Biogeography of the high mountain Lepidoptera in the Balkan Peninsula

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Abstract

Balkanic high mountains represent nearly all types of European vertical zonation. The elevation and vegetation character of the timberline and allied vegetation types (scrubs, tall vs short, closed vs. open rupicolous swards) but also the edaphic traits, etc. considerably influence the biogeographical composition of butterfly and moth assemblages. The habitats of the high elevations are populated by several types of mountain species. They belong to five main biogeographical groups: (i) boreo-montane (“Siberian”) species, often represented by isolated, partly differentiated populations mostly in the coniferous forests zones; (ii) arctic-alpine (in majority Eurasian!) species represented by isolated, most often taxonomically differentiated populations in alpine zones of highest Balkanic mountains; (iii) alpine (nearly exclusively European!) species represented by isolated, mostly taxonomically differentiated populations in subalpine-alpine zones of Balkanic mountains; (iv) Balkanic-oreal species often with isolated populations (subspecies) also in the Southern or Southwestern Alps and Massif Central, in special cases also Appenines and/or in Southern and Eastern Carpathians, as well; (v) oro-Mediterranean-xeromontane species occurring in the southern Balkanic mountains, being either endemic or represented by differentiated subspecies of western Asiatic species. The most typical biogeographical patterns in butterflies and macro-moths are as follows: (i) close connections of the western Balkanic (Dinaric) populations of alpine and arctic-alpine species with southeastern Alpine ones; (ii) close connections of the eastern Balkanic (Thracian) populations of alpine and arctic-alpine species with southern Carpathian ones; (iii) the “Central Balkanic split” in taxonomic subdivision of several alpine and arctic-alpine species; (iv) the southern limit of distribution of boreo-montane, arctic-alpine and alpine species agrees with the “Adamović-line”, i.e. the southern limit of the alpine type of vertical zonation of vegetation; (v) the northern limit of oro-Mediterranean xeromontane species also well agrees with this important line, since these species are connected with the oro-Mediterranean type of vegetation (partly by food plant specialisations, see: endemic Polyommatina or by rupicolous habitats, as some Noctuinae).

Key words: vertical zonation, timberline, boreo-montane, arctic-alpine, alpine, Balkanicoreal, xeromontane, central Balkanic split, Adamović-line.

Introduction

The Balkan peninsula shows essential differences compared with the other Mediterranean peninsulas. It is not barriered by west-eastern high mountains as the Pyrenées and Alps but firmly connected to south-eastern Central Europe by high mountain ranges running from north-west to south-east as the Dinaric mountains on the western flank and the Stara Planina mountains in the East. Both are in South continued in the Shar-Korab massiv, the Albanian Alps and Pindos in one side, and the Rila-Pirin-Rodope massiv on the other. These
mountains often overrange the 2500 m elevation and the highest parts are reaching nearly 3000 m asl. (e.g. Rila, Pirin, Olympos). They regularly have extended plateau-like surfaces above the timberline (North Albanian Alps, Šar Planina, Korab, Rila) and exhibit typical alpine geomorphological features (e.g. Durmitor, North Albanian Alps, Šar Planina, Korab, Rila, Pirin). Thus, the biogeographical character of the Balkan peninsula is rather complex. Its southern and Adriatic parts represent one of the main survival areas (refugia) of the temperate flora and fauna (e.g. Reinig 1937, 1950; de Lattin 1957, 1967; Varga 1977; Taberlet et al. 1998; Hewitt 1999, 2000; Schmitt 2007), with several smaller core areas ('refugia within refugia') and centres of spot-like endemisms (e.g. Bilton et al. 1998; Médail and Diadema 2009; Podnar et al. 2013). It was shown that the Pontic-Mediterranean core areas of the Balkan Peninsula are generally of higher importance for the recolonisation of major parts of Europe than the Atlantic- or Adriatic-Mediterranean ones (Hewitt 1999, 2004; Habel et al. 2005). On the other side, its northern montaneous parts, together with the Carpathians, belonged to the most important extra-Mediterranean refugia as core areas of survival of numerous continental species (e.g. Pinceel et al. 2005; Kotlik et al. 2006; Ursenbacher et al. 2006; Schmitt 2007; Schmitt and Varga 2009, 2012; Varga 2010). In addition, the high mountains of the Balkan peninsula support a rich and biogeographically richly articulated mountain flora and fauna consisting of several biogeographical elements (Varga 1975, 1996; Schmitt 2009; Schmitt and Varga 2009, 2012).

Species diversity, substrate, climate and vegetation

Species numbers
The highest number of alpine and arctic-alpine species is known to occur in the mountains with the most extended alpine belts, e.g. Central and Eastern Pyrénées, Central Alps, highest massifs of the Southwestern and Southern Alps, Southern Carpathians, highest mountains of the Balkan peninsula (Šar-planina, Korab, Rila, Pirin). Thus, e.g. the overall number of oreal species in the Carpathians, belonged to the most important extra-Mediterranean refugia as core areas of survival of numerous continental species (e.g. Pinceel et al. 2005; Kotlik et al. 2006; Ursenbacher et al. 2006; Schmitt 2007; Schmitt and Varga 2009, 2012; Varga 2010). Numerous data of horizontal and vertical distribution of Lepidoptera in the Carpathians and in the Balkanic high mountains have been already published (e.g. by Abadjiev 1992-95, 2001; Alexinschi 1960; Alexinschi and König 1963; Beshkov 1995, 1996, 2009a, 2009b, 2010; Beshkov and Langourov 2004; Buresch and Tuleshkov 1929-1943; Busse and Ockruck 1991; Caradja 1930; Coutsis 1969, 1972; Coutsis et al. 1997; Coutsis and Ghavalas 1991; Daniel 1964; Diószyghy 1929-30, 1936; Drenowsky 1923, 1925, 1928, 1930a, 1930b, 1930c, 1931, 1933, 1936; Goltz 1935-36; Huemer 2010; Beshkov and Langourov 2004; Buresch and Tuleshkov 1929-1943; Busse and Ockruck 1991; Caradja 1930; Coutsis 1969, 1972; Coutsis et al. 1997; Coutsis and Ghavalas 1991; Daniel 1964; Diószyghy 1929-30, 1936; Drenowsky 1923, 1925, 1928, 1930a, 1930b, 1930c, 1931, 1933, 1936; Goltz 1935-36; Huemer et al. 2011; Jaksic 1988; König 1959, 1975, 1982; Koutroubas 1994; Koutsafitiks 1974; Krzywicki 1963; Michieli 1963; Niessolowsky 1929, 1936; Niessolowsky and Woytusiak 1937; Pamperis 1997; Pinker 1968; Popescu-Gorj 1952, 1962, 1963, 1964, 1971), Rákosy 1992a, 1992b, 1995, 1997, 1998; Rebel 1903, 1904, 1911; Rebel and Zerny 1931; Schauder and Jakišić 1989; Sijarić 1971, 1980; Sijarić et al. 1984; Thurner 1948, 1964; Tuleschakov 1929, 1930, 1931, 1932, 1955, 1965; Varga 1971, 1975, 1995, 1999, 2003; Varga & Slivov 1977; Verovnik et al. 2010; Vihodcevski and Gogov 1963; Züllich 1936). The species numbers and the extension of glaciations in SE Europe are presented in Holdhaus (1954) and Varga (1995, 2003). From these data we can conclude, that the total number of species and the number of endemic species are only partly correlated (see also: Huemer 1998; Williams et al. 1999).

The connection of the vertical distribution of Lepidoptera with the climatic conditions and vertical zonation of the vegetation
The distribution of oreal species mostly depends on the elevation of the timberline. However, it is often influenced by the meso- and micro-climatic conditions. Arctic-alpine and alpine species occur e.g. on the northern slopes of the Carpathians at relatively low altitudes because of a suppression of the timberline due to the harsh climatic conditions (e.g. Tatra Mts., Rodna and Retezat Mts.). We can also observe a relatively depressed tree line in the high mountains influenced by the summer aridity of sub-Mediterranean and Mediterranean climatic belts. In these mountains we encounter a scrubby sub-alpine beech forest zone which is under semi-arid conditions followed upwards by a bushy-steppic formation typically consisting of tall grasses (Stipa spp., Festuca paniculata) and low scrubs (e.g. Fabaceae: Cytisanthus radiatus, Chamaecytisus absinthioides, Genista depressa, etc.). Sub-alpine beech forest dominates also on the southern slopes of the Stara Planina, contrasting with the spruce tree-line of northern slopes. The sub-alpine beech or beech-fir forest as the uppermost woody level is widely distributed also in the Dinaric high mountains but also in central Macedonia, e.g. in the Jakupica planina) where the beech-fir timberline is surprisingly followed by
Table 1. Species numbers of arctic-alpine, alpine and Balkanic orreal Macrolepidoptera in some parts of the Carpathians and in Balkan high mountains.

| Faunal type         | North Carpathians | East Carpathians | South Carpathians | Crna Gora-N Albania | Šar-planina & Korab | Rila | Pirin |
|---------------------|-------------------|------------------|-------------------|---------------------|--------------------|------|------|
| Arctic-alpine       | 5                 | 10               | 9                 | 12                  | 11                 | 8    | 8    |
| Alpine              | 19                | 18               | 17                | 19                  | 20                 | 18   | 16   |
| Balkanic orreal     | 0                 | 1                | 2                 | 8                   | 9                  | 9    | 9    |
| Total               | 24                | 29               | 28                | 39                  | 40                 | 35   | 33   |

dense stands of *Pinus montana*. In the karstic high mountains also the zone-inversion is often observed in the cool, deep valleys or in karstic depressions (*dolina*, or called *ponjikve* in the Croatian mountains, Horvat 1959, 1962; Horvat & al. 1974). On the other side, the more continental high mountains of Bulgaria, as Rila and Pirin exhibit a relatively high-lying limit of woody vegetation, formed by spruce and Balkanic coniferous trees as *Pinus peuce* (preferably on acidic substrate) or *P. heldreichii* (on calcareous substrate) followed by tall swards of *Festuca paniculata* and scrubby formation of *Bruckenthalia spiculifolia* and *Daphne oleoides*.

Thus, the Balkan high mountains show in limited dimensions nearly the complete diversity of European vertical zonation or "Stufenfolgen" (Adamović 1909; Horvat 1962; Walter & Straka 1970; Grabherr et al. 1994) of vegetation which shows at least four different major types in the European high mountains. In the Northern and Central Alps the Helvetic type of zonation predominates with a timberline formed by spruce (*Picea abies*), often with groups of *Pinus cembra*. In the continental Inner Alpine areas (e.g. parts of Wallis, Upper Engadin, parts of Ötztaler Alp) the Penninian type of zonation is widespread consisting of three different coniferous belts: a Scotch pine belt (often with birch), a zone of spruce and the highest level is predominated by larch (*Larix decidua*). In the Submediterranean zone either some variations of the Helvetic type can be observed, or the Insubric type of zonation occurs with sub-alpine beech or beech-fir forests, often with inserted tall-grass or scrubby mountain steppe-like formations (parts of Pyrenees, Appenines, Insubric Alps, Dinaric Mts). Finally, the Mediterranean zone is characterised by special types of high mountain coniferous forests (e.g. Balkanic *Abies* species), scrubs, cusheon plant formations and dry grasslands of Oro-Mediterranean type. In the humid high mountains with the Helvetic and Penninian type of vertical zonation the high-lying open biomes are bordered, as a rule, by a nearly continuous timberline. In addition, the zonation of dense alpine scrub- and tall-forb communities ("Krummholz", scrub-like *Pinus*, *Juniperus*, *Betula*, *Rhododendron* and different *Ericaceae*) typifies the "kampfzone" of arboreal and non-arboreal biomes.

