School of Doctoral Studies in Biological Sciences

University of South Bohemia in České Budějovice
Faculty of Science

Ecology and evolution of mountain butterflies

Ph.D. Thesis

RNDr. Irena Klečková

Supervisor: RNDr. Zdeněk Faltýnek Fric Ph.D.
Department of Zoology, Faculty of Science, University of South Bohemia
Institute of Entomology, Biology Centre, Czech Academy of Sciences

České Budějovice 2014

This thesis should be cited as:
Kleckova I 2014. Ecology and evolution of mountain butterflies, Ph.D.Thesis. University of South Bohemia, Faculty of Science, School of Doctoral Studies in Biological Sciences, České Budějovice, Czech Republic, 94 pp.

Annotation

The thesis deals with speciation processes, thermal ecology and habitat use in Holarctic mountain and arctic butterflies. It demonstrates a crucial role of environmental heterogeneity for speciation, survival of butterfly lineages, coexistence of closely related species and, finally, for resource use of sexes with different habitats demands at the level of individual species.

Declaration [in Czech]

This thesis originated from a partnership of Faculty of Science, University of South Bohemia, and Institute of Entomology, Biology Centre of the ASCR, supporting doctoral studies in the Entomology study programme.

Přírodovědecká fakulta
Faculty of Science

BC AVČR

Financial support

Funding was provided by the Grant agency of the Czech Republic (P505/10/2248, P505/10/1630, 206/08/H044, P505/10/2167), Czech Ministry of Education (LC-06073, MSM 6007665801) and the Grant Agency of the University of South Bohemia (106/2010/P, 135/2010/P, 144/2010/P, 145/2010/P, 235 144/2010/P) plus from the contract Motýli Krkonoš (reg.č. 236 CZ.3.22/1.2.00/12.03299).

Acknowledgements

I am very grateful to Zdeněk Faltýnek Fric, supervisor of my PhD. for his guidance during my studies and for igniting my interest in the phylogeny of butterflies. I am thankful to Martin Konvička, supervisor of my MSc. thesis for introduction to ecology of butterflies and Loic Pellissier for fruitful discussions about the combination of evolution and ecology in my research. Many thanks to Kamil Zimmerman for introduction to the program MARK, to Martin Česánek, Jiří Beneš, Michal Zapletal and Kamil Zimmerman for providing specimens for molecular studies, to Niklas Wahlberg for supervising the *Neptis* phylogeny project during my Erasmus stay in Finland, to Pavel Fortunato Matos Maravi for his guidance trough my beginnings with molecular methods, to Michaela Borovanská for being a pleasant companion and helpful advisor during my lab work, to Ilona Černá for her help with the organization of the *Erebia* monitoring, to Simon Segar and Oldřich Říčan for advice on molecular data analyses, and finally to Kateřina Sam, Pavel Šebek, Petr Vlašánek, Philip Butterill, Dita Horázná, David Novotný and Jana Kantorová for creating a friendly environment in the office. I would like to thank my family and friends for support. Finally, I would like to thank to my husband Jan for his love, patience and interest in the subject of my studies and to our son Štěpán simply for being here with us.

List of papers and author's contribution

The thesis is based on the following papers (listed thematically):

I. Phylogeny of a mountain butterfly genus *Oeneis*: biogeographical and ecological speciation processes interact during evolution of Holarctic diversity.
Klečková, I., *Pellissier, L., Česánek, M., Konvička, M., Faltýnek Fric, Z.*
Manuscript
[IK, LP and ZFF conceived the study, IK collected molecular and ecological data, performed majority of data analyses and wrote the manuscript, LP contributed to data analysis and revisions of the manuscript, MC provided samples and contributed by deep knowledge of species ecology and distribution, MK and ZFF also participated on writing the manuscript]

II. Quantitative evidence for biennial life cycle and its spatial variation in the mountain butterfly *Erebia euryale* in the Czech Republic
Klečková, I., *Vrba, P., Konvička, M.*
in revision, European Journal of Entomology
[MK and IK conceived the study, IK coordinated the collection of field data, analysed data and participated in writing the manuscript, MK participated in writing the manuscript and PV contributed to data and figure processing]

III. Thermoregulation and microhabitat use in mountain butterflies of the genus *Erebia*: Importance of fine-scale habitat heterogeneity
Klečková, I., *Konvička, M., Klečka, J.*
Journal of Thermal Biology (2014) 41: 50–58
[IK and JK conceived the study, IK collected field data and contributed to data analyses, JK analyzed majority of the data, IK, JK and MK participated in writing the manuscript].

