

ON THE LIMIT OF ALTITUDINAL RANGE SHIFTS –
POPULATION GENETICS OF
RELICT BUTTERFLY POPULATIONS

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Responses to climate warming vary considerably. Cold-adapted species mostly escape rising temperatures by latitudinal and/or altitudinal range shifts, and often today occur in isolated remnants. In the present study we discuss the genetic consequences of climate warming for five butterfly taxa (*Lycaena helle*, *Erebia epiphron*, *Erebia sudetica inalpina*, *Coenonympha darwiniana* and *C. macromma*) which currently show relict-like distributions at least in parts of their distribution ranges. For all these species, genetic data (microsatellite and/or allozyme polymorphisms) already exist. In general, the situation for such high montane/alpine species in the Alps differs from that in the low-altitude mountains, as the considerably higher elevations of the Alps mean that there is still possibility for further altitudinal shifts, while no such possibilities exist in lower mountain ranges. However, there are considerable differences in the general genetic situation of the five taxa analysed. The genetic structure of the Alpine *L. helle* populations is quite similar to that of the populations in the northern Alps forelands and the lowlands of eastern Europe. However, the lower mountain systems of western Europe all represent considerably differentiated gene pools for this species, so that these might be endangered by climate change. At the contrary, the relict population of *E. epiphron* in the Jeseník Mts is genetically not differentiated from the northern Alps. Taxa such as *Erebia sudetica inalpina*, *Coenonympha darwiniana* and *C. macromma*, which are all confined to certain parts of the Alps, represent endemic gene-pools. Of these taxa, *E. sudetica inalpina* shows low population genetic diversity, while the other two species have high allozyme diversity. Therefore, climate change accompanied by altitudinal range shifts might not have an effect on the genetic composition of the former, but might cause losses of genetic diversity in the latter two taxa. In conclusion, the data of these five taxa show that climate change will have different effects on different species of relict-like distributions.

Key words: climate change, relict species, habitat fragmentation, genetic differentiation, private alleles, extinction scenario, butterflies

INTRODUCTION
RESPONSES TO CLIMATE CHANGE

Many scientific studies have addressed the effects of recent climate changes on distribution patterns (PARMESAN *et al.* 1999, THOMAS & LENNON 1999, PARMESAN & YOHE 2003, ROOT *et al.* 2003, PARMESAN 2006). These changes can

also have severe impacts on species-interactions; thus, spatial mismatches of trophically interacting species can arise as a result of range shifts (SCHWEIGER *et al.* 2008). In addition, many studies were also conducted to analyse species distribution modifications as a consequence of climate change along glacial-interglacial oscillations (COOPE 1994, HEWITT 2004, SCHMITT 2007). These oscillations caused extinction processes of thermophilic species over major parts of Central Europe during the glacial period, or survival in southern refugia (HEWITT 1996, HABEL *et al.* 2005, 2008a, SCHMITT *et al.* 2005b). In contrast to these warm-adapted organisms, boreo-montane and arctic-alpine species might have reached their maximum distributions over the Central European lowlands during glaciations, but then escaped the postglacial warming by migrating to higher altitudes and latitudes (VARGA & SCHMITT 2008, SCHMITT 2009). These species therefore are of great interest in integrating the past distribution history and recent climate-driven changes.

Today, such cold-adapted species are therefore restricted to the highest elevations of low altitude mountains scattered over Central Europe. Here, these species have often already reached the elevation limit and thus cannot respond to further rising temperatures. For these populations, life in complete isolation is enhancing processes of population dynamics, such as population fluctuations (LESICA & ALLENDORF 1995) and population stochasticity (MELBOURNE & HASTINGS 2008). This results in losses of genetic diversity in local sites through drift, which cannot be compensated by immigration from neighbouring populations. Such genetically impoverished populations often suffer from decreased fitness and the accumulation of weakly deleterious alleles (REED & FRANKHAM 2003, ALLENDORF & LUIKART 2006).