The occurrence of the arctic-alpine (e.g. *Zygaena exulans*, *Pyrgus andromedae*, *Erebia pandrose*, *Glacies coracina*, *Gramma quenseli*, *Agrotis fatidica*, etc.) and alpine species (e.g. *Pyrgus cacalae*, *Euphydryas cynthia*, *E. tyndarus-group*, *E. gorge*, *E. pronoe*, *Glacies canaliculata*, *G. noricana*, *G. bentelli*, *Apamea zeta*, etc.) is usually connected with the Helvetic and/or Penninian types of vertical zonation. They need the presence of a “true” alpine elevation with adequate types of vegetation, as the alpine turfs: "*Matten*", cusheon plants, dwarf scrubs of lattice ("*Spalier*”) vegetation, etc. They reach a southern boundary of occurrence in the Balkan peninsula at the “*Adamović-line*” due to the basic change of vertical zonation (Varga 1975, 1977b, 1995a; Varga 2003; Fig. 1).
Figure 1. Southern boundary of arctic-alpine and alpine species on the Balkan peninsula and the Adamović-line. The high mountain systems of southeastern Europe, their number of arctic-alpine marco-Lepidoptera species (numbers in circles) and the occurrence of xeromontane species (triangles). The Adamović line is marked with “A”. The southern boundary of true alpine and arctic-alpine species is marked with broken line. Legend: EC – Eastern Central Alps; JA – Julian Alps; HT – High Tatra & Belanské Tatry; R – Rodna Alps; BC – Bucegi and Piatra Craiului; Rt – Retezat Mts; Tr, Pr, Cv, V – Trebević, Prenj, Cvrstnica, Vranica planina; D – Durmitor & Maglič; NA – N Albanian Alps; S – Šar Planina; Jb – Jablanica; Ko – Korab; R – Rila Mts; P – Pirin Mts; Ro – Rodopi Mts; AB – Ali Botus–Orvilos; F – Falakron; B – Baba Planina (Pelister); G – Galičica Planina; T – Tomor; Gr Grammos; O – Olympos; Sm – Smolika; Ty – Trychonis; Parnassos; Ch – Chelmos; E – Erymanthus; K – Korynthos; T – Taygetos; Pn – Parnon.
The vertical distribution of Balkanic or real species shows several characteristic differences as opposed to the alpine and arctic-alpine species. They are most numerous at the timberline. Their preferred habitats are grasslands in the upper subalpine belts. Only some few species are connected to the (mostly lower!) alpine elevations (2000-2400 m), and they exceptionally also occur at lower altitudes below the timberline (Coenonympha rhodopensis, Erebia orientalis, E. rhodopensis, Aplocera simpliciata). Some other species display a transitional character: they predominantly occur in lower-alpine and sub-alpine elevations with a mosaic-like scrub and grassland vegetation (e.g. in the Pirin Mts: Pinus mugho and Juniperus sibirica, Bruckenthalia spiculifolia and Daphne oleoides dwarf shrubs and grassy vegetation predominated by Festuca paniculata and Stipa spp.), or in steppe-like grasslands with abundant tall-forbs. Typical species of this vegetation type are e.g.: Polyommatus eroides, Boloria graeca, Erebia ottomana, Aplocera lithoxylata, Xestia ocharea, while other species occur mostly in humid sub-alpine meadows and tall-forb habitats, e.g. Lycaena candens. Some Balkanic or real species but mostly the xeromontane species (x) are confined to rocky habitats with scarce vegetation (figs. 16-17), e.g. Agriades dardanus (x), Polyommatus (Agrodiaetus) nepholiptamenos, P. (A.) orphicus (x), Erebia melas, Pseudochazara graeca (x), P. orestes (x), P. cingovskii (x), P. geyeri occidentalis (x), P. graeca (x), Elophos certthius, Hadena clara macedonica (x), H. vulcania urumovi (x), Hadena drenovskyii (x), Rhyacia psamnia starvoiticius (x), Rhyacia (Epilipsia) cervantes (x), Chersotis fimbriola ssp., Chersotis laeta leonhardti (x), Ch. capnistis schnacki (x), Dichagyris (Yigoga) gracilis etoliae (x), Euxoa decora macedonica (x), etc. (Varga 1975, 1996; Schmitt and Varga 2009).

The influence of the substrate and habitat type on the vertical distribution

The vertical distribution of butterflies and moths is generally influenced by substrate type and by the vertical belts of vegetation. The occurrence of some arctic-alpine species, e.g. Melanarta melanopa rupestralis, Pyrgus andromeda seem to be connected with the tundra-like geomorphological formations, as skeletal soils with Dryas octopetala-cusheons, e.g. in Pirin Mts. Many species prefer the slopes covered by erratic blocks or gravel. The apparent petrophyll of several alpine and arctic-alpine species correlates with their sheltering behaviour under harsh weather conditions, e.g. in daily active geometrid species, as Entephria nobiliaria, E. cyanata, Glacies coracina (x) and other species occur mostly in humid sub-alpine meadows and tall-forb habitats, e.g. Lycaena candens. Some Balkanic or real species but mostly the xeromontane species (x) are confined to rocky

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fairly widespread both in the Carpathians and in the western Balkans is *E. epiphron*. Its sister species, *E. orientalis* exclusively occurs in the eastern Balkanic high mountains (Fig. 2) and is subdivided into three subspecies: *E. o. orientalis* in the Rila, *E. o. infernalis* in the Pirin Mts. and *E. o. macrophthalmata* in the Western and Central Stara Planina). *Erebia manto* (as *E. manto osmanica*) occurs exclusively in the Dinarids of Bosnia, *E. albergana* (as *E. albergana phorcys*) at moderate altitudes (1200-1600 m, exceptionally from 700 m) near to the beech-forest timberline, on the southern slopes of the Western and Central Stara Planina and in the Korab Mts. while *E. oeme* is one of the most widely distributed *Erebia* in the subalpine-alpine levels of the Balkanic high mountains, although it is extremely localised and scarce in the Carpathians (Retezat, Făgăraș Mts.). There are relatively few alpine-subalpine butterfly species in the Balkan peninsula which are connected with the rocky and gravelly habitats with scarce vegetation, e.g. *E. gorge* (widespread in European high mountains, Fig. 3), *E. melas* (Balkans, northwestern Dinarids: Nanos, Southern and Eastern Carpathians, Mti Apuseni, Fig. 4); but also several species of the Geometrid moth genera *Glacies*, *Elophos* and *Charissa* (Geometridae) prefer these habitats (Povolny and Moucha 1956, 1958; Varga 1975, 1996, 2003; Varga and Varga-Sipos 2002; Schmitt and Varga 2009).
Figure 3. Distribution of *Erebia gorge* on the Balkan peninsula and in the Carpathians. The populations of the southeastern Alps and western Balcanic mountains are closely related, the populations of the Carpathians and the Bulgarian high mountains belong to another group. Legend: western subspecies: G – *Erebia gorge gorge*; V – *E. gorge vagana*; H – *E. gorge hercegovinensis* (Dinaric Mts); A – *E. gorge albanica*; (the latter with reduction of apical ocelli); eastern subspecies: R – *E. gorge rudkwyki*; FK *E. gorge friderikokenigi*; P – *E. gorge pirinica* (in Rila Mts often in f. triopes).

**Habitat partitioning in closely related species**

The vertical distribution of butterflies is probably influenced also by the competition of closely related species. We only have very scattered data on the butterfly assemblages (e.g. the publications of Balletto *et al.* 1977; 1992a, 1992b; Rákosi 1992a) and on the horizontal vs. vertical dispersion of butterflies in the European mountains (Varga and Varga-Sipos 2002). The interpretation of vertical shifts is based mostly on anecdotic informations and only rarely on the analysis of abiotic vs. biotic factors. It would be necessary to form a data-basis from literary and museal data, and to compare it with the results of recent surveys, carried
out in high mountains of different geographical latitudes. Closely related species often show different types of habitat partitioning. A humid vs. dry habitat partitioning, combined with some vertical shifts, is characteristic for the sibling species of the Boloria pales-species group (Fig. 5). A typical sward vs. gravel partitioning has been observed e.g. in Erebia rhodopensis (grasslands) and E. gorge (gravel) in several Balkanic high mountains (Fig. 6).

Figure 4. Distribution of Erebia melas on the Balkan peninsula and in the Carpathians. Legend: 1 – Erebia melas leonhardi; 2–3 – E. melas acoris (2) and E. melas nanos (3); 4 – E. melas of the Rtanj Planina (probably extinct); 5 – E. melas melas; 6 – E. melas koenigiella (instable altitudinal form of E. m. melas); 7–9 – E. melas carpathicola (7, 8) and E. melas runcensis (9). Legend of the inlayed map: white sector – reddish coloration, black sector – black wing coloration; left side of the circle: male upper- and underside, right side of the circle: female upper- and underside (Hungarian Natural History Museum, Zoological State Collection Munich and coll. Varga, Debrecen).

