palustris* (10), *Ophioglossum vulgatum* (10), *Orthilia secunda* (10), *Potentilla erecta* (10), *Rubus nessensis* (10), *Salix aurita* (10), *Thalictrum lucidum* (10), *Thalictrum simplex* (10), *Veronica longifolia* (10), *Moneses uniflora* (9.5), *Phegopteris connectilis* (9.5), *Valeriana sambucifolia* (9.5), *Matteuccia struthiopteris* (9.5), *Sagina nodosa* (9), *Cirsium canum* (9), *Geranium palustre* (9), *Iris sibirica* (9), *Lythrum tribracteatum* (9), *Rubus idaeus* (9), *Rumex aquaticus* (9), *Rumex thyrsiflorus* (9), *Scorzonera parviflora* (9), *Selinum carvifolia* (9), *Monotropa hypopitys* subsp. *hypopitys* (8.5), *Chrysosplenium alternifolium* (8), *Equisetum telmateia* (8), *Lycopodium tristachyum* (8), *Allium angulosum* (8), *Galium rivale* (8), *Gladiolus imbricatus* (8), *Juncus atratus* (8), *Pyrola rotundifolia* (8), *Cirsium rivulare* (7), *Aster sedifolius* (7), *Euphorbia villosa* (7), *Lythrum virgatum* (7), *Chaerophyllum hirsutum* (6.5), *Epipactis palustris* (6), *Lycopus exaltatus* (6), *Monotropa hypopitys* subsp. *hypophegea* (3.5).

Fig. 2: (A) *Polemonium caeruleum*, Piatra Țibăului, 21.06.2017; (B) *Achillea impatiens*, Borzont Marsh, 08.07.2019; (C) *Vaccinium oxycoccos*, Poiana Stampei at "Turbăria Stampei", 12.05.2016; (D) *Viola epipsila*, Poiana Stampei at "Turbăria Stampei", 07.04.2016; (E) *Spiraea salicifolia*, Borzont Marsh, 08.07.2019; (F) *Cnidium dubium*, Valea Morii Nature Reserve, 08.07.2017 (photographs: Paul-Marian Szatmari)

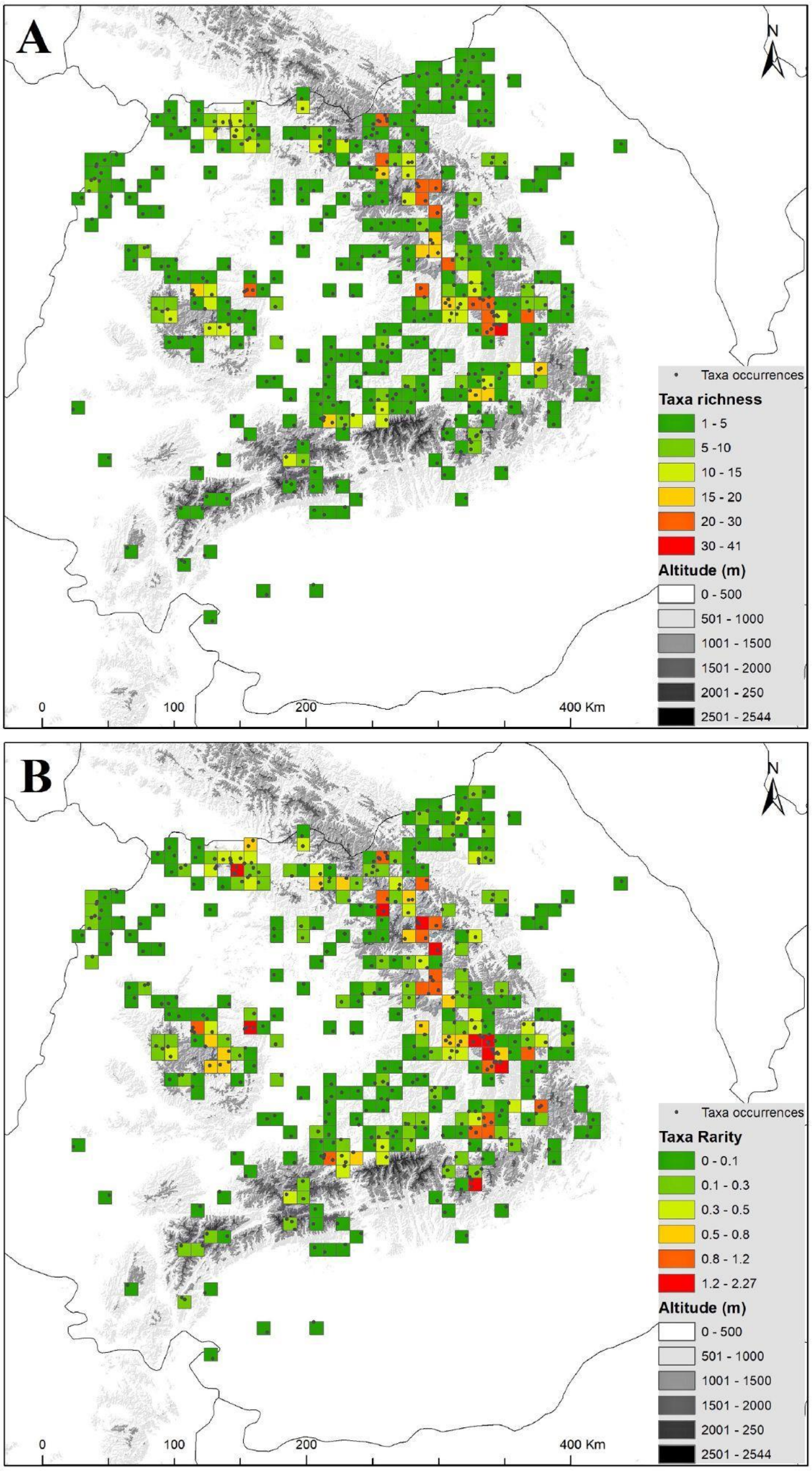

Fig. 3: A. Relict taxa richness hotspots based on distribution recorded in 10 × 10 UTM grid cells; B. Relict taxa rarity hotspots. Grey dots indicate the occurrence of taxa on which the analyses were carried out