In this article, we discuss the genetic data known for five mountain butterfly species (*Lycaena helle*, *Erebia epiphron*, *Erebia sudetica inalpina*, *Coenonympha darwiniana* and *C. macromma*; SCHMITT *et al.* 2005a, 2006, HAUBRICH & SCHMITT 2007, FINGER *et al.* 2009, HABEL *et al.* 2010a, b, c, SCHMITT & BESOLD 2010) in the light of recent global warming. We especially focus on the importance and relevance of relict-like populations of these species and work out the similarities and differences between them.

THE FIVE MOUNTAIN BUTTERFLY TAXA

The lycaenid butterfly Violet Copper *Lycaena helle* (DENIS & SCHIFFER-MÜLLER, 1775) is an example of a combination of postglacial retreat to higher elevations and northwards shift. This species has almost completely lost its lowland

populations over major parts of its former European distribution area, especially at the species' western distribution edge (BOZANO & WEIDENHOFFER 2001). This pattern has led to highly disjunct population remnants, mostly restricted to higher elevations. The species requires cold and moist habitats (BACHELARD & DESCIMON 1999, STEINER *et al.* 2006); further specific habitat characteristics are for example high abundances of the species' larval food plant *Polygonum bistorta* and habitat structures with shrubs and trees (TURLURE *et al.* 2009). The altitudinal range of this species is varying from little above sea level in Scandinavia and north-eastern Europe to an upper limit at about 1.800 m in the Alps and Pyrenees (TOLMAN & LEWINGTON 1998); the lowest occupied habitats in Switzerland are located at about 600 m (SCHWEIZERISCHER BUND FÜR NATURSCHUTZ 1987). Besides the climate warming the recent anthropogenic habitat destruction reinforced further habitat fragmentation (FISCHER *et al.* 1999). This combination has caused extinction of many local populations and the species is listed in appendices II and IV of the Nature 2000 directive (DREWS & PRETSCHER 2003) and many Red Data Books. Thus, *L. helle* is considered one of the most endangered butterfly species in Europe (VAN SWAAY & WARREN 1999).

The Mountain Ringlet *Erebia epiphron* (KNOCH, 1783) shows similar postglacial range shift patterns as *L. helle*, but has retreated to the northern parts of the British Isles rather than to Fennoscandia (KUDRNA 2002). Furthermore, the altitudinal range of the species on average is higher than for *L. helle* (900–2,700 m, populations of lower altitudes are only known for the northern UK) (TOLMAN & LEWINGTON 1998). *Erebia epiphron* is also found in a larger number of Central European low-altitudinal mountains, e.g. in the Jeseník Mts in northern Moravia (SCHMITT *et al.* 2005a).

Some taxa distributed in the same altitudinal belts as *L. helle* and *E. epiphron* are strongly restricted to some small and isolated areas of the Alps. In this article we refer to three taxa: *Erebia sudetica inalpina* WARREN, 1949 endemic to the area of Grindelwald in Switzerland with an altitudinal range from 1,300 to 1,900 m (SONDEREGGER 2005); *Coenonympha darwiniana* STAUDINGER, 1871 restricted to the southern Alps between eastern Valais and western Graubünden (SCHMITT & BESOLD 2010) with an altitudinal range from 800 to 2,100 m (TOLMAN & LEWINGTON 1998); and *Coenonympha macromma* TURATI & VERITY, 1911 endemic to the Alpes Maritimes (SCHMITT & BESOLD 2010) and an identical altitudinal range as its sibling species. All these four Satyrinae species need high-montane to alpine meadows of low to medium vegetation height; their larvae feed on different species of grasses (SCHWEIZERISCHER BUND FÜR NATURSCHUTZ 1987, SONDEREGGER 2005).