The vertical distribution of the alpine species displays a characteristic geographical trend. While they often occur in the Alps and Carpathians near and not exclusively above the timberline, their distribution is shifted essentially higher in the Balkan mountains (Drenovsky 1925, 1928; Rákosy 1992a, b, 2013; Varga 1975, 2003; Varga and Varga-Sipos 2002; Table 2). They do not occur at the sub-alpine meadows, at the clearings of the uppermost coniferous zone or of the ‘krummholz’ belt. These habitats are regularly populated by the Balkanic oreal group of species. The Balkanic oreal butterfly species mostly populate the tall-grass dry or mesic grasslands near or over the timberline (e.g. Festucetum paniculatae, Stipa grasslands), e.g. Boloria graeca, Erebia orientalis, E. rhodopensis, E. ottomana as do also numerous typical Balkanic bush-cricket species such as Psorodonotus spp. and Anterastes sericus. The Balkanic endemic Pinus species, P. heldreichii and P. peuce form light-penetrated, scattered stands and the Balkanic oreal butterfly and
Table 2. Vertical distribution (in 1000 m’s) of some butterfly and day-flying moth species in the Carpathians and in some high mountains of the Balkan Peninsula

| Species                     | Tatra Mts. | Bucegi Mts. | Retezat Mts. | Durmitor Mts. | Šar-planina | Rila Mts. | Pirin Mts. |
|-----------------------------|------------|-------------|--------------|---------------|-------------|-----------|------------|
| Zygama exulans              | 2.0-2.3    |             | 2.1-2.45     | 2.1-2.6       |             |           |            |
| Pyrgus cacaliae             | 1.9-2.3    |             |              |               |             |           |            |
| Pyrgus andromedae           |            |             | 2.2-2.5      | 2.3-2.7       | 2.5-2.7     |           |            |
| Boloria pales              | 1.6-2.3    | 1.8-2.4     | 1.95-2.3     | 2.2-2.65      | 2.2-2.7     | 2.4-2.8   |            |
| Boloria graeca              |            |             | 1.7-2.1      | 1.8-2.25      | 1.6-2.3     | 1.7-2.3   |            |
| Euphydryas cynthia          |            |             |              |               |             |           |            |
| Erebia epiphron             | 1.3-1.9    | 1.5-2.2     | 1.35-2.3     | 1.7-2.2       | 2.1-2.6     |           |            |
| Erebia orientalis           |            |             |              |               |             | 2.1-2.7   | 2.3-2.7   |
| Erebia sudetica             |            |             |              |               | 1.5-1.7     | 1.6-1.95  |            |
| Erebia pharte               | 1.6-2.1    |             |              |               | 1.5-2.1     |           |            |
| Erebia manto                | 1.1-1.7    | 1.25-2.1    |              | 1.3-2.1       |             |           |            |
| Erebia rhodopensis          | 1.7-2.3    | 1.8-2.45    | 1.8-2.35     | 1.9-2.35      | 2.1-2.7     | 2.2-2.75  | 2.4-2.9   |
| Erebia melas                |            |             |              |               | 1.6-2.1     | 1.7-2.2   | 1.55-2.55 |
| Erebia cassioide            | 1.55-2.1   | 1.9-2.3     | 1.95-2.5     |               | 2.2-2.6     | 2.3-2.6   |            |
| Erebia ottomana             |            |             |              |               | 1.55-2.1    | 1.7-2.1   | 1.65-2.25 |
| Erebia pronoe               |            |             |              |               | 1.5-2.1     | 2.0-2.3   | 1.85-2.3  | 2.1-2.3   |
| Erebia pandrose             | 1.75-2.3   | 2.1-2.4     | 1.8-2.4      | 2.1-2.4       | 2.1-2.6     | 2.3-2.75  |            |
| Anaitis simplicia           |            | 1.8-2.2     | 1.6-2.3      | 1.7-2.3       | 1.9-2.5     | 1.95-2.55 |
| Psodos coracinus            | 1.9-2.1    | 2.1-2.3     | 1.9-2.5      |               | 2.5-2.7     | 2.5-2.9   |            |
| Psodos canaliculatus        | 1.9-2.3    | 1.85-2.3    | 2.1-2.5      |               |             |           |            |
| Psodos benteli              | 2.1-2.3    | 2.15-2.4    |             |               |             |           |            |
| Grammia quenselii           | 2.3-2.4    |             |             |               |             |           |            |
| Syngapha rilaecacuminum     |            |             |             |               |             |           | 2.3-2.7   |

Some other Balkanic oreal species are connected with rocky habitats. The *Erebia* species show some interesting combinations of vertical and habitat type partitioning, i.e. swards vs. rocky habitats. The partitioning of the species of the *Erebia pluto* group (Warren 1936) and of the ecologically partly similar species *E. melas* is shown in five mountains (Fig. 6). In several areas of the Alps, Carpathians and Balkanic high mountains more species occur sympatriically, but usually with restricted habitat overlaps. *E. cassioide neleus*, for example, has a relatively wide sub-alpine to alpine range (1550 m - 2100 m) in the Retezat Mts. where the Balkanic *E. ottomana* does not occur, while the Balkanic subspecies *E. cassioide illyromacedonica* and *macedonica* seems to be restricted to the alpine zone (2200 m - 2600 m) in the Šar-planina, and also in the Rila and Pirin Mts., where the sub-alpine zone is occupied by strong populations of *E. ottomana* (Varga and Varga-Sipos 2002; Louy et al. 2014). The petrophilic Balkanic *E. melas* often shows a vertical exclusion with the taxonomically not very closely related alpine *E. gorge* in many Balkanic high mountains (e.g. in Durmitor, Šar-planina, Rila and Pirin Mts.). *E. gorge* is restricted to the alpine zone, where the montane/ sub-alpine *E. melas* does not occur. On the contrary, in the Olympus Mts., where no other *Erebia* spp. occur, *E. melas* occupies a wide range of rocky habitats, to the highest alpine levels (Fig. 6).

1 Incl. Belanské Tatry
Figure 5. Vertical distribution of the *Boloria pales*-group in European high mountains. The niche overlap is between the synpatric species is mostly insignificant.

Figure 6. Vertical distribution of the *Erebia pluto*-group + *E. melas* in European high mountains. The niche overlap is between the synpatric species is mostly insignificant.
We cannot demonstrate based on these mainly anecdotic data the existence of competitive exclusion, however, there is a clear indication of some geographical trends.

**Faunal types in the Balkanic high mountains: patterns of distribution and taxonomic subdivision**

**Main faunal types and patterns of distribution**

The Balkanic high mountains are inhabited by numerous characteristic butterfly and moth species belonging into the following five main biogeographical groups:

(i) Boreo-montane species (Varga 1977b, 2010b). They are mostly connected to the montane-subalpine coniferous zone of the Balkanic high mountains, as e.g. *Erebia euryale*, *Eurois occulta*, *Anaplectoides prasina*, *Papestra biren*, *Polia hepatica*, *Mniotype adusta*, but also regularly to some intrazonal grassy-herbaceous habitats as *Boloria titania* (only in Dinaric high mountains), *Lasionycta proxima*, *Apamea furva*, *A. rubirena*, *Photedes captiuncula*, or to rupicolous formations as *Parnassius apollo*, *Lasionmata petropolitana*, *Xestia ashworthii*, *Epipsilia grisescens*\(^*\), *Standfussiana lucernea*\(^*\), *Hadena caesia*\(^*\). Some species of this type of distribution seem to have a xeromontane origin (see: \(^*\)). Other species, like *Lycaena helle*, *Boloria eunomia* occupy only some very scarce marshy-boggy habitats in the Western and Central Stara Planina.

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**Figure 7.** Vertical distribution of the alpine and Balkanic oreal species in the Pirin Mts. Legend: Horizontal lines 1 – upper limit of grassy vegetation (Vihren, 2915 m), 2 - upper limit of *Pinus montana* (isolated scrubs) ~ 2600 m, 3 – upper limit of *Pinus montana/Juniperus nana* zone ~ 2400 m, 4 – lower limit of Arctic-Alpine cusheon plants and dwarf scrubs ~ 2300 m, 5 – upper limit of *Pinus heldreichii* stands. Vertical lines: 1 – *Boloria graeca*, 2 – *Erebia melas*, 3 – *E. ottomana*, 4 – *E. orientalis*, 5 – *E. rhodopensis*, 6 – *Boloria pales*, 7 – *Euphydryas cynthia*, 8 – *Erebia cassioides*, 9 – *E. gorge*, 10 – *Glacies coracina*.
(ii) Alpine species. The species connected with mesic or humid habitats have, as a rule, a very restricted Balkanic distribution as *Erebia manto* (Fig. 10), *E. albergana*. Some species of the grassy or rupicolous alpine habitats show a rather wide Balkanic distribution, e.g. *Boloria pales* (Fig. 9), *Erebia epiphron* (Fig. 2), *E. gorge* (Fig.3), *E. cassioides* (Figs. 8, 10), *E. pronoe, E. oeme*. These species are – with the exception of *E. epiphron* – much more scarce and/or local in the Carpathians. It is typical that the Balkanic high mountains with the most extended alpine belts, e.g. Durmitor, Šar-planina, Rila, Pirin, support a more diverse assembly of *Erebia* species than the highest parts of the Carpathians. Other species are restricted to the highest western* and/or eastern* Balkanic mountains with long distance disjunctions, e.g. *Pyrgus cacaliae, Euphydryas cynthia* (Fig. 11), *Glacies canaliculata*, *Orphne tenebraria*, *Entephria nobiliaria, Gnophos obfuscatus* (Varga 1975; Schmitt 2009; Schmitt and Varga 2009; Varga and Schmitt 2010).

(iii) The not numerous arctic-alpine species exclusively occur in the highest Balkanic mountains (as Durmitor, North-Albanian Alps, Korab, Šar-planina, Rila, Pirin) like to the Carpathians, as *Zygaena exulans*, *Erebia pandrose, Pyrgus andromedae, Glacies coracina, Pygmaena fusca*. Other arctic-alpine species of the highest Balkanic mountains do not occur in the Carpathians, as e.g. *Melanarta melanopa rupestralis, Agrotis fatidica* (Fig. 12). They are strictly connected to alpine elevations with glacial morphology and dwarf scrub and cushion vegetation (Varga 1975; Schmitt and Varga 2009; Varga and Schmitt 2010). The endemic (Rila, Ossogova) *Sygrapha rilaecacuminum* is the sister species of the arctic-alpine *S. devergens.*

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**Table 3. Vertical distribution of alpine - balkanic-oreal species pairs or groups.**

| Mountains       | Alpine          | Balkanic I          | Balkanic II          |
|-----------------|-----------------|---------------------|----------------------|
| **Boloria pales** |                 |                     |                      |
| Tatra Mts       | 1600-2300 m     |                     |                      |
| Piatra Craiului | 1700-2100 m     |                     |                      |
| Bucegi          | 1800-2400 m     |                     |                      |
| Durmitor        | 1950-2300 m     | 1700-2100 m         |                      |
| Sar-planina     | 2200-2650 m     | 1800-2250 m         |                      |
| Rila            | 2200-2700 m     | 1600-2300 m         |                      |
| Pirin           | 2400-2800 m     | 1700-2300 m         |                      |
| N Pindos        |                 | 1700-2100 m         |                      |
| **Boloria graeca** |                 |                     |                      |
| Tatra Mts       |                 |                     |                      |
| Piatra Craiului |                 |                     |                      |
| Bucegi          |                 |                     |                      |
| Durmitor        |                 |                     |                      |
| Sar-planina     |                 |                     |                      |
| Rila            |                 |                     |                      |
| Pirin           |                 |                     |                      |
| N Pindos        |                 |                     |                      |

**Erebia cassioides**

| Mountains       | Alpine          | Balkanic I          | Balkanic II          |
|-----------------|-----------------|---------------------|----------------------|
| Retezat Mts     | 1550-2100 m     |                     |                      |
| Durmitor        | 1900-2300 m     | 1550-2100 m         |                      |
| Sar-planina     | 1950-2500 m     | 1700-2100 m         |                      |
| Rila            | 2200-2600 m     | 1650-2250 m         |                      |
| Pirin           | 2300-2600 m     | 1700-2350 m         |                      |
| Rodopi Mts.     | 1600-2100 m     |                     |                      |
| N Pindos        |                  | 1700-2500 m         |                      |

**Erebia melas**

| Mountains       | Alpine          | Balkanic I          | Balkanic II          |
|-----------------|-----------------|---------------------|----------------------|
| Tatra Mts       | 1700-2300 m     |                     |                      |
| Bucegi          | 1800-2450 m     |                     |                      |
| Piatra Craiului | 1850-2200 m     |                     |                      |
| Retezat         | 1800-2350 m     | [1800-2100 m]       |                      |
| Durmitor        | 1900-2350 m     | 1600-2100 m         |                      |
| Sar-planina     | 2100-2700 m     | 1700-2350 m         | 2100-2500 m          |
| Rila            | 2200-2750 m     | 1700-2200 m         | 2200-2700 m          |
| Pirin           | 2400-2900 m     | 1550-2550 m         | 2100-2600 m          |
| N Pindos        | 1700-2300 m     | 2100-2300 m         |                      |

**Erebia rhodopensis**
Figure 8. Allo- and parapatric distribution of *Erebia tyndarus*-group in Europa. The Balkanic populations (Durmitor, Maglić, Volujak: *R. cassioides illyrica*; Šar planina, Korab: *E. cassioides illyromacedonica*; Stara Planina: *E. cassioides kinoshitai*; Rila, Pirin: *E. cassioides macedonica*) are allied to the Southern Carpathian *E. cassioides neleus*. Further abbreviations: *c* *E. cassioides cassioides*, *ca* *E. calcaria*, *a* *E. arvernensis*, *ni* *E. nivalis*, *h* *E. hispania*.

