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Butterfly diversity and biogeography on the Croatian karst mountain Biokovo: Vertical distribution and preference for altitude and aspect?

IVA MIHOCI[1], VLADIMIR HRŠAK[2], MLADEN KUČINIĆ[3], VLATKA MIČETIĆ STANKOVIĆ[3], ANTUN DELIĆ[4]
and NIKOLA TVRTKOVIĆ[1]

[1]Croatian Natural History Museum, Department of Zoology, Demetrova 1, 10000 Zagreb, Croatia; e-mails: iva.mihoci@hpm.hr, nikola.tvrtkovic@hpm.hr

[2]University of Zagreb, Faculty of Science, Department of Biology, Marulićev Trg 20/II, 10000 Zagreb, Croatia; e-mail: vhrsak@lipa.botanic.hr

[3]University of Zagreb, Faculty of Science, Department of Biology, Group of Systematic Zoology & Entomology, Rooseveltov trg 6, 10000 Zagreb, Croatia; e-mails: kucinic@zg.biol.pmf.hr, vmicetic@zg.biol.pmf.hr

[4]Faculty of Education, Savska cesta 77, 10000 Zagreb, Croatia; e-mail: a_delic@yahoo.com

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Abstract. Geographic isolation, altitude, climate, landscape and habitat are significant predictors of butterfly diversity in mountain ecosystems. Their diversity and its dependence on altitude, aspect (compass bearing) and biogeographic characteristics of the butterflies were surveyed on the karst mountain Biokovo in southern Croatia. The results affirm that there is a high diversity of butterflies in the study area and the species composition and biogeographic elements are more dependent on altitude than aspect of the mountain. The present study indicates that climate, relief and habitat preferences strongly influence the biogeographic features of species and the relationship between species richness per site and altitude, aspect and the altitude-aspect interaction.

INTRODUCTION

Butterflies are well known taxonomically and ecologically (Kudrna, 1986; Kristensen et al., 2007). Their diversity and geographic patterns, vertical distribution, variation in species richness with altitude and species response to changing altitude, have been a major concern of many researchers interested in mountain biogeography (e.g. Gutiérrez, 1997; Liška & Skyva, 1997; Wettstein & Schmid, 1999; Beneš et al., 2000; Varga, 2003a, b, 2008). Species diversity varies spatially, displaying latitudinal and longitudinal gradients and there are core areas that serve as centres of dispersal and restricted territories where endemic species accumulate (Varga, 1995; Varga & Schmitt, 2008).

In mountain ecosystems, the distribution of species is determined by the suitability of habitat and climate (Storch et al., 2003). The main factors that influence species distribution and diversity include geographic isolation, altitude, climate and features of landscape and habitat such as structure, heterogeneity and quality (e.g. Kudrna, 1986; Fleishman et al., 1998, 2003; Wettstein & Schmid, 1999; Pyrcz & Wojtusiak, 2002; Storch et al., 2003).

Mountain ecosystems, though considered "simple" because the number of species decreases with altitude, are extremely heterogeneous (Haslett, 1997a). The diversity and area/size of habitats at different altitudes affects spatial distribution, species richness, morphology, physiology, life cycle and behavioural patterns (Haslett, 1997b).

Research on the diversity of butterflies occurring on the karst mountain range Biokovo (Dalmatia, southern Croatia) has continued, off and on, since the 19th century (Mann, 1869; Stauder, 1923; Sijarić, 1991a, b; Mihoci & Šašić, 2005). This mountain is a part of the Dinaric karst, which is a mountain range approximately 700 km long and 80–210 km wide that stretches from the Julian Alps along the border between Italy and Slovenia, passes through the Croatian coast and islands, western and southern Bosnia and Herzegovina, and ends in south eastern Montenegro and north western Albania (Tišljar et al., 2002). Mt. Biokovo is closest to the Adriatic Sea (Fig. 1) and as a consequence there are areas on the mountain with continental, montane or Mediterranean climates and vegetation. Certain habitat characteristics of Mt. Biokovo cannot be found elsewhere in the Dinaric karst. To protect these features, the habitat diversity and species listed in the Habitats Directive 92/43/EEC annexes (European Comission, 1992; State Institute for Nature Protection, 2008), Biokovo was declared a Nature Park in 1981 and proposed as a NATURA 2000 site in 2010.

This study determines the influence of altitude and topographic aspect on the distribution and biogeographic characteristics of butterflies on Mt. Biokovo. It also compares the composition and biogeographic characteristics of the species on Mt. Biokovo with those on several other Dinaric karst mountains (Sket, 1994): Mt. Velebit (Croatia) (Mihoci et al., 2007), Mt. Durmitor (Montenegro) (Sijarić et al., 1984), Mt. Učka (Croatia) (Rebel, 1910; Kučinić, 2010) and the complex of Mt. Čvrsnica and Vran (Bosnia and Herzegovina) (Sijarić, 1996; Kučinić et al., 2005). Since similar faunistic research has been done on neighbouring karst areas in the Balkans it was possible

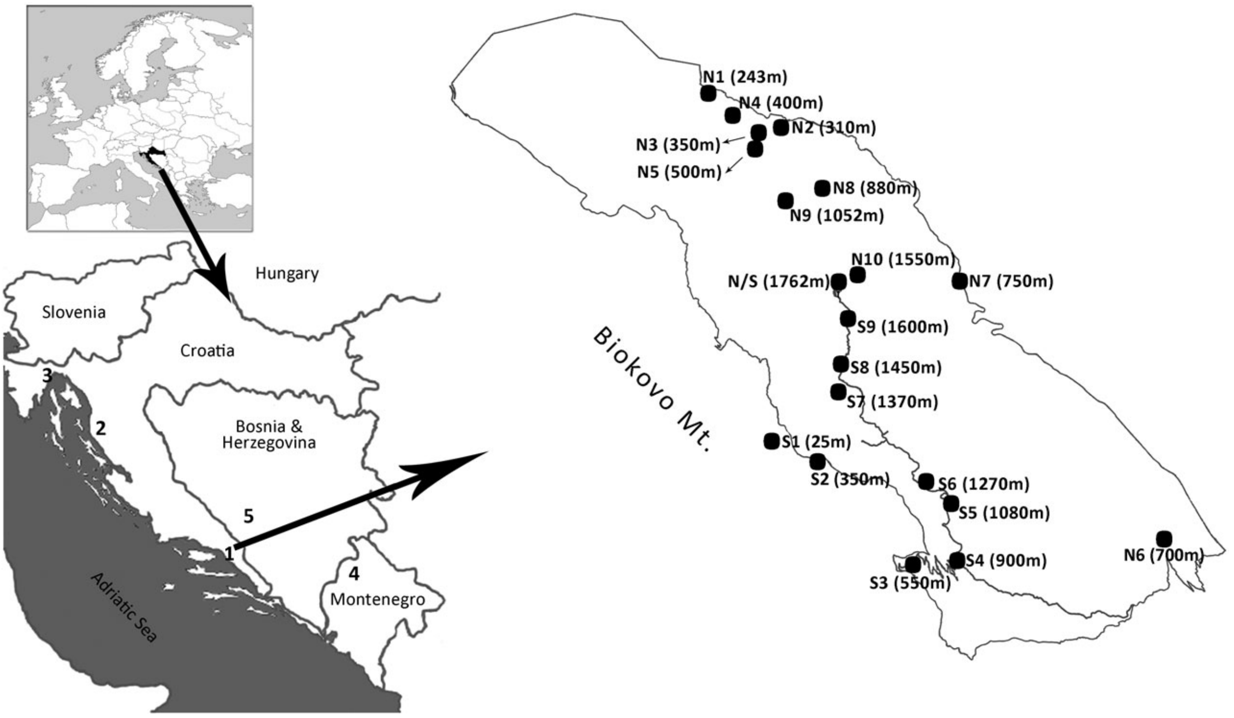


Fig. 1. Study area on Mt. Biokovo, Croatia, with sampling sites per altitude on the northern (N) and southern (S) aspects and positions of neighbouring mountains (1 – Mt. Biokovo, 2 – Mt. Velebit, 3 – Mt. Učka, 4 – Mt. Durmitor, 5 – Mt. Čvrsnica – Vran complex).