The analysis of distribution of glacial relicts highlights several diversity hotspots (Fig. 3A) across the Romanian part of the Carpathian Region (10 × 10 UTM quadrats with ≥21 occurring (sub) species). With only one exception (Valea Morii Nature Reserve), situated in the north-eastern part of the Apuseni Mountains, where 22 taxa have been recorded, most glacial relicts are concentrated in the Eastern Carpathians, along a series of intra-mountain depressions. The highest diversity (41 taxa) is recorded in a single grid cell from the southern part of the Eastern Carpathians (south of the Ciuc Depression). However, a cluster of quadrats indicates the existence of extensive refugial habitats for cold-adapted taxa in this area, with richness values ranging from 26 to 41 (sub) species in five adjacent grid cells overlapping the Ciuc Depression, the south of the Ciuc Mountains, eastern part of the Harghita Mountains and the Bodoc Mountains. Other areas from the Eastern Carpathians harboring high numbers of glacial relicts are found in the southern part of the Nemira Mountains (30 taxa), southern part of the Gurghiului Mountains (21 taxa), Giurgeu Depression (21 taxa), while a second cluster of quadrats (ranging from 22 to 29 taxa in four adjacent quadrats) is located in the Drăgoiasa, Bilbor and Borsec Depressions, known for their richness in cold wetland habitats harbouring such taxa. The northern part of the Eastern Romanian Carpathians are overlapped by two grid cells with high relict taxa richness values, in an area encompassing mostly the Dorna Depression (29 taxa), and Obcina Mestecănișului (21 taxa).

When analysing the distribution of richness in rare taxa (Fig. 3B), however, the 10 × 10 UTM quadrats (with values ranging from 0.01 to 2.27) display a slightly different spatial configuration. In addition to a stronger support for already outlined glacial relict richness hotspots from the Eastern Carpathians and north-eastern part of the Apuseni Mountains, several rarity hotspots emerged independent from the previous high richness areas. The Giurgeu Depression in the central part of the Eastern Carpathians is highlighted as a diversity centre for rare glacial relicts by the presence of several taxa (e.g., *Achillea impatiens*, *Betula humilis*, *B. nana*, *Pedicularis sceptrum-carolinum*, *Stellaria longifolia*, *Viola epipsila*, and *V. palustris*). In addition, another centre of rarity is indicated in the northern part of the Eastern Carpathians (the lower altitude volcanic massifs, where *Empetrum nigrum*, *Lycopodiella inundata*, and *Vaccinium uliginosum* have been recorded), while two regions from the Eastern part of the Southern Carpathians display high values of rarity for glacial relicts, namely the Brașov Depression (including here *Carex hostiana*, *Chimaphila umbellata*, *Cladium mariscus*, *Drosera anglica*, *Liparis loeselii*, *Pedicularis sceptrum-carolinum*, *Primula farinosa*, *Rhynchospora alba*, *Sesleria uliginosa*, and *Tephroseris palustris*) and the Bucegi Mountains, highlighted by the presence of Lăptici peatbog (where *Carex capillaris*, *C. chordorrhiza* and *Salix myrtilloides* occur).

Discussions

A list of putative low altitude glacial relicts in the Romanian flora

The assessment of the relict status of species is mainly based on indirect evidence, such as phylogeographical structure, genetic diversity and distribution analysis, sometimes correlated with direct macrofossil evidence and radiocarbon dating of sedimentary deposits [18]. However, only a few species from our list are directly supported by fossil evidence certifying their presence in the South-Eastern Carpathians during the LGM or Early Holocene. For this reason we have relied on existing evidence from the Western Carpathians [34] and adjacent regions, considering the presence of these species in Romania is even closer to their southern range limit. Based on such macrofossil data, several (sub) species have been proven to occur during the LGM and Late Glacial periods in the Carpathian Region and/or adjacent areas (i.e. *Betula nana*, *Salix myrtilloides*, *Saxifraga hirculus*, *Betula humilis*, *Carex dioica*, *Potamogeton alpinus*, *Empetrum nigrum* subsp. *nigrum*, *Trientalis europaea*, *Carex limosa*, *Scheuchzeria palustris*, *Ligularia sibirica*, *Lycopodiella inundata*, *Rhynchospora alba*, *Comarum palustre*, *Betula pubescens*, *Eriophorum vaginatum*, *Polemonium caeruleum*, *Sparganium minimum*, *Viola palustris*, *Carex lasiocarpa*, *Carex diandra*, and *Cladium mariscus* subsp. *mariscus*), as well as the Early Holocene (Preboreal) (i.e. *Carex chordorrhiza*, *Andromeda polifolia*, *Vaccinium uliginosum* subsp. *uliginosum*, *Vaccinium oxycoccos* (Fig. 2C), *Primula farinosa*, *Drosera rotundifolia*, and *Pedicularis palustris*), while several taxa are supported by pollen and macrofossil remains only from the Middle and Late Holocene (Table 1), which do not exclude however their presence in the LGM.