EXAMPLE: *LYCAENA HELLE*

Genetic data for *L. helle* based on five highly polymorphic microsatellite loci (HABEL *et al.* 2008b) give a clear resolution and strong evidence on a regional (FINGER *et al.* 2009) as well as on the continental level (HABEL *et al.* 2010a, b, c), and are suitable to demonstrate past range shifts (going back at least to the last glacial period) (cf. KIMBERLY & SELKOE 2006).

Postglacial colonisations of Lycaena helle

In a neighbour-joining dendrogram based on genetic distances sensu CAVALLI-SFORZA and EDWARDS (1967) all Fenoscandian samples build one branch most closely related to eastern European populations (Fig. 1). While the Finnish populations are genetically closer to the eastern European ones than the Swedish populations, these similarities mirror the feasibility of this postglacial expansion route (eastern Europe–Finland–Sweden), also reflected in losses of alleles during this colonisation process. This colonisation pathway of *L. helle* from north-eastern Europe via Finland to Sweden mostly coincides with that of *Trollius europaeus* (DESPRES *et al.* 2002) and maybe *Ranunculus glacialis* (SCHÖNSWETTER *et al.* 2003).

Evolution on mountain archipelagos in Lycaena helle

The low-altitude mountains of western Europe provided exclaves of suitable climatic conditions for cold-adapted species during the postglacial warming. These mountain areas are geographically isolated from each other. After colonisation, individual exchanges among these areas have been restricted, as shown, for example, by genetic analyses of *L. helle*: The studied populations of the Massif Central, Madeleine Mountains, Vosges, Ardennes, Eifel and Westerwald represent strongly differentiated and distinct gene pools affected by the strong isolation over several thousands of years (HABEL *et al.* 2010a, c). They are also characterised by private alleles; more than 11% of the total number of alleles analysed are endemic to a single mountain area (Fig. 2). In addition to this genetic uniqueness in microsatellite alleles, morphological characters distinguish the populations of each of these mountain areas so that *L. helle* was split into nine subspecies (MEYER 1982). The combination of distinct genetic and morphological characters may be used to define them as evolutionarily significant units sensu MORITZ (1994) to underpin the high evolutionary value of these relict populations.

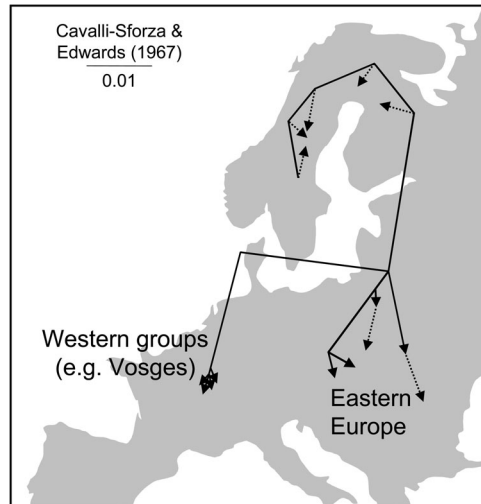


Fig. 1. Neighbour-joining tree based on genetic distances (CAVALLI-SFORZA & EDWARDS 1967) performed on five microsatellite loci, representing the analysed populations of Scandinavia, Finland, eastern Europe (Poland, Lithuania, Romania) and the Vosges. Genetic distances are projected on a map. Solid lines display the genetic distance, arrows show the locations of the sampling sites. Data recalculated from HABEL *et al.* (2010c)