to carry out a cluster analysis of the results of these and our study on Biokovo.

MATERIAL AND METHODS

Study sites

Mt. Biokovo is 36 km long and 9.5 km wide (Fig. 1). It has an oblong shape and is orientated along a northwest-southeast axis. The highest peaks are in the southeast of the range, with the tallest Saint Jure peaking at an altitude of 1762 m (Kušan, 1969). Mt. Biokovo is isolated from other mountain areas in the Dinarids, as it adjoins the Adriatic Sea to the south and is separated from the nearby mountains in Croatia and Bosnia and Herzegovina by a broad lowland plain in the north.

Geomorphologic features of Mt. Biokovo originated during the karstification process in fluvial periods. Bedrock originated from sedimentation, and the main geomorphologic characteristics are due to limestone and dolomite karst, and the occasional water regime (Kušan, 1969; Telbisz et al., 2009). The aspect of the sea-facing side of the mountain is much steeper than that of the mainland side. In mid-range altitudes between 400 and 1100 meters, the sea-facing aspect is composed predominantly of cliffs and steep rocks, features which are absent on the mainland side of the mountain.

The vegetation on Mt. Biokovo includes both older Mediterranean and newer Boreal and European forms, together with different types of xerophytic, mesophytic and submontane vegetation, in which Mediterranean elements dominate. Its geographical isolation has made Mt. Biokovo a hotspot of plant endemism, with over 30 endemics (Šolić, 1983).

Butterfly recording

Butterflies were recorded by standard methods using an entomological net in all the vegetation periods from 1994 to 2004 at 10 sites on the mainland side (northeast aspect) and 9 on the coastal side (southwest aspect) and at the top of St. Jure (N/S) (Fig. 1). The sites sampled at the different altitudes were determined exclusively by the presence of meadow/grassland, especially on the forested northern aspect. In several analyses, localities from the northern (N) and southern (S) aspects were grouped into three altitude zones (Z) (zone 1, NZ1 & SZ1: 0–500 m; zone 2, NZ2 & SZ2: 500–1000 m; zone 3, NZ3 & SZ3: above 1000 m). The same amount of time was spent sampling all the sites visited on five occasions between April and September, but in different years: the southern aspect was visited between 1994 and 2000 and the northern aspect between 2000 and 2004. Sampling at each site was done over a 1-h period, and all butterflies seen and captured in that time were recorded. Butterflies were recorded only on dry, sunny and warm days between 10 a.m. and 5 p.m. (Pollard & Yates, 1993).

Data processing

All the tests below were computed separately for altitude and aspect. The number of species at each locality and the mean altitude for each species were determined on both the northern and southern aspects. Change of species richness with altitude and aspect was demonstrated by a regression-based test. Alpha diversity was calculated using the Shannon-Wiener diversity index (*H*) and the Simpson diversity index (*D*). The Shannon-Wiener index is more sensitive to rare species, but its numerical value is less meaningful than some other indices. In contrast, the Simpson index is relatively insensitive to rare species, making it relatively stable with respect to sample size. It can be used to count infinite and finite populations, as well as binary variables (Whittaker, 1972).

Species turnover rate was determined according to Schoener (1986) and statistical significance demonstrated by a regression-based test.

Faunistic similarity between mountain aspects and altitude zones were calculated using the Sørensen similarity index (*S*) (Sørensen, 1948).

TABLE 1. Total number of species (TSN), average number of species recorded at the sample sites (ASN) on the northern and southern aspects and the Shannon's (*H*) and Simpson's (*D*) diversity indices for the northern and southern aspect of Mt. Biokovo.

Aspect	TSN	ASN	H	D
Northern	88	18.4	2.662	0.9118
Southern	80	17.2	2.442	0.8176

TABLE 2. Total species number (TSN), average species number recorded at sampling sites (ASN) at different altitude zones and the Shannon's (*H*) and Simpson's (*D*) diversity indices for the different altitude zones on Mt. Biokovo.

Altitude zone	TSN	ASN	*H*	*D*
Zone 1 (0–500 m)	79	19.1	2.570	0.835
Zone 2 (500–1000 m)	66	16.6	2.390	0.857
Zone 3 (above 1000 m)	67	17.7	2.712	0.920

Indicator species analysis (ISA) (Dufrêne & Legendre, 1997) was used to determine which species are characteristic of aspects or zones (in two groups). Statistical significance of the indicator values (*IVs*) obtained was tested using a permutation test with 1000 random permutations.

The effect of altitude or aspect on species composition was tested using variance decomposition with score files obtained through simple, between- and within-groups normalized principal component analysis (PCA) (Dolédec & Chessel, 1991). In addition, three generalized linear models (GLM) (McCullagh & Nelder, 1989; Lepš & Šmilauer, 2003) relating species number per site (SNS) to altitude; aspect and the altitude-aspect interaction were computed using a Poisson log model.

Butterflies were categorized biogeographically according to Varga (1975, 1977, 2003a), Sijarić et al. (1984) and Schaider & Jakšić (1989). The categories of Sijarić et al. (1984) and Schaider & Jakšić (1989) were developed specifically for the Dinaric karst area. The percentage of each category was calculated for each altitude zone and aspect for Mt. Biokovo and overall for Mt. Velebit and Mt. Durmitor. The following biogeographical categories were used: CP – Circum-Palearctic, WP – West-Palearctic, NPM – North and Pontic-Mediterranean, PCTSS – Pontic-Caspic-Turkestanic-Southsibiric, SI – Sibiric, OT – Oreo-Tundral, EA – Euro-Alpine, PMO – Pontic-Mediterranean Oreal, XM – Xeromontane, HM – Holo-Mediterranean, AM – Atlantic-Mediterranean, PT – Paleotropic, PAM – Pontic-Atlantic-Mediterranean, NP – Non-Paleartic and SMR – S-Mediterranean Refugia. For all taxa, the categorization of the nominal species was used.

Butterfly diversity was compared using the Bray-Curtis distance for samples collected at five sites: Mt. Biokovo, Mt. Učka, Mt. Velebit, Mt. Durmitor and the complex of Mt. Čvrsnica and Vran.