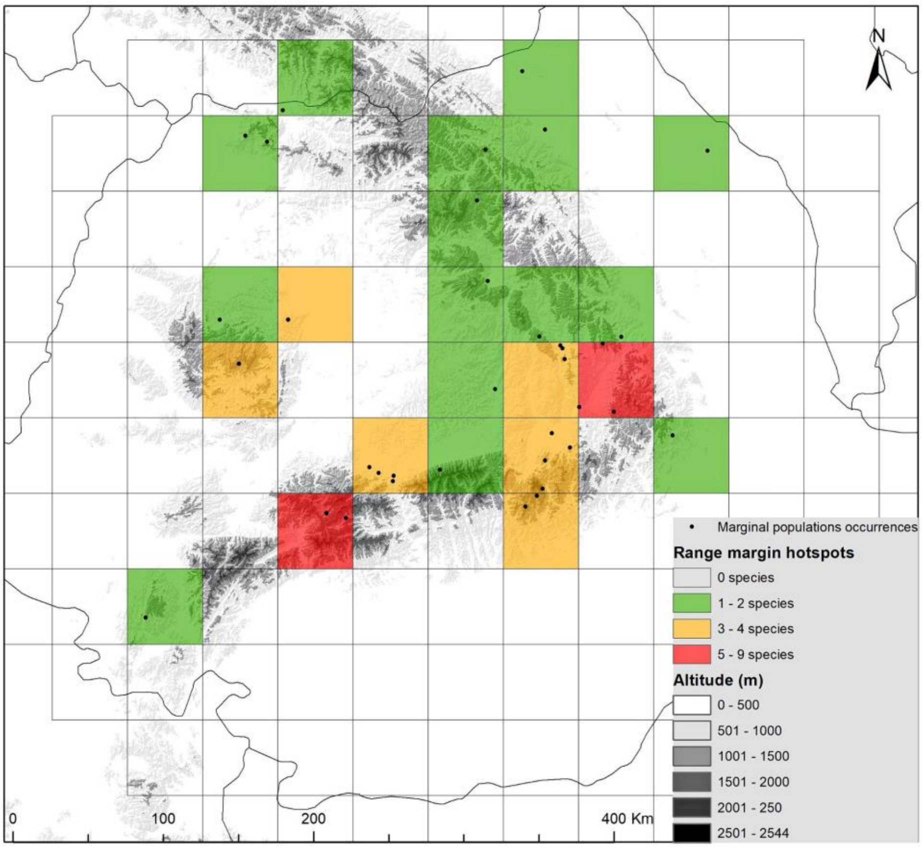

Fig. 4: Range margin hotspots based on occurrence of marginal populations of evaluated taxa recorded in 50 × 50 UTM grid cells

Considering previous knowledge, we identified that 54 out of the 74 taxa proposed by us as glacial relicts in the Romanian flora have been previously included in this category. For example, 52 taxa were initially proposed by Pop [70], from which six (*Vaccinium uliginosum*, *Carex hartmanii*, *Betula pubescens*, *Euonymus nanus*, *Eriophorum gracile* and *Adenophora liliifolia*) were omitted from the Romanian Flora monograph, where only 46 species were mentioned by the same author [72]. Other authors [73] include two additional species in this category (*Crepis sibirica* and *Liparis loeselii*) (Table 1). Conversely, 13 taxa previously considered as glacial relicts in the Romanian flora did not meet the required criteria in order to be included in this category following our evaluation: *Saxifraga mutata* subsp. *mutata* (14.5 total score) - mentioned by Ciocârlan [12] after Morariu and Negruș [60], who discovered the only population in Romania in the fens near Stupini; *Carex appropinquata* (14), [72]; *Carex davalliana* (14) [70]; *Menyanthes trifoliata* (14) [65]; *Ribes nigrum* (14) [72]; *Schoenus nigricans* (14) [62, 15]; *Galium boreale* (12) [70]; *Lycopodium complanatum* (10) [12], *Rubus nesssensis* (10) [70, 72, 12], *Ribes petraeum* (10) [12]; *Monotropa hypopitys* subsp. *hypopitys* (8.5) and subsp. *hypophegea* (3.5) [12], and *Lycopodium tristachyum* (8) [12]. Other species previously considered glacial relicts were not listed due to their limited distribution, being endemic for the mountains of Europe (including Carpathian endemics): *Salix bicolor* (21.5 final score), *Cochlearia borzaeana* (16.5), *Pedicularis limnogena* (15.5), and *Armeria maritima* subsp. *barcensis* (14) [70, 72]. Finally, *Drosera* × *obovata* (23 points), was excluded due to its hybrid nature, even though several authors consider it a valid, non-hybridogenous species [102, 17].