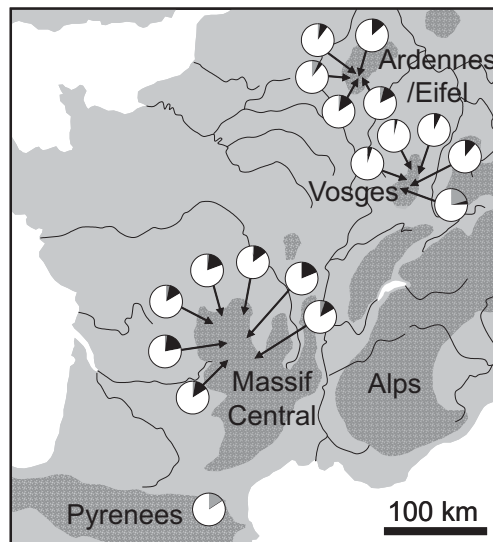


Fig. 2. Allele frequency distributions of *L. helle* populations of the Pyrenees and the western low-altitude mountains (Massif Central, Vosges, Ardennes). The colours in the pie charts indicate the distribution of alleles (white: occurring in several mountain areas, black: exclusive to a single mountain area, grey: exclusively occurring in the respective population). Data taken from FINGER *et al.* (2009) and HABEL *et al.* (2010a, b)

These genetic results also underline that *L. helle* is suffering from anthropogenic habitat deterioration and rising isolation; particularly the populations scattered over the species' western distribution range suffer from the low or even missing exchange rates of individuals (HABEL *et al.* 2010a). Even within the analysed mountain areas, isolation-by-distance systems support the geography-dependent interconnectivity of local populations (FINGER *et al.* 2009).

Predictions for the future distribution of Lycaena helle

A Climate Envelope Model (CEM) (PHILIPS *et al.* 2006) identified and quantified the climatically suitable habitats for *L. helle* and possible connections between them (for details see HABEL *et al.* 2010c). These projections of the climatic envelope into the geographic space allow to assess the potential distribution of the butterfly under the current climate (cf. ARAUJO & WHITTAKER 2005). The resulting areas with a predicted suitability of >75% are restricted to higher elevations and the North, and are all separated from each other by unsuitable areas (HABEL *et al.* 2010c); this models mostly match with the actual distribution of the species (KUDRNA 2002). These results coincide with the genetic picture of isolated remnant population groups aggravated by the low dispersal power of *L. helle* (BINK 1992). This pattern is corroborated by strong genetic differentiation between neighbouring mountain areas like the Ardennes/Eifel complex and the Westerwald (FINGER *et al.* 2009) or even neighbouring populations within such mountain areas (HABEL *et al.* 2010a, b).

Applying different scenarios of climate warming, the climate envelope models (CEMs) suggest a strong decline of potentially suitable habitats, especially at the western edge of the species' distribution. Most of the recent areas of predicted suitability may disappear. Areas with a predicted suitability of 75% remain exclusively over areas of the Jura Mts and the Alps. Areas with a predicted suitability of at least 50% remain in parts of the Massif Central, the Pyrenees and the Vosges. Even over major parts of the Alps, potentially suitable habitats may largely disappear (HABEL *et al.* 2010b).

EXAMPLE: *EREBIA EPIPHRON*

Genetic structures within mountain archipelagos of Erebia epiphron

A study of allozyme polymorphisms of *E. epiphron* also distinguished several strongly differentiated genetic lineages in this species, calling for a variety of different glacial retreats and differentiation centres around and between the moun-

tain systems of Europe. In contrast to *L. helle*, the strongly isolated populations from the Jeseník Mts in northern Moravia was grouped together with the northern Alpine lineage (SCHMITT *et al.* 2006). The genetic constitutions of the other low-altitudinal mountain populations (e.g. Massif Central, Vosges) are still unknown for this species, but are suspected not to be endemic to these areas, as all of them are less isolated from other high mountain populations of the species than the Jeseník Mts.

Genetic constitution of Erebia epiphron in the Jeseník Mts

Nevertheless, *E. epiphron* shows a remarkable variability of genetic diversities in Jeseník Mts. Here, the species is quite common along the main ridge in a large, mostly continuous population, but is also found in an isolated but small area of subalpine grassland west of the main ridge separated from the ridge population by some four kilometres of forest. This small population has a strongly impoverished genetic diversity compared to that of the main ridge, and indications of degeneration such as partial albinisms of the wing coloration have been observed (SCHMITT *et al.* 2005a). Therefore, the genetic make-up maintained by this small population is apparently inadequate for its long-term survival.