Statistical analyses and ISA were conducted using PCOrd-4.37 and PRIMER6 software, whereas inertia decomposition and PCA were conducted using ADE-4 software (Chessel et al., 1998).

RESULTS

A total of 102 species were recorded (Appendix). The most interesting records were the endemic *Zerynthia cerisy dalmacijae* and *Proterebia afra dalmata*, and rare *Papilio alexanor*, all strictly protected taxa in Croatia (Ministry of Culture of Republic of Croatia, 2009). Of the species of *Erebia*, which all typically occur on mountains, only *Erebia melas* was recorded.

Higher species richness and higher average number of species per locality (species density) were recorded on the northern than on the southern aspect (88 vs. 80, 18.4 vs. 17.2), but these differences are not statistically significant (t-test, $p > 0.05$). Similarly, the Shannon (H) and Simpson (*D*) diversity indices were higher on the northern aspect (Table 1). Sørensen's similarity between the two aspects was relatively high ($S = 78.57\%$), with 66 species shared by the two aspects. Of all the species observed, 22 were recorded only on the northern and 14 only on the southern aspect.

The highest number of species occurred in the lowest altitude zone, zone 1 (total 79, 19.1 per locality). Altitude zones 2 and 3 had a nearly equal number of species (Table 2). The Sørensen similarity index between NZ1 and SZ1 was 56.36%, with 31 species shared by the two zones; 35.00% between NZ2 and SZ2; and 52.75% between NZ3 and SZ3, with 24 species shared. Altitude zones 1 and 2 on the northern aspect were the most similar in species composition, with a Sørensen similarity index of 71.43% (Table 3).

On the northern aspect, the total number of species decreased with altitude (NZ1 – 64, NZ2 – 62, NZ3 – 35). Site analysis revealed the highest number of species (>40 per site) at sites N1 (243 m), N3 (350 m), N6 (700 m) and N8 (880 m) (Fig. 2). Conversely, on the southern aspect, the highest number of species (56) was recorded in SZ3, compared to 46 in SZ1 and 18 in SZ2. Site analysis showed the highest number of species at the lowest site S1 (33 species), and 30 at sites S2 (350 m), S6 (1270 m) and S8 (1450 m). Species richness decreases with altitude although not linearly. Regression lines for both aspects are statistically insignificant (N: $p = 0.51$; S: $p = 0.33$).

At the highest mean altitude on the southern aspect, 38 species were recorded, compared to 22 at the highest mean altitude on the northern aspect (Appendix).

On both aspects, species turnover rate (STR) increased with altitude (Fig. 3). The calculated rates indicate that a 95% change in species composition is reached at 1052–1550 m on the northern aspect. On the southern aspect, the highest percentage change (81%) is reached at 1600–1762 m. In general, STR is lower on the southern than on the northern side of the mountain (Fig. 3). A

TABLE 3. Sørensen similarity index (%) between altitude zones on the northern and southern aspects of Mt. Biokovo (NZ1 – 0–500 m on the northern aspect, NZ2 – 500–1000 m on the northern aspect, NZ3 – above 1000 m on the northern aspect, SZ1 – 0–500 m on the southern aspect, SZ2 – 500–1000 m on the southern aspect, SZ3 – above 1000 m on the southern aspect).

Exp./alt. zone	NZ1	NZ2	NZ3	SZ1	SZ2	SZ3
NZ1	–					
NZ2	71.43	–				
NZ3	46.46	47.42	–			
SZ1	56.36	55.56	44.44	–		
SZ2	31.71	35.00	26.42	40.63	–	
SZ3	56.67	67.80	52.75	49.02	29.73	–

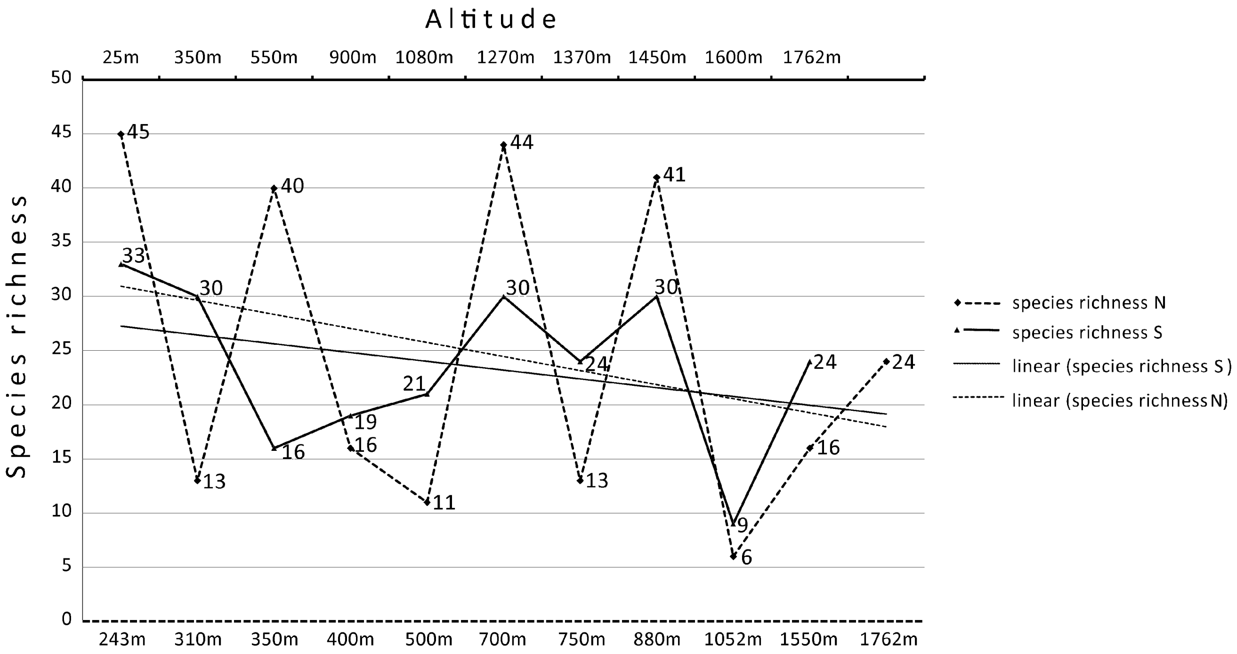


Fig. 2. The species richness at different altitudes on the northern (N – dashed line) and southern (S – solid line) aspects.

regression-based test showed statistical significance for STR on the northern (y = 0.022x + 0.72) ($p < 0.001$) and insignificance on the southern side (y = –0.0002x + 0.759) ($p > 0.05$). Aspects when combined are highly statistically different (t-test, $p < 0.001$) (Fig. 4a, b).

ISA confirmed *Argynnis niobe* (*IV* = 33.3, *P* = 0.042) and *Proterebia afra dalmata* (*IV* = 33.3, *P* = 0.040) as indicator species for the northern and *Hyponephele lycaon* (*IV* = 33.3, *P* = 0.024) and *Chazara briseis* (*IV* = 41.7, *P* = 0.010) for the southern aspect. *Pieris rapae* (*IV* = 40.0, *P* = 0.026) is an indicator species of low altitudes and *Polyommatus amandus* (*IV* = 56.1, *P* = 0.004), *Satyrium spini* (*IV* = 45.4, *P* = 0.012), *Erebia melas* (*IV* = 44.4, *P* = 0.016) and *Hyponephele lycaon* (*IV* = 44.4, *P* = 0.013) of high altitudes. ISA revealed no indicator species for the mid-altitudes.