In total, 45 of the 74 (sub) species evaluated by us as glacial relicts in Romania have been similarly assessed for the Western Carpathians by Dítě et al. [19]. The species *Pedicularis palustris, Sparganium minimum, Carex hostiana* and *Lycopodiella inundata*, mentioned as relicts for the Western Carpathians by various authors [31, 88], were not considered as such by Dítě et al. [19] following their evaluation. However, these taxa show enough relict characters in the Romanian part of the Carpathian Region, and consequently we evaluated them as glacial relicts for this region. Conversely, six species that are considered by Dítě et al. [19] as possible glacial relicts in the Western Carpathians did not fall within this category following our evaluation for the Romanian flora: *Carex appropinquata* (14), *Triglochin maritima* (13), *Angelica archangelica* (12), *Dianthus superbus* (11.5), *Thalictrum simplex* (10), and *Scorzonera parviflora* (9). Dítě et al. [19] included species from more types of habitats than we considered in our study. Our focus was on wetland habitats, which are considered the typical habitats of lowland refugia in southern latitudes for many continental species from the LGM and Early Holocene [33]. Consequently, other species that could be considered relicts for the South-Eastern Carpathians were not included in our evaluation (e.g. *Veratrum nigrum, Kobresia myosuroides, Trifolium lupinaster* or *Stipa eriocaulis*). Witkowski et al. [111] listed only 32 of the 74 taxa evaluated here as glacial relicts for the entire Carpathian Region, of which six taxa (*Carex chordorrhiza, Hammarbya paludosa, Tephroseris palustris, Comarum palustre, Ligularia glauca,* and *Chimaphila umbellata*) were not included in this category before in the Romanian flora. Furthermore, 14 of the 74 species have been discussed as glacial relicts for Central Europe or other neighboring regions, including Romania, in recent literature (Table 1): *Carex vaginata* – Romania and the Carpathians [20], *Calamagrostis purpurea* – Romania and the Carpathians [52], *Pedicularis palustris, Carex hostiana* - Central Europe [31], *Carex capillaris, Schoenus ferrugineus* - Central Europe [10], *Cladium mariscus* - Central Europe and Romania [62, 69, 15, 10], *Salix pentandra* - Hungary and Bulgaria [23, 112], and *Ligularia glauca* - Central Europe [38].

Due to lack of firmer and direct palaeoecological and phylogeographical evidence to support our findings in the case of many other taxa, the results of our evaluation for glacial relict traits in the Romanian flora should be regarded as an overview rather than a definitive list. Moreover, the choice of setting an arbitrary threshold (15 points) for the final evaluation score in order to delimit glacial relicts from the other evaluated species, does not necessarily invalidate the possible relict status of other taxa whose total score falls below that threshold. For example, *Carex appropinquata* (14 points) is considered a possible glacial relict in both the Western [19] and South-Eastern Carpathians [72], as macrofossils of the species uncovered in the Carpathian Region (Mátra Mountains, northern Hungary) date back to the beginning of the Bølling and Older Dryas

Late Glacial Periods (14,615 until 7,050 BP) [66]. *Menyanthes trifoliata* (14 points), a common species in the Arctic, has macrofossils in all the stadials and interstadials of the Late Glacial from the Carpathians [8, 26, 34]. However, its reduced ecological niche conservatism and absence of large discontinuities in its distribution led to this species' lower score in our evaluation. Conversely, the status of several taxa from our list of putative glacial relicts has been strongly debated. For example, *Cladium mariscus* is considered a postglacial relict in Central Europe [69], with a maximum distribution in Europe attained between 9,800-8,000 BP [27]. In the Czech Republic, based on palaeobotanical evidence (fossil seeds), Pokorný et al. [69] indicate that *Cladium mariscus* may have survived in fens throughout the entire Holocene. The distribution of this species in Romania is currently more reduced when compared to the extent of known sites with palaeoecological evidence, confirming its presumed status of postglacial relict [80]. The species is found in Transylvania exclusively in very old alkaline fens (Valea Morii, Hărman, Prejmer, Borsec) which may indicate a strong areal contraction during the middle Holocene. Most likely, the species survived the LGM in permanent fens and colonized the Carpathian Region during the warmer interstadials (Bølling, Allerød, as well as Preboreal-Boreal), so it could not be considered a true glacial relict; therefore, its presence in the LGM is questionable.

Glacial relicts: ecological and biogeographical considerations

A clear distinction between the glacial and postglacial relicts is difficult. Dítě et al. [19] suggested that these species can be differentiated by several ecological traits used in their study that may prove large regional extinctions rather than Early Holocene migrations (e.g., rarity, ecological conservatism, disjunctivity, and niche contraction). This approach is also not conclusive, as some relicts from the Late Glacial and Early Holocene may have not occured in the region before these periods or have been in decline, such as *Cladium mariscus*, a species rather typical for the Boreal period [69]. Some species were more abundant in the LGM (e.g. some peatland species, arctic-alpine scrubs), while others became predominant in the interstadials like Bølling and Allerød from the Late Glacial or in the Early Holocene (e.g. tall-herbs, boreal species of peatlands, species of forest-steppe and open taiga), therefore a clear distinction between relicts from LGM and interstadials is problematic, although macrofossils indicate their presence in both periods, only the proportions being variable. Thus, both *Betula nana*, an arctic species that is continuously present until the Preboreal, and *Scheuchzeria palustris*, generally an indicator of wet and warmer periods, are found in the cold stages [42]. Most marsh species in the current study, however, could have survived the dry period of the LGM in habitats as humid as they are today. For example, *Betula pubescens* and *Comarum palustre* are not strictly related to a particular type of marsh, but were dominant species during the LGM period, as evidenced by the large number of macrofossils discovered in the region [34]. They are also among the most common species in the Arctic [117]. More macrofossil and genetic evidence from future studies could provide stronger evidence regarding the past distribution of the species discussed here.