EXAMPLES: *EREBIA SUDETICA INALPINA*, *COENONYMPHA DARWINIANA*, *C. MACROMMA*

The genetic diversity of mid-altitude endemics of the Alps

In contrast to the low-altitude mountains of Central Europe, mid-altitude species should not be dramatically threatened by climate warming in the Alps as uphill habitat shifts are well possible in Europe's highest mountain system. However, the strongly localised endemic taxa in this group differ in that they express strongly different levels of genetic diversity. Thus, the ringlet *E. sudetica inalpina* has low genetic diversity (HAUBRICH & SCHMITT 2007), but the genetic situation is considerably different for the two endemics *C. darwiniana* and *C. macromma*. The populations of these two species show remarkable genetic diversity (SCHMITT & BESOLD 2010), which is even higher than in the two other representatives of this species complex, the high altitude *C. gardetta* (SCHMITT & BESOLD 2010) and the lowland taxon *C. arcania* (BESOLD *et al.* 2008a); indeed, the populations even reach the extremely high genetic diversities of the very common and fairly widespread congeneric *C. pamphilus* (BESOLD *et al.* 2008b).

THE FUTURE OF RELICT POPULATIONS OF MOUNTAIN BUTTERFLY SPECIES

Many of the populations of *L. helle*, but also of other occurrences of alpine species in the European low-altitude mountains as for example *E. epiphron*, may be highly threatened by climate change in many of their populations in mountain systems without major uphill escape possibilities. These predicted losses of suitable habitats would also involve losses of genetically unique groups of populations. However, whether such lost populations will represent a unique gene pool as in the case of *L. helle* or will be represented by replica in other, higher mountain systems as in the case of *E. epiphron*, need individual analyses in every single case.

The scenario of further climate warming might present a severe threat for the survival of *E. epiphron* in the Jeseník Mts, not only due to the risk of complete loss of habitat in this mountain range, but also as the possibly remaining areas suitable for this species here and possibly many others in the Central European low-altitude mountains will not support the existence of sufficiently large populations of this species conserving gene pools of adequate diversity. This might also be a problem for many other species with regressive populations. Thus, even populations of *L. helle* might disappear in areas predicted as habitat by the CEM models due to degeneration effects of their gene pools (REED & FRANKHAM 2003, SCHMITT & HEWITT 2004).

Finally, quick uphill habitat shifts due to dramatic climatic changes might result in considerable losses of genetic diversity of the affected populations. While such genetic bottlenecks may negatively influence the populations' viability (REED & FRANKHAM 2003), such changes might be critical especially for genetically diverse taxa like *C. darwiniana* and *C. macromma* and possibly also for other local mid-altitude endemics of the Alps which show either such high genetic population diversity or low individual mobility. Therefore, uphill shifts might also negatively impact the highly polymorphic populations of *L. helle*. In contrast, taxa with low genetic diversity like *E. sudetica inalpina* might be less affected by such genetic bottleneck effects due to their genetic poverty so that even a quick up-slope translocation by climate warming, even in the case of reduced available habitat at higher elevations, should not result in any remarkable genetic consequences for this taxon.

Therefore, major and rapid climate-driven uphill shifts in the future might strongly impact the genetic make-up of many mid-altitude populations, especially in the high mountain systems, and particularly in species of generally high genetic diversity, while many of the populations and entire genetic lineages in lower mountain systems might be lost for ever.