Variance decomposition analysis showed that the effect of altitude on the variability in the species composition of butterflies is 2-fold greater than the effect of aspect (Table 4).

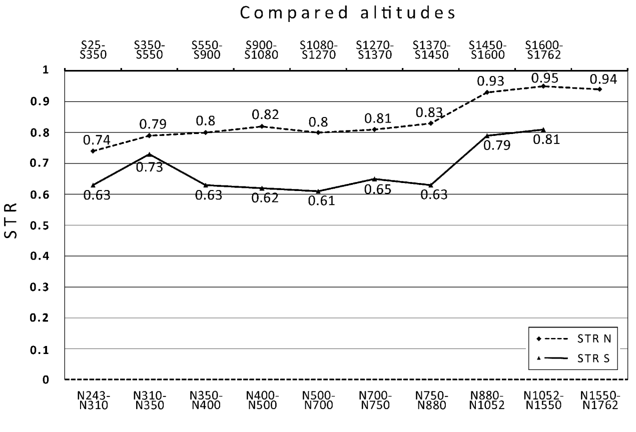


Fig. 3. Species turnover rate (STR) between different and increasing altitudes on the northern (N – dashed line) and southern (S – solid line) aspects.

The General Linear Modelling (GLM) analysis using the model comparing species number per site SNS (predicted vs. observed) with altitude showed that sites S3, N4, N5 and N9 have lower species richness than predicted (below confidence limits), while sites S6, S8, N1 and N8 have higher richness than predicted (Fig. 5a). In the model comparing SNS with aspect, sites N1, N8 and S2 have higher species richness than predicted (Fig. 5b). In the model comparing SNS with the altitude-aspect interaction, sites S3, S9, N4, N5 and N9 have lower species richness than predicted, while sites N1, N8, S2, S6, and S8 have higher richness than predicted (Fig. 5c).

Biogeography

On the southern aspect most of the species were Circum-Palearctic (36.25%) followed by West-Palearctic and North and Pontic-Mediterranean species (21.25% and 20%). Circum-Palearctic species (43.18%) and Pontic-Mediterranean Oreal species (7.95%) prevailed on the northern aspect, while North and Pontic-Mediterranean (20%) and West-Palearctic (21.25%) species were predominant on the southern aspect (Table 5).

With increasing altitude, the proportion of Pontic-Mediterranean Oreal, Holo-Mediterranean, Atlantic-Mediterranean and Paleotropic species decreased, whereas the proportion of Circum-Palaearctic and Pontic-

Table 4. Inertia decomposition analysis – used to test the prominence of altitude or aspect effect on variability in species composition.

	Between groups inertia	Within groups inertia	Total inertia
Aspect	0.74	11.23	13.07
Altitude	1.31	11.76	13.07

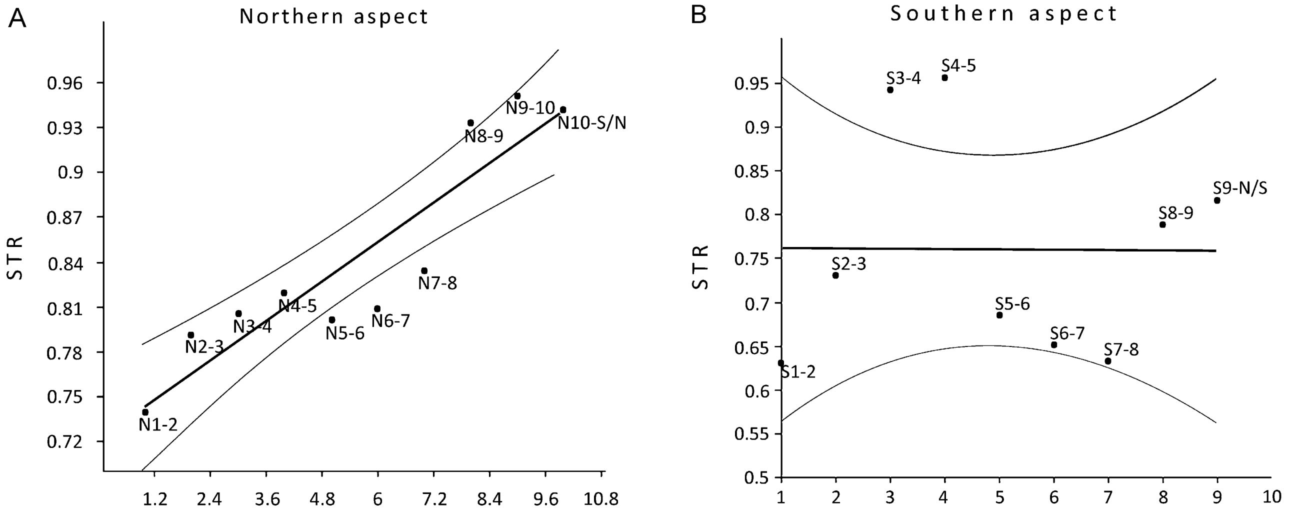


Fig. 4. Linear regression of the species turnover rate (STR). A – northern aspect; B – southern aspect.

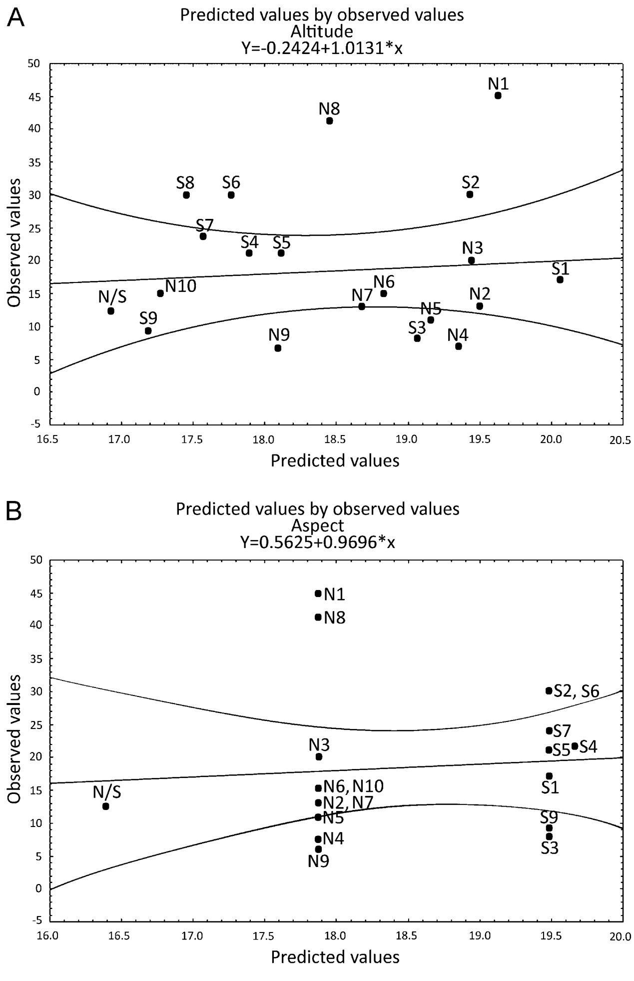
Caspic-Turkestanic-Southsibiric species increased (Table 5).