Comparable to the Alps, the Carpathians played an important role as a major refugium for many cold-adapted species during the interglacial periods [6]. Continental species, currently distributed throughout Eurasia, were considered to be completely absent from Europe during the Ice Age, surviving only in Siberia and Manchuria. They were thought to have arrived in Europe through rapid postglacial migration. However, this concept began to be questioned during 1960-1970, following the distribution analysis of intraspecific taxonomic differentiation. Several studies indicate that the Carpathian Region was a transition zone for species migrating from Siberia, the Arctic or the Caucasus to Western Europe. These migrations were possible due to the frequent climatic fluctuations during the Quaternary, which also favoured the exchange of species and enhanced geneflow among populations from the mountainous areas of Europe (e.g., the Alps, Carpathians and Sudetes). Because the Carpathians and the Sudetes have lower altitudes compared to the Alps, they were not as strongly glaciated as the latter, so the valleys and mountain ranges provided a diversity of habitats where species could find refuge [104]. These refugia include not only species commonly found in the surrounding mountains (the local species pool), but also continental species from Siberia or circumpolar/boreal species that have survived the LGM in the marshes and mountain valleys unaffected by aridity or very low temperatures.

Additional molecular insights, such as genetic differentiation among European populations, led to the emergence of the northern refugia hypothesis, stating their local survival in glacial refugia during the LGM. Multiple examples show that continental species had numerous refugia in Europe, performing only local migrations and reducing the probability of large postglacial migrations between continents as a major re-colonisation process [85]. Therefore, continental species like *Achillea impatiens* (Fig. 2B), *Angelica palustris, Euonymus nanus, Ligularia glauca, Spiraea salicifolia, Adenophora liliifolia, Chimaphila umbellata, Cnidium dubium* (Fig. 2F), and *Viola epipsila* (Fig. 2D) have probably survived in the Carpathian Region during the Ice Age. They are of much older origin, probably migrating to Europe in the Pleistocene, during a favorable, cold, humid climate. According to the hypothesis of Schmitt and Varga [85] these species could have survived the very harsh climate in the same cryptic northern refugia as the European temperate species, being perfectly adapted to harsh winters and arid, cold summers. During the Holocene, they probably retreated together with the arctic and boreal species to mountain depressions, fens and bogs that maintained similar harsh and cooler conditions. Phylogeographical studies mostly focused on alpine species; however, several studies discussed fen or peatland species. For example, a wider and continuous distribution of *Primula farinosa* in the Carpathian Region is supported by the genetic similarity between the Western Carpathian and Eastern Carpathian populations [100] and by pollen records from the Pannonian lowland [32]. Other genetic evidence indicate the presence of certain orchid species in the region that survived during the LGM in fens and then migrated northwards to Fennoscandia, like *Dactylorhiza traunsteineri* and *D. lapponica* [64], while *Liparis loeselii* and *Malaxis monophyllos* show a low genetic diversity that could indicate a late migration from Asia to the Carpathian Region [46]. *Betula humilis* is considered a glacial relict in Central Europe, but genetic analysis of populations from Poland and Belarus reveals that the species may have not survived the LGM in these areas. However, few populations have shown a higher genetic diversity, which could indicate the survival of the species in isolated groups further south, from which they later re-colonized the northern areas. As a result, the Carpathian Region was an important reservoir of *Betula humilis* populations in the LGM [41].

Macrofossil data also certify the presence of many boreal species during the LGM (e.g., *Polemonium caeruleum, Rhynchospora alba, Scheuchzeria palustris, Lycopodiella inundata, Viola palustris, Sparganium minimum*) in the Carpathian Region. During that period, the Carpathian Region and the Pannonian Plain were characterised by scattered boreal forests (Willis et al., 2001), facilitating these species' survival in a northern cryptic glacial refugia, along with temperate woody and grassy species. Stachurska-Swakoń et al. [89] show that the region was covered with widespread mesic and humid meadows, which indicates that these species were already present and did not arrive here in the Early Holocene. Their local extinction has been probably caused by the warm and arid climate of the Boreal and the formation of compact forests in the Atlantic periods, which led to the extension of forest vegetation to the detriment of the existing meadows and marshes.

Vascular plants, sessile organisms, usually display greater dispersal constraints [31] that can lead, within some parts of their areal, to a long-term isolation in suboptimal conditions and the probability that certain populations become relict [19]. Most of the plants included in our study are characterised by larger ecological tolerance and niche breadth across their entire areal than the one displayed by the populations from the Carpathian Region, spanning from wetland to mesic habitats. However, their long-term isolation in marginal populations led to habitat niche contraction and a decrease in their capacity to re-colonize a wider area. This phenomenon is most prominent in some of the taxa reaching high scoring values in our evaluation: *Betula nana, Ledum palustre, Carex chordorrhiza, Carex loliacea, Carex vaginata, Andromeda polifolia, Salix myrtilloides, Salix starkeana, Saxifraga hirculus,* and *Trichophorum alpinum*. Such species can develop on open ground in the harsh conditions of tundra, as well as in peatlands and nearby springs and fens. Moreover, *Trientalis europaea, Euonymus nanus, Malaxis monophyllos* and *Chimaphila umbellata* can survive in both highly humid (including peatlands) environments and dry, acidic forests. *Polemonium caeruleum, Calamagrostis canescens, Calamagrostis stricta, Angelica palustris* and *Cnidium dubium* can survive in dryer conditions for a few months, while *Crepis sibirica, Polemonium caeruleum,* and *Ligularia glauca* can adapt to both mesophilic tall-herb communities and wetlands. All these species' ecological plasticity and higher adaptability than the one displayed by their relict populations probably enhanced their initial dispersal into refugia across the Carpathian Region, where more competitive flora of the Holocene could not establish itself.