Figure 9. Distribution of *Boloria pales* on the Balkan peninsula and in the Carpathians. The western Balkanic populations are connected with the Eastern Alpine nominotypic subspecies. The Southern Carpathian populations (*B. pales carpathomeridionalis*) are related to the Eastern Balkanic *B. pales rilaensis*. 
Figure 10. Distribution of *Erebia manto* (black circles) and *E. cassioides* (open circles) in the high mountain systems of southeastern Europe. *E. manto* is widely distributed in the Carpathians, partly as the nominotypic subspecies (N-NE Carpathians), partly as *E. manto trajanus* (E and S Carpathians). It occurs as *E. manto osmana* only in some high mountains of Bosnia. *E. cassioides* occurs in the western Balkan Peninsula as *E. cassioides illyrica* (Crna Gora) and *illyromacedonica* (FYR Makedonia and Greek Macedonia), and as *E. cassioides kinoshitai* (Stara Planina) and *E. cassioides macedonica* (Rila, Pirin) in the eastern high mountains of the peninsula.

(iv) The Balkanic-oreal species belong to the most typical members of the fauna of Balkanic high mountains. Most species of this group are quite generally distributed, e.g. *Colias caucasica balcanica*, *Boloria graeca* (Fig. 13), *Erebia ottomana* (Fig. 14), *E. melas* (Fig. 4), *Coenonympha rhodopensis*, while *C. orientalis* has a rather local distribution in the southern Dinaric mountains. Oppositely, the sister species of *Erebia epiphron*, *E. orientalis* (Fig. 2) is restricted to the three eastern Balkanic high mountains Stara Planina, Rila and Pirin (Varga 1975; Schmitt 2009; Schmitt and Varga 2009; Varga and Schmitt 2010). *E. rhodopensis* is the sister species of the SW alpine *E. aethiopella* and is very typical for the higher levels of the Balkanic high mountains (Fig. 15).
Figure 11. Distribution of Euphydryas cynthia in Europe. c – Euphydryas cynthia cynthia; a – Euphydryas cynthia alpicola; l – Euphydryas cynthia leonhardi; d – Euphydryas cynthia drenovskyi. The population of the Rila Mts shows some parallel characters (e.g. reddish submarginal spots in males, less dichrous females) with the nominotypic subspecies. The population of the Pirin Mts is characterised by whitish submarginal spots in males and more dichrous colouration in females, as in the subspecies E. cynthia alpicola.

(v) The oro-Mediterranean-xeromontane species are generally restricted to the southern Balkanic high mountains, e.g. Colias aurorina heldreichii*, Polyommatus iphigenia nonacriensis*, P. aroaniensis*, P. eleniae*, P. nephohiptamenos*, P. menelaos*, P. andronicus*, P. (A.) orphicus* Pseudochazara graeca*, P. sintenisi*, P. geyeri occidentalis*, (Fig. 16) Agriades dardanus, (cf. Varga 1975, 1996; Varga and Schmitt 2009). The species marked with * are Balkan endemics, which most probably passed through their process of speciation here and at least survived the last glaciation in close proximity to their recent occurrences (Varga 1975, 2003).

Briefly reviewing the main biogeographical connections, we can outline some general trends as follows.
(i) The western Balcanic (Dinaric) populations of alpine and arctic-alpine species show most often close connections with the southeastern (calcareous!) Alpine ones;
(ii) Oppositely, the eastern Balcanic (Thracian) populations of alpine and arctic-alpine species regularly have close connections of with the Carpathian ones, often with direct links to the Southern Carpathians;
(iii) The “Central Balcanic split” was observed in the taxonomic subdivision of several alpine and arctic-alpine species;
(iv) The southern limit of distribution of boreo-montane, arctic-alpine and alpine species agrees with the “Adamović-line”, i.e. the southern limit of alpine type of vertical zonation of vegetation;
(v) The northern limit of oro-Mediterranean xeromontane species also well agrees with this important line, since these species are connected with the oro-Mediterranean type of vegetation (partly by food plant specialisations, see: endemic Polyommatina or by rupicolous habitats, as some Noctuinae, mostly Noctuinae).
These connections and splits will be analysed in details in the next paragraph.

**Taxonomic subdivision of Balkanic high mountain species**

Many morphological studies show close biogeographical connections but also discontinuities between (i) the western Balkan and the (ii) eastern Balkan mountain systems. These two systems are separated by the central Balkan depression along the rivers Vardar and Southern Morava, a typical migration route through the central Balkans (see below). Good examples for these divergences are the fritillary *Boloria pales* (Fig. 9) as well as the ringlets *Erebia pandrose* and *E. gorge* (Fig. 3) (Varga 1975). Thus, the wing patterns of *B. pales* clearly separate the populations from the western Balkan mountains (*B. pales contempta*) from the eastern mountain areas (*B. pales rilaensis*) (Varga 1972a, 1975); on the other hand, the oro-Mediterranean relative *Boloria graeca* (Fig. 13) is indistinguishable with its populations from Durmitor, Šar Planina, Grammos,
Figure 13. Distribution of Boloria graeca. Legend: Balcan peninsula southern part: B. graeca graeca; Balcan peninsula NW and E part: B. graeca balcanica; SW Alps: B. graeca tendensis. B. graeca graeca and B. graeca balcanica are only slightly differentiated (probably as a geographical cline!).

Figure 14. Distribution of Erebia ottomana in Europa and on the Balkan peninsula. Legend: o – E. ottomana ottomana (Ulu dagh), b – E. ottomana balcanica, bu – E. ottomana bureschii, d – E. ottomana drenovskii, be – E. ottomana benacensis, t – E. ottomana tardenota.
Rila and Pirin. Morphological studies of the male genitalia of *Erebia pandrose* (Cupedo 2007) revealed that the western Balkan populations (from Durmitor) seem to belong to the *sthennyo* group and hereby are linked with the southeastern Alps (*E. pandrose marmolata, E. pandrose infraclara*), whereas the eastern Balkan populations (Rila: *E. pandrose amnicolorata*) resemble the Carpathian *pandrose* group (*E. pandrose roberti, E. pandrose cibiniaca; Varga 1972b*). In *Erebia cassioides*, the high mountain ranges of the western and southern Balkans belong to the subspecies *E. cassioides illyrica* and *illyromacedonica* (Lorković 1953), whereas the populations of the eastern Balkans belong to the subspecies *E. cassioides macedonica* (Rila and Pirin) and *kinoshitai* (Stara Planina, Beshkov 1996) closely related to the southern Carpathian *E. cassioides neleus* (Fig. 10). A similar case in noctuid moths is represented by the sibling species *Apamea michielii* (western Balkans: endemic for the Durmitor, N-Albanian Alps, Jakupica und Šar Planina; Varga 1977, 2010b) and *A. maillardii* (eastern Balkans: Stara Planina, Vitosha, Rila, Pirin, but also most other high mountain systems of Europe, as Pyrenées, Alps, Carpathians).

Scattered exclaves of Balkanic oreal elements exist in many montaneous regions of Southern Europe, most often differentiated from the Balkan populations on subspecific level (Varga 1975; Schmitt and Varga 2009; Louy et al. 2014), as in southern France, (e.g *Erebia ottomana tardenota* in Massif Central, Fig. 14), in different parts of the southern Alps (e.g. *E. ottomana benacensis, Boloria graeca tendensis, Aplocera simpliciata*), central Italy (e.g. *Coenonympha rhodopensis italicata*), the southwestern Carpathians (e.g. *E. m. melas, C. rhodopsis schmidtii, Aplocera simpliciata*), the northwestern Dinarids (e.g. *E. melas nanos*), the eastern Carpathians (e.g. *E. melas carpathicola*) and the Apuseni Mts. (e.g. *E. melas runcensis*) (Fig. 4). However, no general pattern of these exclaves can be obtained so that all of them apparently represent individual (and thus specific) cases. The glacial refugial character of some southern Alpine regions is also supported by the occurrence of endemic species of other groups, e.g. flightless Coleoptera (Holdhaus and Lindroth 1939; Holdhaus 1954), Micro-moths (*Sattleria* spp., Huemer 1998) or Geometridae: *Glacies spitzi, G. baldensis* (Wolfsberger 1966, 1971; Varga and Schmitt 2010). In the case of the exclaves in the southern and eastern Carpathians and also Mt. Apuseni a late glacial range expansion from the Balkanic mountains via the region of the Iron Gate into the southwestern Carpathians is probably the most likely scenario for this type of disjunction. However, further genetic studies are urgently needed to test this hypothesis, since only the Balcanic and Italian populations of *Coenonympha rhodopensis* were studied until yet (Louy et al. 2013). These surveys have shown that the disjunct range of *C. rhodopensis* at the Balkan Peninsula is most likely the result of a postglacial up-hill shift of its distribution.

![Figure 15. Distribution of Erebia rhodopensis and related species. Legend: rh – E. rhodopensis, ae – E. aethiopella, g – E. gorgone.](image-url)
Discussion

Ecological vs historical explanations of patterns of distribution

The Balkanic mountain systems are nested in a system of biogeographical links among the European high mountain systems. Several of these links can be explained by the recent ecological constraints. Thus, also their distributional history can be hypothesised. Other connections are not evident and need to be studied in
details (e.g. by molecular analyses) in the future. A predominant link exists between the Alps and the Balkan high mountain systems, but some of these elements are absent in the Carpathians (Varga 1975; Schmitt and Varga 2009). This pattern was observed in three eco-geographical groups: (i) high alpine and (ii) arctic-alpine species (e.g. *Euphydryas cynthia*, Fig. 13, *Pyrgus andromedae*, *Orphne tenebraria*, *Pygmaena fusca*, *Melanarta melanopa rupestralis*, Fig. 12), cold-continental steppe species of high altitudes in Europe (e.g. *Arctia flavia*, *Agrotis fatidica*; like in some Orthoptera, e.g. *Podismopsis relicta*, *Gomphocerus sibiricus*, *Aeropedellus variegatus*), but also in some meso-hygrophilous species of lower altitudes (i.e. the subalpine level) (e.g. *Boloria eunomia*, *E. albergana*).