Comparison of biogeographic proportions of species from Mt. Biokovo, Mt. Velebit (Croatia) and Mt. Durmitor (Montenegro) revealed that Circum-Palearctic species accounted for the highest share of species (< 35%), while the proportion of North and Pontic-Mediterranean and Pontic-Mediterranean Oreal species was higher on Mt. Biokovo than on Mt. Velebit or Mt. Durmitor. The share of Sibiric species was several times higher on Mt. Velebit and Mt. Durmitor than on Mt. Biokovo. No Euro-Alpine species were recorded on Mt. Biokovo, in contrast to the other two mountains (Table 6).

The cluster analysis grouped Mt. Velebit and Mt. Durmitor (78% similarity) and Mt. Biokovo and Mt. Učka (68%). Based on butterfly diversity, the complex on Mt. Čvrsnica and Vran is more similar to Mt. Velebit and Mt. Durmitor than to that on Mt. Biokovo or Mt. Učka (Fig. 6).

DISCUSSION AND CONCLUSIONS

The position of Mt. Biokovo on the Adriatic Sea coast, at the border between the continental and Mediterranean climate, as well as its isolation from surrounding mountains, has resulted in a high degree of endemism (Šolić, 1983) and great diversity of habitats (Kušan, 1969). The



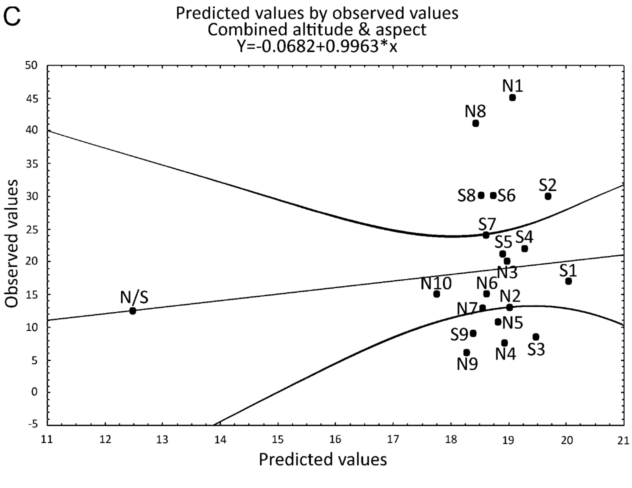


Fig. 5. The GLM analysis. A – model comparing observed with predicted species number at sites at different altitudes on the mountain; B – model comparing observed and predicted number of species at sites on the northern and southern aspects of the mountain; C – model comparing observed and predicted numbers of species at sites with altitude-aspect combined.

Table 5. Number and proportion of species in each biogeographic group in altitude zones and on the northern and southern aspects of Mt. Biokovo (CP – Circum-Paleartic, WP – West-Palearctic, NPM – North and Pontic-Mediterranean, PCTSS – Pontic-Caspic-Turkestanic-Southsibiric, SI – Sibiric, PMO – Pontic-Mediterranean Oreal, HM – Holo-Mediterranean, AM – Atlantic-Mediterranean, PT – Paleotropic, PAM – Pontic-Atlantic-Mediterranean and NP – Non-Paleartic; Alt. zone 1 – 0–500 m, Alt. zone 2 – 500–1000 m, Alt. zone 3 – above 1000 m, N – north-eastern aspect, S – south-western aspect) (Varga, 1975, 1977; Sijarić et al., 1984; Schaider & Jakšić, 1989; Varga, 2003a).

Biogeographic qualification	Alt. zone 1	Alt. zone 2	Alt. zone 3	N	S
CP	32 (40.50)	27 (40.91)	28 (41.79)	38 (43.18)	29 (36.25)
WP	14 (17.72)	13 (19.70)	13 (19.40)	16 (18.18)	17 (21.25)
NPM	16 (20.25)	9 (13.63)	12 (17,91)	13 (14.77)	16 (20.00)
PCTSS	3 (3.80)	3 (4.55)	4 (5.97)	5 (5.68)	4 (5.00)
SI	1 (1.27)	1 (1.52)	1 (1.49)	2 (2.27)	1 (1.25)
PMO	5 (6.33)	6 (9.09)	3 (4.48)	7 (7.95)	4 (5.00)
HM	2 (2.53)	1 (1.52)	1 (1.49)	2 (2.27)	1 (1.25)
AM	2 (2.53)	1 (1.52)	1 (1.49)	1 (1.14)	2 (2.50)
PT	2 (2.53)	1 (1.52)	1 (1.49)	1 (1.14)	2 (2.50)
PAM	1 (1.27)	3 (4.55)	2 (2.99)	2 (2.27)	3 (3.75)
NP	1 (1.27)	1 (1.52)	1 (1.49)	1 (1.14)	1 (1.25)
Total	79 (100.00)	66 (100.00)	67 (100.00)	88 (100.00)	80 (100.00)

present study indicates that 53% of the Croatian butterfly fauna occurs on Mt. Biokovo (e.g. Lorković, 1989; Mihoci et al., 2005, 2006; Perković, 2006; Mihoci & Šašić, 2009; Polak, 2009). The butterfly fauna on the southern and northern slopes is similar, probably because species ranges overlap (S = 78.57%) as the northern and southern localities are relatively close together. On the other hand, the Sørensen index indicated differences in the composition of the fauna in different altitude zones, in particular the isolation of species at mid-altitudes on the southern aspect.

Table 6. Proportion of species in each biogeographic group on Mt. Biokovo, Mt. Velebit and Mt. Durmitor (CP – Circum-Paleartic, WP – West-Palearctic, NPM – North and Pontic-Mediterranean, PCTSS – Pontic-Caspic-Turkestanic--Southsibiric, SI – Sibiric, OT – Oreo-Tundral, EA – Euro-Alpine, PMO – Pontic-Mediterranean Oreal, XM – Xeromontane, HM – Holo-Mediterranean, AM – Atlantic-Mediterranean, PT – Paleotropic, PAM – Pontic-Atlantic-Mediterranean, NP – Non-Paleartic and SMR – S-Mediterranean Refugia) (Varga, 1975, 1977; Sijarić et al., 1984; Schaider & Jakšić, 1989; Varga, 2003a).