The distribution analyses of glacial relicts in low altitude wetlands confirm the hypothesis of Hájek et al. [30], according to which these rare species could survive in five types of marshes: (i) oligotrophic peat bogs in the high mountain areas with siliceous or volcanic bedrock, such as the whole series of volcanic mountains with acid substrate in the western part of the Eastern Carpathians or the mountains in the Bucovina region from the northern part of the Eastern Romanian Carpathians; (ii) slightly acidic or moderately alkaline fens along the mid-altitude mountain depressions (e.g. the poor fens with *Drosera anglica* and *Saxifraga hirculus* from the Ciuc Depression); (iii) alkaline rich fens from intramountain depressions (e.g. Ciuc, Giurgeu, Drăgoiasa, Bilbor, and Borsec Depressions); (iv) infiltrations of mineral waters rich in limestone at the base of the calcareous mountains (e.g. the springs at the base of Rarău Mountains, with *Carex vaginata*); (v) alkaline fens from low altitudes around mineral rich springs (e.g. the Bârsa, Făgăraș and Sibiu Depressions, the Valea Morii Natural Reserve, the Dumbrava Harghitei Natural Reserve from Vlăhița - western foothills of the Harghita Mountains) and the eastern foothills of the Vlădeasa Mountains (Călăţele peatbog, where *Dactylorhiza lapponica* and the only *Pedicularis sceptrum-carolinum* and *Salix pentandra* populations from the Apuseni Mts. were known). Among these types of marshes, the alkaline fens are considered to be among the richest habitats in relict species [31]. The stability of these mires is maintained by the constant flow of springs, groundwater and streams extremely rich in minerals, which act as a buffer tempering climatic fluctuations and reduce vegetation successions, maintaining the constant and favourable conditions for the survival of some relict populations of cold-adapted species [32]. The most species-rich alkaline fens in the Carpathian region are also the oldest [74, 27]. Thus, the rich fens of Hărman, Prejmer, Bilbor, Drăgoiasa, Borsec, Ciuc and Giurgeu Depressions in the Eastern Carpathians and Valea Morii from north-eastern edge of the Apuseni Mountains, are also the most valuable wetland ecosystems of the South-Eastern Carpathians, essential in preserving rare and relict species (e.g., *Tofieldia calyculata*, *Dactylorhiza traunsteineri*, *Primula farinosa*, *Cladium mariscus*, *Sesleria uliginosa*, *Schoenus nigricans*, *S. ferrugineus*, and *Liparis loeselii*).

Hotspots of diversity, rarity and range-margin in cold-adapted relict populations from the South-Eastern Carpathians

Following the analysis of species distribution, several important richness, rarity and range margin hotspots of cold-adapted species in the Romanian part of the Carpathian Region were highlighted (Fig. 3, 4). These are mainly located along the intra-montane depressions in the Eastern Carpathians, however, several range margin or rarity hotspots were outlined also in the Southern Carpathians and the Apuseni Mountains.

In the central and southern part of the Eastern Carpathians, the continental climate, characterised by colder and dryer conditions during both winter and summer, together with the existence of extensive marshes here contributed to preserving a high number of cold-adapted taxa. The annual average temperature of Ciuc and Giurgeu depressions (5.9° - 6°C), as well as total annual precipitations (< 600 mm) are particularly low for intra-montane depressions situated at 640 – 816 m a.s.l. [70]. Palynological data confirm that the intra-montane depressions of the Eastern Carpathians kept their cold, continental climate throughout the Holocene, as well as their wetlands, which were not affected by the Boreal warming, thus offering adequate conditions for the survival of cold-adapted species to present day. Pine and spruce were present throughout this period, and large amounts of alder pollen, ferns and swamp species indicate the perpetuation of these marshes in the region, being fed by the Olt and Mureș rivers [75, 24]. As a result, the large intramountain basins from the Eastern Carpathians (Giurgeu, Ciuc, and Drăgoiasa-Bilbor-Borsec), acted as major low altitude refugia for relict populations of cold-adapted species [70]. Moreover, the neighboring Nemira, Bodoc, and Harghita Mountains, very rich in wetlands as well, contributed to the present-day conservation of relict species in this region (e.g., *Betula nana*, *Calamagrostis purpurea*, and *Stellaria longifolia*).

Similarly, the cold climate characterising the northern part of the Eastern Carpathians (the eastern part of the Maramureș Mountains, the Rodna Mts., the Obcinele Bucovinene, and the Călimani Mountains), the Dornelor Depression, and the Suceava Plateau, have led to the preservation of extensive pine-covered peatlands that harbored a high number of relict species in this area [70, 5]. Here, rich precipitations during mid-summer (June-July), had a beneficial effect on relict species by maintaining local wetland habitats and a cooler climate [24]. These conditions favored not only the prevalence of spruce forest vegetation at lower altitudes, but also the emergence of extensive marshes and peat bogs covered with woody species (e.g. *Pinus sylvestris*, *Picea abies*, *Betula* spp.), more specific to the vegetation of central Siberia and a high number of cold-adapted relicts, e.g., *Betula nana*, *Carex loliacea*, *Viola epipsila*, *Trientalis europaea*, and *Salix starkeana* in Lucina peat bog (Obcinele Bucovinene) and Dornelor Depression, and *Ligularia glauca*, *Pedicularis sceptrum-carolinum*, *Chimaphila umbellata*, *Euonymus nanus*, *Ligularia sibirica* and *Salix starkeana* in the Suceava Plateau at 300 m [70, 59].