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REFERENCES

- ALLENDORF, F. W. & LUIKART, G. (2006) *Conservation and the genetics of populations*. Blackwell Publishing, Oxford, UK, 642 pp.
- ARAUJO, M. & WHITTAKER, R. (2005) Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography* **14**: 529–538.
- BACHELARD, P. & DESCIMON, H. (1999) *Lycaena helle* (Denis & Schiffermüller, 1775) dans le Massif Central (France): une analyse écogéographique (Lepidoptera: Lycaenidae). *Linneana Belgica* **17**: 23–41.
- BESOLD, J., HUCK, S. & SCHMITT, T. (2008a) Allozyme polymorphisms in the Small Heath *Coenonympha pamphilus*: Recent ecological selection or old biogeographical signal? – *Annales Zoologici Fennici* **45**: 217–228.
- BESOLD, J., SCHMITT, T., TAMMARU, T. & CASSEL-LUNDHAGEN, A. (2008b) Strong genetic impoverishment from the centre of distribution in southern Europe to peripheral Baltic and isolated Scandinavian populations of the pearly heath butterfly. *Journal of Biogeography* **35**: 2090–2101.
- BINK, F. A. (1992) *Ecologische Atlas van de Dagvlinders van Noordwest-Europa*. Schuyt, Haarlem, 512 pp.
- BOZANO, G. C. & WEIDENHOFFER, Z. (2001) *Guide to the butterflies of the Palearctic Region. Lycaenidae. 1. Lycaeninae*. Omnes Artes, Milano, 62 pp.
- CAVALLI-SFORZA, L. L. & EDWARDS, A. W. F. (1967) Phylogenetic analysis: Models and estimation procedures. *Evolution* **21**: 550–570.
- COOPE, G. R. (1994) The response of insect faunas to glacial-interglacial climatic fluctuations. *Philosophical Transactions of the Royal Society of London B* **344**: 19–26.
- DESPRES, L., LORIOT, S. & GAUDEUL, M. (2002) Geographic pattern of genetic variation in the European globeflower *Trollius europaeus* L. (Ranunculaceae) inferred from amplified fragment length polymorphism markers. *Molecular Ecology* **11**: 2337–2347.
- DREWS, M. & PRETSCHER, P. (2003) Schmetterlinge (Insecta, Lepidoptera) der FFH-Richtlinie. In: Das europäische Schutzgebietssystem Natura 2000, Ökologie und Verbreitung von Arten der FFH-Richtlinie in Deutschland. *Schriftenreihe für Landschaftspflege und Naturschutz* **69**: 445–448.
- FINGER, A., ZACHOS, F. E., SCHMITT, T., MEYER, M., ASSMANN, T. & HABEL, J. C. (2009) The genetic status of the Violet Copper *Lycaena helle* – a relict of the cold past in times of global warming. *Ecography* **32**: 382–390.
- FISCHER, K., BEINLICH, B. & PLACHTER, H. (1999) Population structure, mobility and habitat preferences of the violet copper *Lycaena helle* (Lepidoptera: Lycaenidae) in Western Germany: implications for conservation. *Journal of Insect Conservation* **3**: 43–52.
- HABEL, J. C., FINGER, A., SCHMITT, T. & NÈVE, G. (2010a): Changing over time: 15 years of isolation influence the population genetic structure of the endangered butterfly *Lycaena helle*. *Journal of Zoological Systematics and Evolutionary Research* [in press]