Biogeo-graphic qualification	MT. BIOKOVO No.species / biogeo. percentage	MT. VELEBIT No.species / biogeo. percentage	MT. DURMITOR No.species / biogeo. percentage
CP	38 (37.25)	50 (36.50)	49 (37.69)
WP	19 (18.63)	23 (16.79)	18 (13.85)
NPM	20 (19.61)	19 (13.87)	17 (13.08)
PCTSS	6 (5.88)	8 (5.84)	9 (6.92)
SI	2 (1.96)	13 (9.49)	14 (10.77)
OT	–	–	2 (1.54)
EA	–	6 (4.38)	8 (6.15)
PMO	7 (6.86)	6 (4.38)	6 (4.62)
XM	–	1 (0.73)	1 (0.77)
HM	2 (1.96)	2 (1.46)	1 (0.77)
AM	2 (1.96)	2 (1.46)	1 (0.77)
PT	2 (1.96)	2 (1.46)	1 (0.77)
PAM	3 (2.94)	3 (2.19)	2 (1.54)
NP	1 (0.98)	1 (0.73)	1 (0.77)
SMR	–	1 (0.73)	–
Total	102 (100.00)	137 (100.00)	130 (100.00)

Differences in butterfly composition may be explained by relief characteristics, vertical stratification of vegetation cover, habitat heterogeneity and climate. Climate, for example, is well known to affect the distribution of butterflies (Van Swaay et al., 2010). In addition, butterfly diversity is strongly associated with vegetation structure and composition (Fleishman et al., 2005), which differ significantly at different altitudes in the area studied. In particular, the differences in butterfly composition between the northern and southern aspects in the mid-altitude zone probably reflect differences in geomorphology: the coastal slope is composed mainly of cliffs and steep rocks, while there are no vertical cliffs on the mainland side of the range, where forests and small isolated grasslands prevail (Kušan, 1969; Marincić et al., 1972; Lukšić, 1995; Penzar & Penzar, 1995; Ridanović & Šimunović, 995). For the same reasons, the similarity of the local climate and vegetation of the forested low- and mid-altitude zones on the northern aspect (Kušan, 1969;

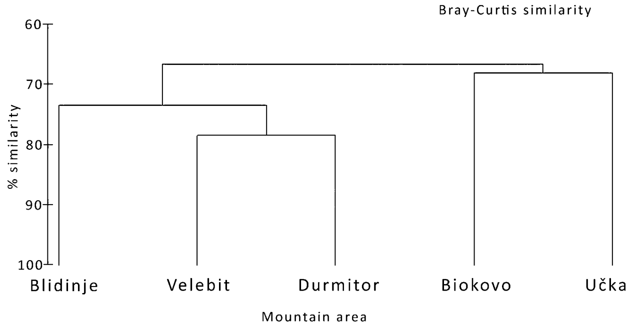


Fig. 6. Cluster analysis of butterfly species composition on Mt. Biokovo, Mt. Velebit, Mt. Učka (Croatia), Blidinje (Mt. Čvrsnica & Vran complex) (Bosnia and Herzegovina) and Mt. Durmitor (Montenegro).

Lukšić, 1995; Mihljević, 1995; Penzar & Penzar, 1995) probably accounts for their nearly identical butterfly species diversity. Site analysis revealed a non-linear decrease in species richness on both aspects, which reflect non-linear relief, non-linear change of vegetation cover and site patch areas decreasing with altitude.

On the southern aspect, more species were found at the highest mean altitude, while more species were found at the lowest mean altitude on the northern aspect. These results are expected if the vertical species distribution is a response to climatic conditions (Settele et al., 2008, Van Swaay et al., 2010), which are hotter on the southern than on the northern aspect (Kušan, 1969; Penzar & Penzar, 1995). Therefore, some species may be highly threatened by recent climate change, such as the high-mountain species *Erebia melas* or *Coenonympha rhodopensis*. Some mountain (e.g. *E. melas*, *C. rhodopensis*) and lowland species (*Zerynthia cerisyi dalmacijae*, *Z. polyxena*, *Leptotes pirithous*, *Lampides boeticus*) were found only at high and low altitudes (Appendix).

Butterfly diversity was higher on the northern aspect due to the predominance of suitable small, calcareous, semi-natural grasslands and forest edge habitats. The richest plant and insect communities in Europe occur in calcareous grasslands (Wallis de Vries et al., 2002). The southern aspect is dominated by cliffs and rocky slopes with a scant and specific vegetation comprised mostly of chasmophytes (Kušan, 1969; Mihljević, 1995; Ridanović & Šimunović, 1995). These habitats are less suitable for butterflies, since few of the species of plants occurring there are larval host-plants or a source of nectar for the adults. In contrast to the present study, a peak in butterfly diversity is recorded at mid-altitudes in mountain areas that do not have the specific geomorphology and climate of Mt. Biokovo (Gutiérrez, 1997; Pyrcz & Wojtusiak, 2002). As pointed out by Hodkinson (2005), maximum species richness of terrestrial insects may occur at the highest, lowest or middle altitude, or show no trend with altitude.

The increase in species turnover rate with altitude on the southern aspect probably reflects changes in habitat structure: Aleppo pine forests at the lower altitudes gradually give way to steep chasmophytic cliffs and rocks, while the higher altitudes are rich in mountain grasslands and edge habitats associated with black pine and beech forests (e.g. Kušan, 1969). The greatest change in the fauna on the southern aspect occurred at 1600–1762 m (sites S9-S/N). Site S9 is located between two narrow sinkholes and is an area subject to a high anthropogenic influence (mountain hut, tourists, road vicinity). Site S/N, at the top of the mountain, features wide, open calcareous slopes rich in vegetation the composition of which is influenced by that of the vegetation on both aspects of the mountain and is least affected by human disturbance. Similarly, the highest number of species on the southern aspect occurred at S1 (33) and S2 (30), where meadows are rich in nectar plants and well-preserved in a botanical reserve. High butterfly richness was also recorded at sites S6 and S8, which have habitat characteristics similar to those of S1 and S2, and confirmed by the GLM analysis using models relating species richness to altitude and the aspect-altitude interaction.

On the northern aspect, a 95% change in species composition occurred at 1052–1550 m (N9–10). In fact, the change in species composition is significant, since there are several high-mountain species at site N10 and only a few at N9. The two sites also differ in terms of altitude and habitat composition: N9 is an isolated meadow surrounding several ponds, whereas N10 is a wide open grassy slope above a beech forest.

On Mt. Biokovo butterfly diversity and composition changes almost twice as much with altitude as with aspect. Numerous authors have pointed out that altitude is one factor that determines climate patterns and changes in floristic composition, both of which strongly affect species distribution (Wettstein & Schmid, 1999; Pyrcz & Wojtusiak, 2002; Storch et al., 2003; Eyre et al., 2005).

The present study revealed that several species, and two in particular, can be used as indicators. On the northern aspect, the endemic *P. afra dalmata* is an indicator species of mid-altitude regions with extensive semi-natural grasslands and edge habitats, rich in the larval-host plant *Festuca* spp. and *Juniperus* bushes for feeding (Mihoci & Šašić, 2005). This taxon lacked suitable habitats at all of the sites on the southern aspect.

Erebia melas is an indicator species of the highest altitude zone. This xeromontane species is the only *Erebia* recorded on Mt. Biokovo and similarly on Mt. Olympus in Greece (Varga, 1975; Sijarić et al., 1984; Mladinov & Lorković, 1985; Mihoci et al., 2007). On both mountains *E. melas* occupies a wide range of rocky habitats, usually up to the highest alpine levels (Varga & Varga-Sipos, 2005). In contrast, Mt. Velebit (Croatia), the longest mountain on the Dinaric karst, has 11 of the 12 *Erebia* species occurring in this country (Mihoci et al., 2007). *E. melas* on Mt. Biokovo defines the southern edge of *Erebia* species distribution in Croatia (Mladinov & Lorković, 1985; Jakšić, 1988). The absence of other *Erebia* species on Mt. Biokovo is attributable to the limited presence of high-mountain meadows rich in grasses. These are replaced by rocky slopes with sparse grasses and an unfavourable climate with long and intense summer droughts, high temperatures and infrequent precipitation (Kušan, 1969; Penzar & Penzar, 1995). The "*Erebia* favourable" habitat occurs on Mt. Velebit where there are 11 species of *Erebia* and on Mt. Durmitor in Montenegro where there are 12 species. These mountains have a favourable climate and widespread alpine and subalpine meadows and semi-natural grass-covered slopes (Sijarić et al., 1984; Forenbacher, 2001; Nikolić, 2004).