The Eastern Carpathians did not constitute only a climatic refuge for cold-adapted species, but also acted as a transitional zone for Asian species and a contact zone between the Asian and European biotas, possibly representing another explanation for the high number of relicts whose main populations reside here. The continental species have established in the region mainly during the preglacial and glacial periods [54] (e.g., *Achillea impatiens*, *Euonymus nanus*, *Ligularia glauca*, and *Spiraea salicifolia*), a similar case as for some boreal relict species (e.g. *Ligularia sibirica*, *Salix starkeana*, *Betula humilis*, and *Polemonium caeruleum*), and arctic species (e.g., *Betula nana*, *Potamogenton alpinus*, *Carex vaginata*, *Carex chorrdorrhiza*, *Saxifraga hirculus*, and *Trientalis europaea*). Many of these species are no longer found in the Southern Carpathians or the Apuseni Mountains, while some of them did not advance to the Western Carpathians (e.g., *Carex loliacea*, *Achillea impatiens*, and *Euonymus nanus*). The importance of this region as a contact zone is highlighted also by the existence of several endemic species whose closest relatives are of Asian origin: *Silene zawadzkii*, probably diverging from an ancestral Asian species [67]; *Hepatica transsilvanica*, whose hybrid origin were previously shown, with the Eastern Carpathians acting as contact area between Central Asian *Hepatica falconeri* and European species *Hepatica nobilis* [4]; *Astragalus roemeri*, whose probable origins are related also to Asian ancestors [3].

The Southern Carpathians are poorer in low-altitude glacial relicts, both in terms of diversity and abundance, many of which are common in the marshes and mires of the Eastern Carpathians and the Apuseni Mountains. Climate during the Holocene and lack of extensive depressions that limited the establishment of wetlands, did not allow the *in situ* resilience of cold-adapted relicts, even though some of them being recorded through palynological information dating from the Late Glacial Period (e.g., *Betula nana*, *Trientalis europaea*) [55]. However, the main areas harboring extensive lower-altitude peatlands are richer in cold-adapted species found here at their southern range limit. These are mainly located in the upper Sebeș Valley (Frumoasa and Tărtărău valleys) and Oașa Depression, where large populations of the subalpine species *Salix bicolor* reside at the lowest altitude in Romania, i.e. 1200-1400 m, *Andromeda polifolia*, *Vaccinium oxycoccos*, and *V. microcarpum* [70], Cindrel at Boița (*Stellaria longifolia*) and the Lăptici peatbog in the upper montane level of the Bucegi Mountains (1500 m), currently in an advanced state of degradation, where the only population of *Salix myrtilloides* fom Romania was known [17] and also harboring the southernmost populations of *Carex chordorrhiza* and *C. capillaris* (the latter ocurring also in the Sebeș Valley).

Paleoclimate proxies helped to reconstruct the differing trends in climatic oscillations throughout the Holocene between the northwestern and the southwestern regions of Romania, the former being influenced by oceanic air masses from the Atlantic richer in precipitations [24], while the latter by the submediterranean climate, with warm and dry air masses [95, 14]. The wetter climate of the Apuseni Mountains and the northern volcanic ridges of the Eastern Carpathians during the Holocene, especially between 8,000 and 5,000 years BP [25], contributed to the perpetuation of mires harboring glacial relicts that are absent from the southwestern part of the Carpathians. Here, the peatlands are resembling to a higher degree the Atlantic and Northern European ones. The vast plateaus of the Apuseni Mountains are home to the largest number of peat bogs in Romania [11], these originating mainly during the Late Glacial Period [78], and harboring many cold-adapted relicts, e.g., *Drosera intermedia*, *Pedicularis limnogena*, *Carex magellanica* subsp. *irrigua*, *C. limosa*, *C. pauciflora*, and *Rhynchospora alba*.

Finally, the north-western lowland region of Romania is highlighted by the occurrence of several glacial relicts at low-altitudes, which have survived here due to local microclimates and extensive marshes in the past and whose continuity was documented by previous palynological research [56, 105]. The most noticeable are the wetlands from the Nir Plain, where relict species such as *Calamagrostis stricta*, *Calamagrostis canescens*, *Angelica palustris*, and *Betula pubescens* survive at 120 m altitude [94], and the alluvial alder forest from Săcueni locality along the Ier Valley [2], where the presence of *Carex diandra* was first recorded from the region.