The interpretation of these distribution patterns is more or less obvious in the first two groups: The southeastern Alps and the Balkan high mountain systems are connected via mountain areas of lower altitude in the northwestern part of the peninsula; these most probably served as corridors (or even major retreats) linking both areas of high mountain systems during glacial conditions, demonstrated e.g. by the occurrences of *Erebia styx trentae* in the southeastern Alps, of *E. stirius* in the northwestern Dinarids (Nanos) and Velka Kapela (Lorković 1952), and of *E. gorge vagana* in the Velebit (Fig 3). With the postglacial warming, most of the alpine species disappeared from the lower northwestern Balkanic mountains and only survived in the Alps or also in the considerably higher and geographically more extended mountain areas of the western and south-central Balkans (*E. gorge*).

The lack of several alpine species in the Northern Carpathians might have two mutually exclusive reasons, but both might be true in single cases. (i) No glacial centres of survival existed in the region of the Northern Carpathians so that no postglacial retreat was possible into this region. This version may be preferable in the case of calcareous rocky and ravine habitats, which are restricted in the Carpathians (e.g. Belánská Tatry), but rather extended in the Dinaric mountain systems of the Balkan Peninsula. (ii) These species also could survive in the Northern Carpathian region and possibly could retreate into the higher mountain areas responding the postglacial warming, but their habitats became too restricted and fragmented during the climatic optimum (i.e. the Atlanticum) since the high plateau-like surfaces are here also rather restricted, in contrast to some of the high mountain systems (Korab, Šar planina, Rila, Pirin) of the Balkan Peninsula with considerably higher elevations in average and also larger high alpine plateau-like areas. This latter argumentation is also supported by the fact that the plateau-like Bucegi massif in the southeastern Carpathians is much richer in alpine and arctic-alpine species (e.g. *Zygaena exulans*, *Glacies coracina*, *G. bentelii*, *Grammia quenselii*; Fig. 12) than the sharp ridge-like High Tatra or Făgăraș Mountains. However, the absence from the Carpathians is much more difficult to explain in the group of species typical for the subalpine level, as e.g. *E. albergana*, *E. oeme* (occurs locally in the Southern Carpathians only, see: Dinca et al. 2010; Rákosy et al. 2011) As these species prefer less extreme conditions, their habitats are even more abundant in the Carpathian region than at the drier Balkan Peninsula. Therefore, their absence or extremely restricted range in the Carpathians cannot be explained by recent or postglacial ecologic conditions, but more likely by much older distribution patterns and stochastic processes.

**Refugia, centres of dispersal, phylogeography**

Recently, numerous surveys were carried out for alpine species (reviewed e.g. in Schönswetter et al., 2005; Schmitt, 2009) and a considerable variety of distributional patterns has been demonstrated. Particularly well studied are the phylogeographic structures of high mountain plant species in the Alps (e.g. Stehlík et al. 2000; Schönswetter et al., 2003, 2005; Triebsch Schönswetter 2003), but also the Pyrenees and Carpathians are already mostly understood (Schmitt 2009; Ronikier et al. 2008; Ronikier 2011). However, large hyatuses of knowledge are still evident for the high mountain systems of the Balkan Peninsula, despite of the fact that this region has the highest diversity of smaller or larger high mountain systems and maybe the most variable connections to some other mountain systems of Europe, in particular to the southeastern Alps and southern Carpathians (Varga 1975, 2003). The high mountain systems of the Balkan Peninsula therefore represent a natural “laboratory” of evolutionary processes in mountain species (Louy et al. 2014). Despite of these circumstances, phylogeographic surveys on butterflies from the Balkan high mountain systems are still scarce.

The genetic data on the mountain forest species *E. euryale* indicate an extended glacial refugium in the eastern Balkans (Schmitt and Haubrich 2008; Varga 2008); refugial areas of this species in the western Balkan Peninsula are likely, but have not been studied so far. These data coincide with the high importance of this region as glacial forest refugia (Willis et al. 1995, 2000; Farcas et al. 1999; Wohlfarth et al. 2001; Björkman et al. 2003; Willis and van Andel 2004; Varga 2008). Furthermore, the populations from Bulgaria...
and the southern Carpathians are genetically undistinguishable, thus supporting the idea that the glacial distribution in Bulgaria was linked with the southern Carpathians, most probably via the hilly area around the Iron Gate, the passage of the Danube through the southwestern Carpathians (Schmitt & Haubrich 2008).

The arctic-alpine *E. pandrose* shows remarkable differentiation at the mtDNA level of its Bulgarian haplotypes from the populations of the Central Pyrenees, Alps and of Scandinavia; this supports a separate centre of glacial survival in the Rila Mts., possibly connected with the Carpathian populations (Varga 1975; Cupedo 2007; Schmitt 2009) and well separated from the large zonal distribution on the „Mammoth steppe“ during the glaciations. The latter resulted in the postglacial colonisation of the most parts of the Alps, Pyrenees and Scandinavia (Schmitt et al. 2008) while the southeastern Calcareous Alps (Dolomites, Julian Alps, etc.) and the Dinaric high mountains were populated by a third main group, possibly related with the also relict-like *E. sthennyo* (Varga 1975, Cupedo 2007). The calcareous mountains of the Dinarids could serve both as served as retreats and/or stepping stones to the southeastern Alps since calcareous substrates predominate in both regions.

**Erebia cassioides** belongs to the most typical alpine butterfly species of the Balkanic high mountains but also of the southwestern Carpathians (Fig. 10). According to the most recent surveys (Louy et al. 2014) the level of differentiation among the Balkan populations of *E. cassioides* reaches a considerably high level, only achieved by mountain butterfly species or species groups with high genetic differentiation among regional groups (e.g. *Erebia epiphron*, Schmitt et al. 2006; *Erebia melampus-sudetica* group, Haubrich and Schmitt 2007; *Coenonympha arcania-gardetta-darwiniana-macromma* group, Schmitt and Besold, 2010). It means that the true alpine species, similarly to the arctic-alpine ones had a highly scattered pattern of distribution during the last glacial maximum on the Balkan peninsula and could survive mostly or exclusively in the moderately high elevations of the glaciated alpine massifs, thus often having a central Balkanic split not only in their range but also in the pattern of genetic and/or morphological differentiation (see: *Boloria pales, Erebia epiphron* group, *E. gorge, E. cassioides, E. pandrose*).

Contrasting to the former group, the Balkanic oreal species generally do not show a similarly strong genetic differentiation among the Balkanic high mountains. Both *Erebia ottomana* (Louy et al. 2014) and *Coenonympha rhodopenensis* (Louy et al. 2013) show a relatively shallow differentiation in this region. Considerable splits seem to exist only in large-distance disjunctions as e.g. in Monte Baldo (*E. ottomana benacensis*) or Mt. Terminillo (*C. rhodopenensis italicca*). The recently started parallel survey of *E. melas* and *E. rhodopenensis* will possibly show the role of habitat differences on phylogeographic patterns in two phylogenetically not very closely related species.

A rather special group of “mountain” species of the Balkan Peninsula is formed by those species occurring mostly or exclusively in the southern part of the peninsula (mainly in the high mountains of the Peloponnisos and southern Greece: e.g. Tymfi, Parnassos), often connected with rupicolous habitats dominated by thorny cusheon plant formations (Astragalo-Acantholimetalia alliance) widely distributed in the arid mountains of Asia Minor and Central Asia. These species do not occur in those mountain systems with the Central European vertical zonation (German: Stufenfolge) of vegetation due to the lack of suitable habitats (e.g. *Colias aurorina, Dichagyris gracilis, Chersotis laeta, Ch. capnistis*; Fig. 17). Therefore, their northern distribution limits practically coincides with the Adamović line (fig. 1), i.e. with the southern boundary of the Central European vegetation type at the Balkan Peninsula (Horvat et al. 1974). These species most probably represent old preglacial relicts of the European fauna demonstrating the significance of the Aegean Land Arc for the faunal genesis of southeastern Europe (Varga 2012).

Furthermore, considering the distribution of species, many of the Balkanic endemics have not reached the Carpathian Basin (*Pieris balcana, Colias aurorina heldreichi, C. caucasica balcicana, Boloria graeca, Pseudochazara graeca, P. geyeri, P. orestes, P. cingovskii* (Fig. 16) *Erebia orientalis* (Fig. 2), *Proterebia afra dalmata* or only some peripheral parts as the Retezet (e.g. *Erebia melas melas* (Fig. 4), *Coenonympha rhodopenensis* [also small exclaims in Italy]). Several of these species belong into two major groups of Balkanic endemics: (i) The endemisms of southern Greece as relics of old Trans-Aegean connections (*Dichagyris gracilis etolae, Rhyacia psammia stavroitiacus, Chersotis capnistis, Ch. zukovskiyi hellenica*; Fig. 17) and (ii) the Macedonian arid massifs as centres of stenochorous species not reaching the southern Carpathians (e.g. *P. graeca, P. geyeri, P. cingovskii*; Fig. 16). Furthermore, the filter-corridor of the Iron Gate prohibited the expansion of several Balkanic and stationary Pontic-Mediterranean elements into the Carpathian Basin (e.g. *Pieris balcana, Kirtinia roxelana, Pseudochazara anthelea, Hipparchia syriaca*, *Coenonympha leander*; the latter two species had historical occurrences also in the Banat, N of the Danube, see Rákosy 2013). Another part of the stationary Pontic-Mediterranean species occur only either in semi-
arid, climatically transitional lower hilly areas of Macedonia or in Thracia (e.g. *Lycaena ottomana*, *Hipparchia fatta*, *Pseudochaera anthelea*). Other species (as *Allancastria cerysi*, *Melanargia larissa*) show a wider distribution also along the Adriatic coast. Note that the majority of the species restricted to the Balkan Peninsula in Europe extend their ranges to Asia Minor or even further east mirroring the often strong cohesiveness between the Balkan Peninsula and Asia Minor, i.e. the Pontic-Mediterranean refugial area sensu de Lattin (1957, 1967).