- HABEL, J.C., MEYER, M., EL MOUSADIK, A. & SCHMITT, T. (2008a) Africa goes Europe: The complete phylogeography of the Marbled White butterfly species complex *Melanargia galathea/lachesis*. *Organisms, Diversity and Evolution* **8**: 121–129.
- HABEL, J. C., MEYER, M., SCHMITT, T. & ASSMANN, T. (2008b) Polymorphic microsatellite loci in the endangered butterfly *Lycaena helle* (Lepidoptera: Lycaenidae). *European Journal of Entomology* **105**: 361–362.
- HABEL, J. C., RÖDDER, D., SCHMITT, T. & NÈVE, G. (2010b) Global warming will affect genetic diversity of *Lycaena helle* populations. *Global Change Biology* [in press]
- HABEL, J. C., SCHMITT, T., MEYER, M., FINGER, A., RÖDDER, D., ASSMANN, T. & ZACHOS, F. (2010c) Biogeography meets conservation: The genetic structure of the endangered lycaenid butterfly *Lycaena helle* (Denis & Schiffermüller, 1775). *Biological Journal of the Linnean Society* **101**: 155–168.
- 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. (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society* **58**: 247–276.
- HEWITT, G. M. (2004) Genetic consequences of climatic oscillation in the Quaternary. *Philosophical Transactions of the Royal Society of London B* **359**: 183–195.
- KIMBERLY, A. & SELKOE, R. J. T. (2006) Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers. *Ecology Letters* **9**: 615–629.
- KUDRNA, O. (2002) The distribution atlas of European butterflies. *Oedippus* **20**: 1–342.
- LESICA, P. & ALLENDORF, F. W. (1995) When peripheral populations are valuable for conservation. *Conservation Biology* **9**: 753–760.
- MELBOURNE, B. A. & HASTINGS, A. (2008) Extinction risk depends strongly on factors contributing to stochasticity. *Nature* **454**: 100–103.
- MEYER, M. (1982) Révision systématique, chorologique et écologique de *Lycaena helle* Denis & Schiffermüller, 1775 (Lycaenidae). 3^e partie: l'écologie. *Linneana Belgica* **8**: 451–466.
- MORITZ, C. (1994) Defining evolutionarily significant units for conservation. *Trends in Ecology and Evolution* **9**: 373–375.
- PARMESAN, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* **37**: 637–669.
- PARMESAN, C. & YOHE, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.
- PARMESAN, C., RYRHOLM, N., STEFANESCU, C., HILL, J. K., THOMAS, C. D., DESCIMON, H., HUNTLEY, B., KAILA, L., KULLBERG, J., TAMMARU, T., TENNENT, W. J., THOMAS, J. A. & WARREN, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**: 579–583.
- PHILLIPS, S. J., ANDERSON, R. P. & SCHAPIRE, R. E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**: 231–259.
- REED, D. H. & FRANKHAM, R. (2003) Correlation between fitness and genetic diversity. *Conservation Biology* **17**: 230–237.
- ROOT, T. L., PRICE, J. T., HALL, K. R., SCHNEIDER, S. H., ROSENZWEIG, C. & POUNDS, J. A. (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57–60.
- SCHMITT, T. (2007) Molecular biogeography of Europe: Pleistocene cycles and postglacial trends. *Frontiers in Zoology* **4**: 11.