The composition of the fauna revealed by biogeographic analysis was expected to reflect the geographical position, climate and ecological characteristics of Mt. Biokovo (Kušan, 1969; Penzar & Penzar, 1995). As expected West-Palearctic, North and Pontic-Mediterranean, Atlantic-Mediterranean and Paleotropic species were predominant on the southern aspect of the mountain, which experiences a Mediterranean climate. On the northern aspect, in contrast, Circum-Paleartic, Pontic-Caspic-Turkestanic-Southsibiric, Sibiric and Pontic-Mediterranean Oreal species are predominant. The finding that Mt. Biokovo has a more similar fauna to Mt. Učka (68%) than to other Dinarid mountains demonstrates the influence of the Adriatic Sea, which results in a Mediterranean climate on the coastal slopes and a continental one on mainland slopes. Both Mt. Biokovo and Mt. Učka lack high-mountain species, such as *Coenonympha gardetta* Prunner, *Lycaena candens* Herrich-Schaffer, *Polyommatus eros* Ochsenheimer, *Polyommatus pyrenaicus* Boisduval and *Erebia* spp. (Mann, 1869; Rebel, 1910; Stauder, 1923; Sijarić, 1991a, b; Kučinić, 2010) unlike Mt. Velebit, Mt. Durmitor or the complex of Mt. Čvrsnica and Vran (e.g. Sijarić et al., 1984; Sijarić, 1996; Kučinić et al., 2005; Mihoci et al., 2007). These findings are consistent with those of Varga & Schmitt (2008), who found fewer alpine and arctic-alpine butterflies in the north western Dinarids than in the longer and higher mountains of northern Albania, Montenegro (Mt. Durmitor), Macedonia and western Bulgaria.

Comparison of the biogeographic characteristics of Mt. Biokovo, Mt. Velebit and Mt. Durmitor suggests that altitude and the continental and alpine climate accounts for the great similarity in composition of species of butterfly on Mt. Velebit and Mt. Durmitor (78%). The greater influence of continental and alpine climate depends on the geographical position and greater heights of Mt. Velebit and Mt. Durmitor compared to Mt. Biokovo (Sijarić et al., 1984; Forenbacher, 2001).

The most common species on all three mountains are Circum-Palearctic species, which is consistent with their dominance in the European fauna (Varga, 1977). However, there is a several-fold lower number of Sibiric species on Mt. Biokovo than on Mt. Velebit and Mt. Durmitor. Even more interestingly, there are no Euro-Alpine species on Mt. Biokovo whereas there are eight on Durmitor. These differences in biogeographical proportions clearly reflect differences in the geographical positions, altitude and habitat characteristics of the mountains.

In conclusion, the present study indicates that the composition and biogeographic features of butterfly species can vary significantly, even over a small area such as the southern and northern aspects of one mountain. This variation reflects the diversity of habitats and the changes in climate and geomorphology with altitude and aspect.

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Appendix. List of the butterflies recorded and their occurrence in the different altitude zones on Mt. Biokovo (NZ1 – 0–500 m on the northern aspect, NZ2 – 500–1000 m on the northern aspect, NZ3 – above 1000 m on the northern aspect, SZ1 – 0–500 m on the southern aspect, SZ2 – 500–1000 m on the southern aspect, SZ3 – above 1000 m on the southern aspect), MA(N) – mean altitude of species on northern aspect, MA(S) – mean altitude of species on southern aspect, BQ – biogeographical qualification: CP – Circum-Paleartic, WP – West-Palearctic, NPM – North and Pontic-Mediterranean, PCTSS – Pontic-Caspic-Turkestanic-Southsibiric, SI – Sibiric, PMO – Pontic-Mediterranean Oreal, HM – Holo-Mediterranean, AM – Atlantic-Mediterranean, PT – Paleotropic, PAM – Pontic-Atlantic-Mediterranean and NP – Non-Paleartic. Systematics follows Karsholt & Razowski (1996) and biogeography Varga (1975, 1977), Sijarić et al. (1984), Schaider & Jakšić (1989) and Varga (2003a). Biogeographical categories according to Sijarić et al. (1984) and Schaider & Jakšić (1989) are used as they are especially modified for the Dinaric karst area.

Species	NZ1	NZ2	NZ3	SZ1	SZ2	SZ3	MA(N)	MA(S)	BQ
Erynnis tages (L.)	–	–	+	–	–	–	1550		CP
Carcharodus lavatherae (Esper, 1783)	–	+	–	–	–	+	880	1410	PAM
Carcharodus floccifera (Zeller, 1847)	–	–	–	+	–	–		350	AM
Pyrgus sidae (Esper, 1784)	+	+	–	–	–	–	619		PMO
Pyrgus armoricanus (Oberthür, 1910)	–	–	–	–	+	–		550	PAM
Pyrgus alveus (Hübner, 1803)	+	–	–	–	–	–	350		CP
Thymelicus lineola (Ochsenheimer, 1808)	–	+	–	–	–	–	880		CP
Thymelicus sylvestris (Poda, 1761)	+	+	–	–	–	+	625	1467	PAM
Thymelicus acteon (Rottemburg, 1775)	–	+	–	–	–	+	675	1450	CP
Ochlodes venata (Bremer & Grey, 1853)	+	–	–	–	–	+	243	1450	CP
Zerynthia polyxena (Denis & Schiffermüller, 1775)	–	–	–	+	–	–		25	NPM
Zerynthia cerisy dalmacijae (Sala & Bollino, 1994)	–	–	–	+	–	–		25	NPM
Parnassius mnemosyne (L.)	–	+	+	–	–	+	1035	1450	PCTSS
Iphiclides podalirius (L.)	+	+	+	+	+	+	624	905	WP
Papilio machaon L.	–	–	+	+	+	–	1762	308	CP
Papilio alexanor Esper, 1800	+	+	–	–	–	–	512		PMO
Leptidea sinapis (L.)	+	+	+	+	–	+	415	925	NPM
Anthocharis cardamines (L.)	+	+	–	+	+	–	527	308	CP
Euchloe ausonia (Hübner, 1804)	+	+	–	–	+	–	459	550	WP
Aporia crataegi (L.)	+	+	+	–	–	+	708	1450	CP
Pieris brassicae (L.)	+	+	–	+	–	+	491	855	CP
Pieris mannii (Mayer, 1851)	+	+	–	+	+	+	507	830	NPM
Pieris rapae (L.)	+	+	–	+	–	+	442	187	CP
Pieris ergane (Geyer, 1828)	+	+	+	+	–	+	785	1202	NPM
Pieris napi (L.)	+	+	–	+	–	–	574	350	CP
Pontia daplidice (L.)	+	–	+	+	–	+	1056	552	CP
Colias croceus (Fourcroy, 1785)	+	+	+	+	+	+	777	550	PT
Colias hyale (L.)	–	+	–	–	–	+	880	1175	NPM
Colias alfacariensis Ribbe, 1905	+	+	–	–	–	+	538	1270	NPM
Gonepteryx rhamni (L.)	+	+	+	–	–	+	643	1363	CP
Gonepteryx cleopatra (L.)	+	–	–	–	–	–	385		NPM
Lycaena phleas (L.)	+	–	–	+	–	–	243	25	CP
Lycaena thersamon (Esper, 1784)	–	–	–	+	–	–		25	WP