![Figure 17. Distribution of some xeromontane Noctuidae species at the Balkan Peninsula. Legend: ♦ Rhyacia helvetina schepleri; □ Dichagryis celsicola goateri; ● Chersotis capnistis schnacki; O Rhyacia psammia stavroitiacus.](image-url)
Aspects of nature conservation: are high mountain butterflies and moths threatened?
The arctic-alpine and also some alpine species are confined only to the highest parts of the Balkanic high
mountains although they can locally occur in high numbers, e.g. *Zygaena exulans* in Durmitor, or
*Euphydryas cynthia*, *Erebia cassioiides* and *Apamea zeta* in Rila Mts. It is more frequent however, that they
are not only strictly localised but also scarce as *Pyrgus andromedae*, *Pygmaena fusca*, *Orphne tenebraria*,
*Entephria nobiliaria*, *Melanarta melanopa rupestralis*, *Agrotis fatidica*, etc. Their occurrences are generally
restricted to some special types of habitats, as tundra-like cusheon (*Silene acaulis*, *Androsace* spp.,
*Dianthus* spp., *Gentiana* spp.) and dwarf scrub (*Dryas octopetala*, *Salix reticulata*, etc.) vegetation and do not reach a
high number of individuals (*Pyrgus andromedae*, *Melanarta melanopa rupestralis*, *Agrotis fatidica*). Thus,
these populations together with their habitats may become more restricted or even extinct due to climate
warming in the future, especially near to the southern limit of alpine type vertical zonation. Other sources of
threat are the growing pressure of alpine skiing in several Balkanic high mountains (extremely e.g. in the not
protected part of the Šar-planina) and the expansion of *Pinus mugho* due to the abandonment of traditional
grazing (e.g. on some plateau-like parts of the Rila Mts.). Thus, their categorisation is mostly Vulnerable to
Data Deficient, the latter mostly in strictly localised species of hardly accessible habitats (e.g. *Syngrapha
rilaeacatum* or *Glacies* spp.).

Oppositely, the Balkanic oreal species are much less threatened. Their populations are generally, or
at least locally rather strong, even of such Balkanic endemic species as *Erebia orientalis* or *E. rhodopensis*.
They are hardly affected by the shift upwards due to warming since their habitats are extended tall-grass
formations of Balkanic type which have a high resilience against summer aridity. They also need, however, a
moderate grazing pressure in their habitats to reduce the expansion of *Juniperus nana* and/or *Pinus mugho*.
Thus they are most often not threatened or characterised as Least Concern (see Abadjiev and Beshkov 2007;
Beshkov, [http://www.nmnhs.com/butterfly_areas_bg/species.php](http://www.nmnhs.com/butterfly_areas_bg/species.php)). The occurrence of Mediterran-
neromontane species is usually connected with special edaphic conditions, e.g. scree, ravines with abundant
rupicolous grasslands. Such habitats are most often used for extensive grazing only or completely unused.
Thus, these species are mostly threatened only by the small extension and fragmentation of their habitats,
often connected with limited number of individuals (e.g. *Agriades dardanus*, *Polyommatus araoensis*,
*Pseudochazara orestes*, *P. cingovskii*). Unfortunately, the ecological information on such species is often
scarce, espacially on the night active species, as the xeromontane Noctuiinae moths (e.g. *Rhyacia psammia*,
*Chersotis*, *Dichagyris* and *Euxoa* spp.).

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References
Abadjiev, S. (1992-1995) Butterflies of Bulgaria I-III, Veren, Sofia.
Abadjiev, S. (2001) An Atlas of the Distribution of the Butterflies in Bulgaria (Lepidoptera: Hesperioidea &
Papilionoidea). Pensoft Publishers, Sofia–Moscow, 335 pp.
Abadjiev, S.K. & Beshkov, S. (2007) Prime butterfly areas in Bulgaria. Pensoft Publishers, Sofia–Moscow,
222 pp.
Adamović, L. (1909) Pflanzengeographische Stellung und Gliederung der Balkanhalbinsel. *Denkschriften
der Akademie der Wissenschaften Wien*, 80, 405–495.
Alexinschi, A. (1960) Contribuțiuni la cunoașterea faunei Macrolepidopterelor din Masivul Rodna, cu
considerații sistematice, ecologice și zoogeografice. *Anali științifice Universităței I. Cuza, Iași*, 6,
729–754.
Alexinschi, A. & König, F. (1963) Contribuțiuni la cunoașterea faunei de Lepidoptere din Munții Lotru și
Parâng. *Comunicare de Zoologie*, 2, 137–149
Balletto, E., Barberis, G. & Toso, G.G. (1982a) Aspetti dell'ecologia dei Lepidotteri Ropaloceri nei consorzi erbacei delle Alpi Italiane. *In: Struttura delle zoocenosi terrestri, II.2. I Pascoli Altomontani - Promozione della Qualità dell'Ambiente*, Roma, pp. 11–96.

Balletto, E., Lattes, A. & Toso, G.G. (1982b) Le comunità di Lepidotteri Ropaloceri come strumento per la classificazione e l'analisi della qualità degli alti pascoli Italiani. *In: Struttura delle zoocenosi terrestri, II.2. I Pascoli Altomontani - Promozione della Qualità dell'Ambiente*, Roma, pp. 97–139.

Balletto, E., Toso, G., Barberis, G. & Rossaro, B. (1977) Aspetti dell’ecologia dei lepidotteri ropaloceri nei consorzi erbacei alto appenninici. *Animalia*, 4, 277–343.

Beshkov, S (1995) Contribution to the knowledge of the Bulgarian lepidoptera fauna (Lepidoptera, Macrolepidoptera). *Phegea*, 23, 201–218

Beshkov, S (1996) A new subspecies of *Erebia cassioides* (Reiner and Hohenwarth, 1792) from Bulgaria: *Erebia cassioides kinoshitai* ssp.n. (Lepidoptera, Nymphalidae: Satyrinae). *Phegea*, 24, 109–124.

Beshkov, S. (2009a) Short contribution on the macrolepidoptera fauna of the Republic of Montenegro (Crna Gora, Balkan Peninsula) (Lep.: Geometridae, Noctuidae) with a report of two new genera and four new species for the country. *Entomologist’s Record and Journal of Variation*, 121 (6), 298–301.

Beshkov, S. (2009b) Two new Macrolepidoptera genera and fifteen new Macrolepidoptera species for the Republic of Montenegro (Crna Gora, Balkan Peninsula), collected in Durmitor National Park. Tara Canyon (Lep.: Geometridae, Noctuidae). *Entomologist’s Record and Journal of Variation*, 121 (5), 243–248.

Beshkov, S. (2010) Contribution on the Bulgarian Macrolepidoptera fauna (Lepidoptera: Geometridae, Noctuidae). *Entomologist’s Record and Journal of Variation*, 122 (4), 175–181.

Beshkov, S. & Langourov, M. (2004) Butterflies and Moths (Insecta: Lepidoptera) of the Bulgarian part of Eastern Rhodopes. *In: Beron P., Popov A. (Eds), Biodiversity of Bulgaria. 2. Biodiversity of Eastern Rhodopes (Bulgaria and Greece)*. Pensoft & National Museum of Natural History, Sofia, pp. 525–676.

Bhagwat, S.A. & Willis, K.J. (2008) Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? *Journal of Biogeography*, 35, 464–482.

Bilton, D.T., Mirol, P.M. Mascheretti, S., Fredga, K., Zima, J. & Searle, J.B. (1998) Mediterranean Europe as an area of endemism for small mammals rather than a source for northwards postglacial colonization *Proceedings of the Royal Society London B*, 265, 1219–1226.

Björkman, L., Feurdean, A., & Wohlfarth, B. (2003). Late- Glacial and Holocene forest dynamics at Stere- goiu in the Gutaiului Mountains, Northwest Romania. *Review of Palaeobotany and Palynology*, 124, 79–111.

Buresch, I. & Tuleschkow, K. (1929-43) Die horizontale Verbreitung der Schmetterlinge in Bulgarien. Teile I-V. *Mitteilungen des naturwissenschaftlichen Institutes Sofia*, 2, 145–250; 3, 145–248; 5, 211–288; 8, 289–347; 9, 349–422; 16, 79–188.

Busse, R. & Ockruck, F. (1991) Ein Beitrag zur Kenntnis der Schmetterlingsfauna des Pirin-Geberigen im Süd-Westen Bulgariens (Lepidoptera). *Phegea*, 19 (1), 5–20.

Caradja, A. (1930) Beiträge zur Lepidopteren-Fauna der südlichen Dobrogea insbesondere der sogenannten “Coasta de Argint”. *Académie Roumaine. Buletin de la Section Scientifique*, 13 (3), 1–21, pl. I–VI.

Coutsis, J. (1969) List of Grecian Butterflies. *Entomologist*, 102, 264–268

Coutsis, J. (1972) List of Grecian Butterflies. Additional records. *Entomologist's Record*, 84, 145–151, 165–167

Coutsis, J., Dils, J., Ghavalas, N. & van der Poorten, D. (1997) A new Erebia species for the Greek fauna (Lepidoptera, Nymphalidae, Satyrinae). *Phegea*, 25, 169–172.

Coutsis, J. & Ghavalas, N. (1991) *Agriades pyrenaicus* (Boisduval, 1940) from N. Greece and notes on *Apatura metis* (Freyer, 1829) from NE. Greece (Lepidoptera, Lycaenidae, Nymphalidae). *Phegea*, 19, 133–138.

Cupedo, F. (2007) Geographical variation and Pleistocene history of the *Erebia pandrose – sthennoyo* complex (Nymphalidae: Satyrinae). *Nota lepidopterologica*, 30, 329–353.

Dinca, V., Cuvelier, S., Zakharov, E.V., Hebert, P.D.N. & Vila, R. (2011) Biogeography, ecology and conservation of *Erebia oeme* in the Carpathians. *Annals de la Societé Entomologique de France*, 46 (3–4), 486–498.

Diószezgy, L. (1929-30) Die Lepidopterenaufna des Reteyzet-Gebirges I. *Verhandlungen und Mitteilungen des siebenbürgischen Vereins für Naturwissenschaften Herrmannstadt*, 79-80, 188–289.
Diószeghy, L. (1936) Die Lepidopterafauna des Retyezat-Gebirges II. Verhandlungen und Mitteilungen des siebenbürgischen Vereins für Naturwissenschaften Herrmannstadt, 86, 84–85.

Drenovsky, A.K. (1925) Die vertikale Verteilung der Lepidopteren in den Hochgebirgen Bulgariens. Deutsche entomologische Zeitschrift [1925], 29–75, 97–125.

Drenovsky, A.K. (1928) Die Lepidopterafauna auf den Hochgebirgen Bulgariens. Sbornik bulgarska Akademia Naukite, 23, 1–120, 1 Karte, 1 Schema (In Bulgarian).

Drenowski, A.K. (1930b) Neue Lepidopterenarten aus Bulgarien. Izvestia ot bulgarskoto entomologsko Drzhtsvo, 5, 175–188 (In Bulgarian).

Drenowski, A.K. (1931) Beitrag zur Insektenfauna Bulgariens u. Mazedonien. II. (Lepidoptera, Hymenoptera, Diptera und Orthoptera). Izvestia ot bulgarskoto. entomologsko Druzhstvo, 9, 237–256 (In Bulgarian).