The importance of conserving relict populations

Relict species are valuable elements for local and regional biodiversity, while also serving as models in understanding the effects of climate change on organisms across time [22, 38, 1]. However, they are also the most susceptible to local extinctions. The rare, endemic and relict species show a visible population decline due to alteration and fragmentation of habitat, while their populations sometimes manifest a depletion of intra-populational genetic diversity [87], affecting their viability. These populations are more prone to be affected by climate change and human impact also due to the fragility of the wetland habitats, with ecosystem fragmentation and disturbances generated by the introduction of alien species being highly relevant [36]. This aspect is highlighted also when considering that over 15% of the glacial relicts identified here are considered Vulnerable, almost 15% Endangered (*Achillea impatiens*, *Calla palustris*, *Carex dioica*, *Euonymus nanus*, *Ligularia glauca*, *Malaxis monophyllos*, *Polemonium caeruleum*, *Rhynchospora alba*, *Saxifraga hirculus*, *Schoenus ferrugineus*, and *Sparganium minimum*), over 20% are Critically endangered (*Angelica palustris*, *Betula humilis*, *B. nana*, *Carex chordorrhiza*, *C. loliacea*, *Chimaphila umbellata*, *Drosera anglica*, *Drosera intermedia*, *Hammarbya paludosa*, *Liparis loeselii*, *Pedicularis sceptrum-carolinum*, *Potamogeton alpinus*, *Primula farinosa*, *Salix starkeana*, *Sesleria uliginosa*, *Tofieldia calyculata*, *Trientalis europaea*, *Viola epipsila*, and *Viola palustris*), while three taxa are considered to be Extinct (*Ledum palustre*, *Tephroseris palustris*, and *Trichophorum alpinum*), based on the latest overview on plant species red lists from Romania [39]. In order to efficiently preserve the populations of relict species, a prerequisite is to know their origin, genetic diversity, current distribution, and local population development. Even though the distribution of relict taxa is better known than for other, more wide-spread species, information about the structure and size of populations is missing in most cases, making any conservation measure less efficient [59]. Moreover, the distribution knowledge for the vascular flora of Romania is still incomplete, this being valid also for relict elements (over 20% of the taxa in our list still remain unassessed for their extinction risk).

Growing evidence indicates that isolated, disjunct populations may possess a high genetic diversity, often as a result of adaptation to different ecological conditions. Some of these marginal populations are good indicators of glacial refugia, based on the presence of ancestral lineages in their DNA profiles [41]. Consequently, the preservation of their high genetic variability is important for maintaining the evolutionary potential of the species [41]. For example, *Primula farinosa* populations in the Carpathians are genetically well demarcated from those occurring throughout the rest of Europe [100]. This differentiation is reflected also in the ecological niche characteristics, making the Carpathian Region a harbour for some of the most threatened lineages of the species, a particularity that favoured the adaptation of the species to different ecological conditions compared to the mountainous and continental regions of Eurasia [99, 113]. Consequently, the conservation value of relict species is very high due to their biogeographical uniqueness, their indicator value for distribution history and, in some cases their ability to withstand the stress caused by ecological changes over long periods of time [77].

Conclusions

Our study is the first attempt that aims to establish, through a numerical approach, a list of species showing increased glacial relict characteristics occurring in low altitude wetland habitats from the Romanian part of the Carpathian Region. For this purpose, we evaluated the biogeographical and ecological characteristics of selected (sub) species. Out of 171 evaluated taxa, 74 have totalled at least 15 points based on our scoring system, highlighting them as putative glacial relicts. The lack of complete genetic history or fossil information concerning these species make such a numerical approach an even more important option for the delineation of relict elements in the flora of Romania. Further studies including additional species are required; however, we believe that our results will contribute to a better understanding of the distribution, ecological and biogeographical particularities of glacial relict elements in the Romanian flora.

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RELICTE GLACIARE DIN ZONE DE JOASĂ ALTITUDINE ÎN FLORA ROMÂNIEI

(Rezumat)

Relictele glaciare reprezintă populații izolate de specii adaptate regiunilor reci, fiind rămășițe ale distribuției lor în trecut de la latitudini mai sudice față de arealul lor principal din prezent, specii care au supraviețuit in situ departe de zona lor de distribuție actuală odată ce epoca glaciară s-a încheiat. Ne propunem să identificăm, pe baza unei evaluări numerice care utilizează un sistem de punctare aplicat pentru 14 criterii ecologice și biogeografice, cele

mai probabile relicte glaciare ale florei vasculare din partea românească a Regiunii Carpatice. Selecția noastră de taxoni (specii și subspecii) include în principal organisme adaptate climatului rece, care apar în zonele umede din depresiunile intramontane și zonele periferice din regiunile joase, în timp ce speciile care apar mai ales în zonele montane înalte ale Carpaților au fost excluse. Ca urmare, din 171 de taxoni evaluați, 74 sunt considerați ca având caractere clare de relicte glaciare în flora României. În plus, pe baza evaluării distribuției lor, au fost evidențiate hotspoturile de bogăție, raritate și limita marginală pentru acești taxoni în România. Atât bogăția, cât și raritatea relictelor glaciare au arătat cele mai mari valori în Carpații Orientali, ca urmare a suprafețelor extinse de depresiuni intramontane ce adăpostesc vaste zone umede. Pe lângă această zonă principală de răspândire și supraviețuire pentru aceste specii adaptate la frig, au fost identificate mai multe potențiale refugii pe baza distribuției taxonilor extrem de rari în partea de nord-est a Munților Apuseni și în partea de est a Carpaților Sudici (Munții Bucegi). Distribuția populațiilor marginale ale relictelor glaciare din România delimitează două zone de concentrare a acestor taxoni bine individualizate, prima în partea de sud a Carpaților Estici, iar a doua în partea de vest a Carpaților Sudici, de-a lungul văilor și depresiunilor intramontane adânci. Datorită distribuției lor limitate, izolate și a fragilității habitatelor în care apar, astfel de populații sunt mai predispuse să fie afectate de impactul negativ generat de activitățile umane și de schimbările climatice. Prin urmare, studiul nostru poate servi și ca un instrument util pentru eficientizarea măsurilor de conservare prin evidențierea riscului de dispariție a relictelor glaciare din România și prin indicarea zonelor umede de joasă altitudine care necesită o monitorizare mai atentă și măsuri urgente de protecție.

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