Callophrys rubi (L.)	+	+	–	+	–	–	599	188	CP
Satyrium w-album (Knoch, 1782)	+	–	–	–	–	–	356		NPM
Satyrium spini (Denis & Schiffermüller, 1775)	–	+	–	–	–	+	880	1490	WP
Satyrium ilicis (Esper, 1779)	+	+	+	–	–	–	763		NPM
Satyrium acaciae (F.)	+	–	–	–	–	+	243	1080	WP
Lampides boeticus (L.)	–	–	–	+	–	–		25	PT
Leptotes pirithous (L.)	–	–	–	+	–	–		25	NPM
Celastrina argiolus (L.)	+	–	–	+	–	–	276	25	CP
Pseudophilotes vicrama (Moore, 1865)	+	+	–	–	–	+	660	1080	AM
Scolitantides orion (Pallas, 1771)	+	+	–	+	–	–	515	350	PCTSS
Glaucopsyche alexis (Poda, 1761)	+	–	–	–	–	–	301		CP
Plebeius argus (L.)	+	–	+	–	–	+	513	1762	CP
Plebeius idas (L.)	+	+	–	–	–	+	495	1490	CP
Aricia agestis (Denis & Schiffermüller, 1775)	+	+	+	+	+	+	536	757	CP
Aricia artaxerxes (F.)	+	–	–	–	–	–	500		SI
Polyommatus semiargus (Rottemburg, 1775)	+	+	–	–	–	–	562		CP
Polyommatus escheri (Hübner, 1823)	–	–	+	–	–	+	1550	1450	WP
Polyommatus dorylas (Denis & Schiffermüller, 1775)	–	–	+	–	–	+	1550	1270	NPM
Polyommatus amandus (Schneider, 1792)	–	+	–	–	–	+	880	1422	SI
Polyommatus icarus (Rottemburg, 1775)	+	+	–	+	+	+	536	915	CP
Polyommatus daphnis (Denis & Schiffermüller, 1775)	–	–	–	–	–	+		1270	NPM
Polyommatus bellargus (Rottemburg, 1775)	+	+	–	+	+	–	558	485	WP
Polyommatus coridon (Poda, 1761)	–	+	–	–	–	+	750	1225	NPM
Libythea celtis (Laicharting, 1782)	+	+	+	+	–	–	783	25	CP
Argynnis paphia (L.)	+	+	–	+	–	+	570	900	CP
Argynnis pandora (Denis & Schiffermüller, 1775)	+	+	–	+	–	+	532	1110	CP
Argynnis aglaja (Linnaeus, 1758)	+	+	–	–	–	+	515	1354	CP
Argynnis adippe (Denis & Schiffermüller, 1775)	+	+	+	–	–	+	713	1270	CP
Argynnis niobe (L.)	+	+	+	–	–	–	809		CP
Issoria lathonia (L.)	+	+	+	+	–	+	816	773	CP
Brenthis hecate (Denis & Schiffermüller, 1775)	–	+	–	–	–	+	751	1270	WP
Boloria euphrosyne (L.)	+	+	+	–	–	–	848		CP
Vanessa atalanta (L.)	+	–	+	+	–	+	880	810	WP
Vanessa cardui (L.)	+	+	+	+	–	+	917	1023	NP
Inachis io (L.)	–	–	+	–	–	+	1762	1450	CP
Aglais urticae (L.)	–	–	+	–	–	+	1762	1485	CP
Polygonia egea (Cramer, 1775)	+	+	–	+	–	+	562	774	NPM
Nymphalis antiopa (L.)	–	+	+	–	–	–	1321		CP
Nymphalis polychloros (L.)	+	–	–	–	–	–	385		WP
Nymphalis xanthomelas (Esper, 1781)	+	–	+	–	–	–	897		PCTSS
Melitaea cinxia (L.)	+	+	–	+	+	+	592	633	CP
Melitaea trivia (Denis & Schiffermüller, 1775)	–	+	–	–	–	–	880		WP
Melitaea didyma (Esper, 1778)	+	+	+	+	–	–	736	188	CP
Limenitis camilla (L.)	+	–	–	–	–	–	356		CP
Limenitis reducta Staudinger, 1901	+	+	–	–	+	+	551	1090	HM
Neptis sappho (Pallas, 1771)	–	–	–	–	–	+		1370	PCTSS
Neptis rivularis (Scopoli, 1763)	–	+	–	–	–	–	880		PCTSS
Pararge aegeria (L.)	+	+	–	+	–	–	513	25	WP
Lasiommata megera (L.)	+	+	+	+	+	+	589	638	WP
Lasiommata maera (L.)	+	+	–	+	–	+	486	1025	CP
Coenonympha rhodopensis Elwes, 1900	–	+	–	–	–	+	675	1410	PMO
Coenonympha pamphilus (L.)	–	+	+	+	+	+	906	849	CP
Pyronia tithonus (L.)	+	–	–	–	–	–	350		NPM
Pyronia cecilia (Vallantin, 1894)	–	–	–	+	–	–		188	NPM
Maniola jurtina (L.)	+	+	+	+	–	–	901	188	WP
Hyponephele lycaon (Rottemburg, 1775)	–	–	–	–	–	+		1293	WP
Hyponephele lupinus (O. Costa, 1836)	+	+	+	–	–	+	759	1175	WP
Proterebia afra dalmata (Godart, 1824)	+	+	–	–	–	–	492		PMO
Erebia melas (Herbst, 1796)	–	–	+	–	–	+	1762	1473	PMO
Melanargia galathea (L.)	+	+	–	–	+	+	473	1220	NPM
Melanargia larissa (Geyer, 1828)	+	–	–	–	+	–	243	550	PMO
Satyrus ferula (F.)	–	+	–	+	–	+	675	997	WP
Minios dryas (Scopoli, 1763)	–	–	+	+	–	+	1762	860	PCTSS
Hipparchia fagi (Scopoli, 1763)	–	–	–	+	–	+		1143	NPM
Hipparchia syriaca (Staudinger, 1871)	–	+	+	+	+	–	1017	462	PMO
Hipparchia semele (L.)	+	+	+	+	–	+	683	738	WP
Hipparchia statilinus (Hufnagel, 1766)	–	–	–	+	–	–		25	NPM
Brintesia circe (F.)	+	–	–	–	–	–	300		HM
Chazara briseis (L.)	–	–	–	+	+	+		765	WP