Farcas, S., de Beaulieu, J.–L., Reille, M., Coldea, G., Diaconeasa, B., Goeury, C., Goslar, T. & Jull, T. (1999). First 14C datings of Late Glacial and Holocene pollen sequences from Romanian Carpathes. Comptes Rendus de l’Academie de Science de Paris, Sciences de la vie, 322, 799–807.

Grabherr, G., Gottfried, M. & Pauli, H. (1994) Climate effects on mountain plants. Nature, 369, 448.

Goltz, v. H. (1935-1936) Die Erebien Siebenbürgens. Verhandlungen und Mitteilungen des siebenbürgischen Vereins für Naturwissenschaften Herrmannstadt, 86, 1–30.

Habel, J.C., Schmitt, T. & Müller, P. (2005) The fourth paradigm pattern of postglacial range expansion of European terrestrial species: the phylogeography of the Marbled White butterfly (Satyrinae, Lepidoptera). Journal of Biogeography, 32, 1489–1497.

Haubrich, K. & Schmitt, T. (2007). Cryptic differentiation in alpine-endemic, high-altitude butterflies reveals down-slope glacial refugia. Molecular Ecology, 16, 3643–3658.

Hewitt, G.M. (1999). Post-glacial re-colonization of European biota. Biological Journal of the Linnean Society, 68, 87–112.

Hewitt, G.M. (2000). The genetic legacy of the Quaternary ice ages. Nature, 405, 907–913.

Hewitt, G.M. (2004). Genetic consequences of climatic oscillations in the Quaternary. Philosophical Transactions of the Royal Society of London B, 359, 183–195.

Holdhaus, K. & Lindroth, C. (1939) Die europäischen Koleopteren mit boreo-alpiner Verbreitung. Annalen des Naturhistorischen Museums in Wien, 50, 123–293

Holdhaus, K. (1959) Die Pflanzenwelt Südosteuropas als Ausdruck der erd- und vegetations-geschichtlicher Vorgänge. Acta Societatis Botanicae Poloniae, 28, 382–408.

Horvat, I. (1962) Die Vegetation Südosteuropas im klimatischen und bodenkundlichen Zusammenhang. Mitteilungen der österreichischen geographischen Gesellschaft, 1, 136–160

Horvat, I., Glavač, V., & Ellenberg, H. (1974) Die Vegetation Südosteuropas. G. Fischer, Stuttgart.

Huemer, P. (1998) Endemische Schmetterlinge der Alpen – ein Überblick (Lepidoptera). Stajfia (Linz), 55, 229–256.

Huemer, P., Krpac, V., Plössl, B. & Tarmann, G. (2011) Contribution to the fauna of Lepidoptera of the Mavrovo National Park (Republic of Macedonia). Acta Entomologica Slovenica, 19 (2), 169–186.

Jackson, S. (1988) Provisional distribution maps of the butterflies of Yugoslavia (Lepidoptera, Rhopalocera). Jugoslavensko entomološko društvu Zagreb, Posebno izdanje I, pp. 215.

König, F. (1959) Răspânderea orizontală și verticală a lepidopterelor din Retezat, Godeanu-Tarcu și Pietrii-Petreanu. Studii și Cercetări Acad. R.P. România (Timișoara), 6, 126–139.

König, F. (1975) Catalogul colectiei de Lepidoptere a Muzeului Banatului, Timișoara.

König, F. (1982) Montane, subalpine, alpine und boreo-alpine Schmetterlingsarten aus den rumänischen Karpathen. Studii și Comunicare (Reghin), 2, 229–236.
Kotlík, P., Deffontaine, V., Mascheretti, S., Zima, J., Michaux, J.R. & Searle, J.B. (2006). A northern glacial refugium for bank voles (Clethrionomys glareolus). *Proceedings of the National Academy of Sciences of the USA*, 103, 14860–14864.

Koutsaftikis, A. (1974) *Erebia rhodopensis* (Nicholl, 1900), espece nouvelle pour la Grece (Lep.: Nymphalidae, Satyrinae). *Phegea*, 22, 9–13.

Krzewicki, M. 1982. Der gegenwärtige Stand der Tagfalterfauna Polens unter besonderer Berücksichtigung ihre Bedrohung. *Nota Lepidopterologica*, 5, 3–16.

Krzewicki, M. (1963) *Przyczynek do znajomości fauny Tatr Polskich* (Lepidoptera). *Annales Zoologici*, 21 (12), 151–222.

Lattin, G. De. (1957) *Die Ausbreitungszentren der holarktischen Landtierwelt*. *Verhandlungen der deutschen Zoologischen Gesellschaft* Hamburg (1956), 380–410.

Louy, D., Habel, J.C., Abadjiev, S. & Schmitt, T. (2013) Genetic legacy from past panmixia: High genetic variability and low differentiation in disjunct populations of the Eastern Large Heath butterfly. *Biological Journal of the Linnean Society*, 110, 281–290.

Louy, D., Habel, C.J., Abadjiev, S., Rákosy, L., Varga, Z., Rödder, D. & Schmitt, T. (2014) Molecules and models indicate diverging evolutionary effects from parallel altitudinal range shift in two mountain Ringlet butterflies. *Biological Journal of the Linnean Society - Manuscript ID BJLS-3069.R1*

Lorković, Z. (1952) Beiträge zum Studium der Semispezies. Spezifität von *Erebia styrius* Godt. and *styx* Fr. (Satyridae). *Zeitschrift für Lepidopterologie* (Krefeld), 2, 159–176.

Lorković, Z. (1953) Spezifische, semispezifische und rassische Differenzierung bei *Erebia tyndarus* Esp. (I-II.) *Traveaux de l’Institute Biologie experimentale de l’Academie de Yougoslavie*, 11-12, 163–192, 193–224.

Louy, D., Habel, J.C., Abadjiev, S. & Schmitt, T. (2013) Genetic legacy from past panmixia: High genetic variability and low differentiation in disjunct populations of the Eastern Large Heath butterfly. *Biological Journal of the Linnean Society*, 110, 281–290.

Lommel, F., Diadema, K. (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography*, 36, 1333–1345.

Michie, S. (1963) Beitrag zur Kenntnis der Makrolepidopterenfauna Mazedoniens (NR Makedonija). *Acta Musei Macedonici Scientiarum Naturalium*, 9, 2/78, 15–33.

Niessolowsky, W. (1929) *Motyle wiekse Tatr polskich*. *Pol. Akadem. Umetn. Prace monograf. fizjogr.* (Krakow) 5, 1–88.

Niessolowsky, W. (1936) *Pieris napi L. subsp. bryoniae Ochs. unter besonderer Berücksichtigung der Karpathen-Formen*. *Annales Musei Zoologici Polonici*, 11, 213–236.

Niessolowsky, W. & Woytusiak, R.J. (1937) Über die Verbreitung der geographischen Formen von *Erebia manto* Esp. in den Karpaten. *Bulletin de l’Academie Polonaise des Sciences, Ser. B.*, 11, 111–126.

Ozenda, P. (1988) Die Vegetation der Alpen im europäischen Gebirgsraum. G. Fischer, Stuttgart New York.

Pamperis, L. (1997) The Butterflies of Greece. Bastas and Plessas, Athens.

Pinceel, J., Jordaens, K., Pfenninger, M. & Backeljau, T. (2005) Rangewide phylogeography of a terrestrial slug in Europe: evidence for Alpine refugia and rapid colonization after the Pleistocene glaciations. *Molecular Ecology*, 14, 1133–1150.

Popescu-Gorj, A. (1952) *Revizuirea speciilor genului Erebia* Dalm. din Carpații Românești (grupa epiphron). *Anal. Acad. R.P.R., Seria Geol., Geogr., Biol.*, 4, pp. 1–21.

Podnar, M., Madaric, B.B. & Mayer, W. (2014) Non-concordant phylogeographical patterns of three widely codistributed endemic Western Balkans lacertid lizards (Reptilia. Lacertidae) shaped by specific habitat requirements and different responses to Pleistocene climatic oscillations. *Journal of Zoological Systematics and Evolutionary Research*, 52, 119–129.

Popescu-Gorj, A. (1962) Revision des especes du genre Erebia Dalm. des Carpathes de la Roumanie (groupes pluto et tyndarus). *Travaux de Museum d'Histoire Naturelle "Grigore Antipa",* 3, 205–223.

Popescu-Gorj, A. (1963) Genul Erebia Dalm. (Lepidoptera, Satyridae) și răspândirea sa verticală în masivul Bucegi. *Acad. R.P.R. Ocrotirea Naturii*, 7, 53–62.

Popescu-Gorj, A. (1964) Catalogue de la collection de Lépidopteres "Prof. A. Ostrogovich" du Muséum d'Histoire Naturelle "Grigore Antipa". Bucharest.
Popescu-Gorj, A. (1971) Ergebnisse der Albanien-Expedition 1961 des "Deutschen Entomologischen Institutes" 82. Beitr.: Lepidoptera, Satyridae I (genus Erebia Dalman). *Beiträge zur Entomologie*, 21 (3/6), 509–516

Povolny, D. & Moucha, J. (1956) On the high mountain Geometridae of the genus Psodos Treitschke, 1828 (Lepidoptera, Geometridae). *Acta entomologica Musei nationalis Pragae*, 30, 140–179

Povolny, D. & Moucha, J. (1958) Kritischer Nachtrag zur Kenntnis der Taxonomie und Zoogeographie der Gattung Psolos Tr. (Lepidoptera, Geometridae). *Acta entomologica Musei nationalis Pragae*, 32, 181–190.

Rákosy L (1992a) Tagfaltergemeinschaften des Retezat-Gebirges (Rhopalocera + Grypocera) (Karpaten, Rumänien). *Nota lepidopterologica*, Suppl. 4, 118–128.

Rákosy L (1992b) Macrolepidoptere din Parcul național de Retezat. In: Popovici, J (Ed.), *Parcul National Retezat - Studii ecologice* (Brasov), pp. 254–280.

Rákosy, L. (1995) Die Noctuidae Siebenbürgens. *Nachrichten des Entomologischen Vereins Apollo*, Frankfurt a.M., Suppl. 13, 1–109.

Rákosy, L (Ed.) (1997) Entomofauna parcurilor nationale Retezat si Valea Cernei. Societates lepidopterologica romana Cluj-Napoca, pp.1–243.

Rákosy, L (1998) Die endemischen Lepidopteren Rumäniens. *Stypia* (Linz), 55, 257–280.

Rákosy, L. (2013) Butterflies of Romania (Fluturi diurni din Romania [in Roman]) Edit. Mega, Cluj-Napoca.

Rebel, H (1903) Studien über die Lepidopterenfauna der Balkanländer I. Bulgarien und Ostrumelien. *Annalen des K.K. Naturhistorischen Hofmuseums*, Wien, 18, 11–346.

Rebel, H (1904) Studien über die Lepidopterenfauna der Balkanländer II. Bosnien und Herzegovina. *Annalen des K.K. Naturhistorischen Hofmuseums*, Wien, 19, 8–377.