IV. Woodland and grassland mosaic from a butterfly perspective: habitat use by *Erebia aethiops* (Lepidoptera: Satyridae)
Slámová, I., *Klečka, J., Konvička, M.*
Insect Conservation and Diversity (2013) 6: 243–254
[MK and IK (=IS) conceived the study, IK collected field data, IK, MK and JK analysed data and wrote the manuscript]

Co-authors agreement: Irena Klečková declares that she is the first and corresponding author of papers I, III and IV and she is the first author of paper II with major contributions as stated above.

....
Irena Klečková

Contents

INTRODUCTION

Astonishing diversity of life on the Earth is shaped by interactions of random factors (e.g. Kimura 1983, Hubbel 2001) with regional history (e.g. MacArthur and Wilson 1967), by selective pressure of abiotic factors (e.g. Berteaux et al. 2004, Vila et al. 2011) and, finally, by biotic interactions (e.g. MacArthur and Pianka 1966, Pierce et al. 2002, Nylin and Wahlberg 2008). The abiotic factors and biotic interactions take effect via species traits such as physiological limits (Vila at al. 2011, Condamine et al. 2012) and habitat use (cf. Thomas et al. 2006). Thus, studies of drivers of evolution start at the species level (e.g. Jiggins 2008), continue at the level of higher taxonomic groups (e.g. Wahlberg et al. 2009) and finish at the level of macroecological studies (e.g. Gaston 2000, Hubbel 2001, Bale et al. 2002). Good knowledge of both, evolutionary drivers of biodiversity and ecological processes, can extend our understanding of diversity of life as well as guide conservation activities in human altered environments (cf. Parmesan 2006).

I chose butterflies as a wonderful model group and I studied them in the field and in the lab. In the field, I used Mark-Recapture method to collect data about butterfly population structure and behaviour, further I studied butterfly thermoregulation in relationship to habitat structure and finally, together with a huge number of dedicated students, I participated in long term monitoring of mountain butterflies. In the lab, I isolated and amplified DNA from dry specimens and used the resulting molecular data to reconstruct the phylogeny of one genus of mountain butterflies, *Oeneis*, and study geographical and ecological drivers of its diversification. I started to work on butterflies of the genus *Erebia* Dalman, 1816 (Lepidoptera: Nymphalidae, Satyrinae), which have already become a traditional object of ecological (e.g. Konvicka et al. 2002, Cizek et al. 2003, Kuras et al. 2003, Vrba et al. 2012) and biogeographical (Konvicka et al. 2009, Konvicka et al. 2014) studies in my working group. Next, I extended my work to include butterflies of the genus *Oeneis* Hübner, [1819] (Lepidoptera: Nymphalidae, Satyrinae), which shares many ecological traits with the genus *Erebia* and probably also has similar evolutionary history. Both genera inhabit the coldest areas of the Holarctic region; i.e high mountain ranges and the arctic. They evolved a wide range of adaptations to harsh and unpredictable environment, such as an isolation layer of dense long scales on wings and body, the ability to flight in low temperatures (I personally observed *Erebia* butterflies flying above snow), tolerance of larvae to low temperatures or prolonged development of the larvae. In my thesis, I asked several questions about (I) the role of geographic and ecological speciation in the evolution of Holarctic cold-dwelling butterflies, (II) possible sources of differentiation of abundance synchronicity among *Erebia euryale* (Esper, 1805) populations of mountain ranges of the Czech Republic, (III) the role of species traits (e.g. habitat preferences, thermal requirements) for species distribution at large, continental, scale and microhabitat use at the local scale and (IV) the importance of butterfly behaviour, as the most plastic response to environmental changes, for demarcation of suitable habitat and for species distribution in a human altered environment.

History of mountain and arctic biota

Understanding the present distribution of individual species and their habitat preferences is not possible without the knowledge of the history of the landscape at both local and continental scales. The evolution of cold dwelling biota of the Holarctic region was shaped especially by Cenozoic climatic changes and by mountain orogenies, which induced speciation and shaped biogeography of recent species (cf. Hewitt 2004). The evolutionary processes in Holarctic cold-dwelling biota have been increasingly studied in alpine and arctic plants (Nagy and Grabherr 2009, Eidesen et al. 2013). However, knowledge about evolution of Holarctic mountain butterflies is still rather fragmentary, contrary to tropical mountains, which provided fascinating information about ecological and neutral evolutionary processes (e.g. Willmott et al. 2001, Hall 2005, Jiggins 2008, Chamberlain et al. 2009, Matos Maravi et al. 2013). First, tropics, and especially their mountains, are continuous source of fascination for biologist and thus, research is targeted to these areas, second, tropical mountains were more stable during their history, which makes detection of evolutionary processes simpler. On the contrary, the history of northern hemisphere was more complex (Sanmartin et al. 2001, Sanmartin and Ronquist 2004) and thus, understanding biogeography and evolutionary history of its biota is more difficult.