- SCHMITT, T. (2009) Biogeographical and evolutionary importance of the European high mountain systems. *Frontiers in Zoology* **6**: 9.
- SCHMITT, T. & BESOLD, J. (2010) Up-slope movements and large scale expansions: The taxonomy and biogeography of the *Coenonympha arcania*–*darwiniana*–*gardetta* butterfly species complex. *Zoological Journal of the Linnean Society* **159**: 890–904.
- SCHMITT, T. & HEWITT, G. M. (2004) The genetic pattern of population threat and loss: a case study of butterflies. *Molecular Ecology* **13**: 21–31.
- SCHMITT, T., CIZEK, O. & KONVICKA, M. (2005a) Genetics of a butterfly relocation: large, small and introduced populations of the mountain endemic *Erebia epiphron silesiana*. *Biological Conservation* **123**: 11–18.
- 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. & SEITZ, A. (2005b) Are *Polyommatus hispana* and *Polyommatus slovacus* bivoltine *Polyommatus coridon* (Lepidoptera: Lycaenidae)? – The discriminatory value of genetics in the taxonomy. *Organisms, Diversity & Evolution* **5**: 297–307.
- SCHÖNSWETTER, P., PAUN, O., TRIBSCH, A. & NIKFELD, H. (2003) Out of the Alps: colonization of Northern Europe by East Alpine populations of the glacier buttercup *Ranunculus glacialis* L. (Ranunculaceae). *Molecular Ecology* **12**: 3373–3381.
- SCHWEIGER, O., SETTELE, J., KUDRNA, O., KLOTZ, S. & KÜHN, I. (2008) Climate change can cause spatial mismatch of trophically interacting species. *Ecology* **89**: 3472–3479.
- SCHWEIZERISCHER BUND FÜR NATURSCHUTZ (1987) *Tagfalter und ihre Lebensräume, Arten, Gefährdung* Schutz. Fotorotar, Egg, 516 pp.
- SONDEREGGER, P. (2005) *Die Erebien der Schweiz*. Selbstverlag, Biel/ Bienne, 712 pp.
- STEINER, R., TRAUTNER, J. & GRANDCHAMP, A.-C. (2006) Larvalhabitate des blauschillernden Feuerfalters (*Lycaena helle*) am schweizerischen Alpennordrand unter Berücksichtigung des Einflusses von Beweidung. *Abhandlungen aus dem Westfälischen Museum für Naturkunde* **68**: 135–151.
- THOMAS, C. D. & LENNON, J. J. (1999) Birds extend their ranges northwards. *Nature* **399**: 21.
- TOLMAN, T. & LEWINGTON, R. (1998) *Die Tagfalter Europas und Nordwestafrikas*. Franckh-Kosmos Verlag, Stuttgart, 319 pp.
- TURLURE, C., VAN DYCK, H., SHTICKZELLE, N. & BAGUETTE, M. (2009) Resource-based habitat definition, niche overlap and conservation of two sympatric glacial relict butterflies. *Oikos* **118**: 950–960.
- VAN SWAAY, C. A. M. & WARREN, M. (1999) *Red Data Book of European butterflies (Rhopalocera)*. *Nature and environment* 99. Council of Europe Publishing, Strasbourg.
- VARGA, Z. & SCHMITT, T. (2008) Types of areal and oreotundral disjunctions in the western Palearctic. *Biological Journal of the Linnean Society* **93**: 415–430.

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Checklist of the Fauna of Hungary

Volume 3. Macrolepidoptera

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This is the third volume of the series "Checklist of the fauna of Hungary" launched in 2001 published by the Hungarian Natural History Museum. The present volume follows the Microlepidoptera (Vol. 2) making complete the checklist of the Lepidoptera fauna of Hungary. The volume divided into three chapters: introduction, checklist and index of scientific names and their authors.

The annotated checklist contains, besides the taxonomic list of the Macrolepidoptera taxa recorded from Hungary, a double biogeographical categorisation of each species. The major part of the extensive Introduction list, shortly explain and illustrate by examples the biogeographic and ecological categories used. The faunal type defined as "an assemblage or aggregation of groups of species-group level taxa (or in certain cases subspecies) which can be attributed to given core areas", while the faunal element defined as a species-group level taxon belonging to the given faunal type, indicating their type of distribution in a finer scale. Ten faunal types (number of faunal elements in parentheses) are represented in the Hungarian Macrolepidoptera fauna: Extra-Palaeartic (10), Transpalaeartic (4), Boreo-continental "Siberian" (4), Southern continental (6), Western Palaeartic (11), Pannonian endemic (1), Carpathian (4), Alpine (5), Xeromontane (2), Eremic (2). Altogether 106 faunal component categories describing the ecological demands of the species based mostly on the bionomy and habitat requirement of the given species.

In the Checklist chapter the following information given for all the 1259 species (552 genera) listed: the generic name with the author and the year of publication; the valid name of the species-group name with the author and the year of publication in the current generic combination; the faunal type and faunal element categorization of the given species, completed with the faunal component category; and when necessary, a concluding remark is given providing brief details of taxonomic and/or nomenclatural information concerning with the taxon under discussion.

Lepidopterans play an important role in ecosystems and are equally favoured by professionals and non-professionals. Based on the information provided in this volume readers can characterise not only a given species but will be able to evaluate a given area through the qualification of the composition of its lepidopteran fauna. We presume that beside basic sciences it will have a wide and successful application in the practice of agriculture, forestry and nature conservation as well.

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