Rebel, H (1911) Die Lepidopterenfauna von Herkulesbad und Orsova. *Annalen des K.K. Naturhistorischen Hofmuseums*, Wien 25, 353–430.

Rebel, H, & Zerny, H (1931) Die Lepidopterenfauna Albaniens. *Denkschriften der Kaiserlichen Akademie der Wissenschaften*, Wien, 103, 19–61.

Reinig W (1937) Die Holarktis. G. Fischer, Jena.

Reinig W (1950) Chorologische Voraussetzungen für die Analyse von Formenkreisen. *Syllegomena Biologica, Festschrift für O. Kleinschmidt*, 364–378.

Ronikier, M. (2011) Biogeography of high-mountain plants in the Carpathians: An emerging phylogeographical perspective. *Taxon*, 60 (2), 373–389.

Ronikier, M., Ciesłak, E. & Korbecka G 2008. High genetic differentiation in the alpine plant *Campanula alpina* Jacq. (Campanulaceae): evidence for glacial survival in several Carpathian regions and long isolation between the Carpathians and the Eastern Alps. *Molecular Ecology*, 17, 1763–1775.

Schmitt, T. & Besold, J. (2010) Upslope movements and large scale expansions: the taxonomy and biogeography of the *Coenonympha arcania* –*C. darwiniana* –*C. gardetta* butterfly species complex *Zoological Journal of the Linnean Society*, 159, 890–904.

Schmitt, T. & Haubrich, K. (2008) The genetic structure of the mountain forest butterfly *Erebia euryale* unravels the late Pleistocene and Postglacial history of the mountain coniferous forest biome in Europe. *Molecular Ecology*, 17, 2194–2207.

Schmitt, T., Hewitt, G.M. & Müller, P (2006) Disjunct distributions during glacial and interglacial periods in mountain butterflies: *Erebia epiphron* as an example. *Journal of Evolutionary Biology*, 19, 108–113.

Schmitt, T. & Varga, Z. (2009) Biogeography of the butterflies of the Carpathian Basin and the Balkan Peninsula. In: Stloukal, E., Hensel, K., Holec, P. et al. (Eds.): *Vývoj prírody Slovenska*. Faunima, Bratislava, pp. 143–166 + 253–275.

Schmitt, T. & Varga, Z. (2012) Extra-Mediterranean refugia: The rule and not the exception? *Frontiers in Zoology* 9: 22-doi:10.1186/1742-9994-9-22.
Schönswetter, P., Stehlik, I., Holderegger, R. & Tribsch, A. (2005) Molecular evidence for glacial refugia of mountain plants in the European Alps. *Molecular Ecology*, 14, 3547–3555.

Schönswetter, P., Tribsch, A. & Niklfeld, H. (2003) Disjunctions in relict alpine plants: phytogeography of *Androsace brevis* and *A. wulfeniana* (Primulaceae). *Botanical Journal of the Linnean Society*, 141, 437–446.

Sijarić, R. (1971) Faunisticka istrazivanja Rhopalocera (Lepidoptera) na kompleksu hercegovackih visokih planina (Prenj, Cvrsnica i Cabulja). *Glasnik zemaljskog Muzeja* (Sarajevo), 10, 163–184.

Sijarić, R., Lorković, Z., Carnelutti, J. & Jakšić, P. (1984) Fauna Durmitora I. Rhopalocera (Lepidoptera). *Crnogorska Akademija Nauka i Umjetnosti Tišnjak, Posebno izdanje* 13, pp. 95–194.

Stehlik, I., Holderegger, R., Schneller, J.J., Abbott, R.J. & Bachmann, K. (2000) Molecular biogeography and population genetics of alpine plant species. *Bulletin des Geobotanischen Institutes der Eidgenössichgen Technischen Hochschule*, 66, 47–59.

Taberlet, P., Fumagalli, L, Wust-Saucy, A-G. & Cosson, J-F. (1998) Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology*, 7, 453–464.

Thurner, J. (1964) Die Lepidopterenfauna Jugoslavisch Mazedoniens. I. Rhopalocera, Grypocera and Noctuidae. *Prirodonaučen Muzej Skopje, Posebno izdanje*, pp. 1–159.

Varga, Z. (1971) Die Erebien (Lep.: Satyridae) der Balkanhalbinsel und der Karpaten II. Die Verbreitung und subspezifische Gliederung von *Erebia epiphron* Knoch, 1793 mit Beschreibung einer neuen Unterart: *E. epiphron infernalis* ssp. nova. *Acta biologica Debrecina*, 9, 221–226.

Varga, Z. (1972a) Taxonomic division and distribution of the adder (*Vipera berus*) as inferred from mitochondrial DNA sequence data. *Molecular Ecology*, 15, 3425–3437.

Varga, Z. (1972b) Die Verbreitung und subspezifische Gliederung von *Erebia pandrose* (Bkh.) (Lep.: Satyridae) mit Beschreibung einer neuen Unterart *E. pandrose ambicolorata* ssp.n. *Acta biologica Debrecina*, 9, 227–235.

Varga, Z. (1975) Geographische Isolation und Subspeziation bei den Hochgebirgs-Lepidopteren der Balkanhalbinsel. *Acta entomologica jugoslavica*, 1, 5–39.

Varga, Z. (1977a) Die Verbreitung und taxonomische Gliederung von *Apamea maillardii* (Hübner-Geyer, 1834) und *A. zeta* (Treitschke, 1825) (Lep. Noctuidae) in der Balkanhalbinsel. *Acta biologica Debrecina*, 13, 283–291.

Varga, Z. (1977b) Das Prinzip der areal-analytischen Methode in der Zoogeographie und die Faunenelemente-Einteilung der europäischen Tagschmetterlinge. *Acta biologica Debrecina*, 14, 223–285.

Varga, Z. (1989a) The origin and division of the northern-montane disjunct areas in Palaearctic Lepidoptera: their importance in solving zoogeographical and evolutionary problems. *Acta biologica debrecina*, 21 (1988-89), 91–116.
Varga, Z. (1995a) Isolates of arctic-alpine Lepidoptera in Southeastern Europe. *Proceedings of the 9th Congress of EIS, Helsinki* (1993), pp. 140–151.

Varga, Z. (1995b) Geographical Patterns of Biodiversity in the Palaearctic and in the Carpathian Basin. *Acta zoologica hungarica*, 41, 71–92.

Varga, Z. (1996) Biogeography and Evolution of the oreal Lepidoptera in the Palaearctic. *Acta zoologica hungarica*, 42, 289–330.

Varga, Z. (1999) Die Erebi en der Balkanhalbinsel und Karpaten IV. Übersicht der subspezifischen Gliederung und der Verbreitung der Erebia-Arten in der Balkanhalbinsel und in den Karpaten (Lepidoptera, Nymphalidae, Satyrinae). *Entomologica romanica*, 3, 15–29.

Varga, Z. (2003) The Geographical Distribution of High Mountain Macrolepidoptera in Europe. In: Grabherr, G. & Nagy, L. (Eds.) *Alpine Biodiversity in Europe*. Springer-Verlag, pp. 239–257.

Varga, Z. (2010a) Extra-Mediterranean refugia, post-glacial vegetation history and area dynamics in Eastern Central Europe. In: Habel, J. & Assmann, Th. (Eds.), *Relict species: Phylogeography and Conservation Biology*. Springer-Verlag, pp. 57–87.

Varga, Z. (2010b) Biogeography of West Palaearctic Noctuidae. In: Fibiger, M., Ronkay, L., Yela, J.L. & Zilli, A. (Eds.), *Noctuidae Europaeae 12 (incl. Suppl. 1-12)*, Entomological Press, Sorø, pp. 265-274.

Varga, Z. & Schmitt, Th. (2008) Types of oreal and oreotundral disjunctions in the western Palearctic. – *Biological Journal of the Linnean Society*, 93, 415–430.

Varga, Z. & Slivov, A.V. (1977) Beitrag zur Kenntnis der Lepidopterenfauna der Hochgebirge in Bulgarien. In: *Terrestrial Fauna of Bulgaria*. Bulgarian Academy of Sciences, pp. 167–190.

Varga, Z. & Varga-Sipos, J. (2002) Vertical distribution of the alpine Lepidoptera in the Carpathians and in the Balkan peninsula in relation to the zonation of the vegetation. *Pirineos*, 156, 69–86.

Verovnik, R., Micevski, B., Durič, M., Jakšič, P., Keymeulen, A., van Swaay, C. & Veling, K. (2010) Contribution to the knowledge of the butterfly fauna of the Republic of Macedonia (Lepidoptera: Papilionoidea & Hesperioidea). *Acta entomologica Slovenica*, 18, 31–46.

Vihodcevsky, N. & Gogov, D. (1963) Beitrag zur Schmetterlingsfauna des Vitosa-Gebirges. *Izvestia zoologiceskata Institutata Sofia*, 14, 227–235 (In Bulgarian).

Walter, H. & Straka, H. (1970) *Arealkunde. Floristisch-historische Geobotanik*. Ulmer, Stuttgart.

Warren, B.C.S. (1936) *Monograph of the genus Erebia*. British Museum (Natural History), London, vii + 407 pp.; 104 Pls.

Williams, P., Humphries, C., Araújo, M., Lampinen, R., Hagemeijer, W., Gasc. J-P. & Mitchell-Jones, T. (2000). Endemism and important areas for representing European biodiversity: a preliminary exploration of atlas data for plants and terrestrial vertebrates. *Belgian Journal of Entomology*, 2, 21–46.

Willis, K.J., Rudner, E. & Sümegi, P (2000) The full-glacial forests of central and southeastern Europe. *Quaternary Research*, 53, 203–213.

Willis, K.J. & van Andel, T.H. (2004) Trees or no trees? the environments of central and eastern Europe during the Last Glaciation. *Quaternary Science Reviews*, 23, 2369–2387.

Willis, K.J., Sümegi, P., Braun, M. & Toth, A (1995) The late Quaternary environmental history of Bátorliget, NE Hungary. *Palaeogeography, Palaeoclimate, Palaeoecology*, 118, 25–47.

Wohlfarth, B., Hannon, G., Feurdean, A., Ghergari, L., Onac, B.P. & Possert, G. (2001). Reconstruction of climatic and environmental changes in NW Romania during the early part of the last deglaciation (~15,000–13,600 cal yr BP). *Quaternary Science Reviews*, 20, 1897–1914.

Wolfsberger, J. (1966) Eine neue Art der Gattung Psodos Tr. vom Monte Baldo in Oberitalien (Lep., Geometridae). *Memoria Museo civico Storia naturale*, 14, 449–454.

Wolfsberger, J. (1971) Die Makrolepidopteren-Fauna des Monte Baldo in Oberitalien. *Editio Museo civico Storia naturale Verona*, 333 pp. + Taf. XX.

Zühlisch, R. (1936) Beitrag zur Macrolepidopterenfauna des Rilogeberges in Bulgarien. *Zeitschrift des Österreichischen Entomologischen Vereines Wien*, 21 (7/8), 49–55.