The history of Holarctic cold-dwelling butterflies is connected with the emergence of grasslands and the appearance of alpine and arctic habitats. Butterfly lineages, which recently inhabit mountains and arctic, originated in newly emerging grassland biomes in the Oligocene (34-23 Ma) (Peña et al. 2011, Condamine at al. 2012). Emergence of these biomes was conditioned by abrupt climate cooling and their expansion was supported by desiccation of the centres of continents in a rain shadow of mountain ranges. During the Oligocene (Scotese 2001) grasslands spread from Asia (Briggs 1995, Condamine et al. 2012) to Europe after the closure of the Turgai strait among the continents. These lowland grasslands (Sanmartin et al. 2001, Retallack 2001) were inhabited by specialized butterflies (Peña and Wahlberg 2008, Peña et al. 2011) pre-adapted for colonization of forest-free alpine zone. Alpine grasslands similar to the ones we see today probably emerged during this time (cf. Wing 1987, Moores and Fairbridge 1998, English and Johnston 2004, Nagy and Grabherr 2009). Species colonizing them from the lowlands adapted to the harsh alpine conditions and consequently diverged in this novel environment. Only some evolutionary lineages of grassland butterflies were able to spread to high mountains and the filtering effect of harsh mountain environment is obvious from genetic structure of recent mountain assemblages (Machac et al. 2011, Pellissier 2013a). Colonization of mountains by other lineages has continued since then. For example, many high alpine plants originated from lowland species later in Pleistocene (Comes and Kadereit 2003). In contrast to plants, butterfly lineages seem to be rather conservative in their thermal or habitat requirements, which demarcate their distributions in biomes (cf. Albre et al. 2008, Vila et al. 2011, Condamine et al. 2012). Speciation of butterflies was thus probably driven primarily by geographic speciation, but ecological speciation also played an important role at least in some taxa (cf. Rundle and Nosil 2005). The interactions among these processes are not well known and may vary across altitudinal and latitudinal gradients.

Uplift of mountains induced speciation of many butterfly lineages (Kodandaramaiah and Wahlberg 2009, Leneveu et al. 2009). Geographic and ecological speciation processes interact in the creation of diversity of mountain butterflies. Ecological speciation should be induced by availability of novel environment and narrow altitudinal zonation (obvious as parapatric speciation) or e.g. by negative interactions among related taxa (occurence in sympatry or in secondary sympatry; Janzen 1967, Rundle and Nosil 2005). Geographic speciation should be induced by heterogeneous geomorphology (cf. Fjeldsa and Lovett 1997) or by climatically induced fragmentation of ranges (cf. Fiedler and Strutzenberger 2013). During cold periods, alpine biota retracted to lowland refuges from glaciated tops. Subsequent warm periods induced uphill shifts of the alpine biota from these lowland refugia and fragmentation of the glacial ranges. The hypothesis of the enhanced rate of speciation during warm periods) is supported by data in plants (Kadereit et al. 2004). The Alps, Himalaya and adjacent mountain ranges (e.g. Altai and Sayan) went trough a period of uplift in the Miocene (23-5 Ma) (Wang et al. 2004, De Grave et al. 2007). The uplift of Himalaya and adjacent ranges was the most intensive around 13-7 Ma (Valdiya 2002). The most intensive uplift of European mountains occurred later, between 10 and 2 Ma (Ager 1975). Recent alpine habitats are expected to be established ca 10 Ma (Nagy and Grabherr 2009). These periods of intensive uplifts are congruent with enhanced rate of speciation in alpine organisms (Kadereit at al. 2008, Hörandl and Emadzade 2011). Thus, phylogenies of mountain butterfly lineages should also display enhanced diversification rates during periods of rapid uplift.

A large part of alpine biota of European mountains has the evolutionary origin in the mountains of Asia (Kodandaramaiah and Wahlberg 2009, Nagy and Grabherr 2009). Similarly, mountains of North America share high proportion of alpine species with mountains of Asia (Nagy and Grabherr 2009). For alpine plants, the origin of disjoint species ranges covering North America and Asia is assumed to be a consequence of long distance dispersal (Kadereit and Baldwin 2012), or alternatively mountains of North America might have been a refuge for alpine biota (Weber et al. 2003). The refugial character is considered to be a consequence of fragmentation of past continuous ranges (Weber et al. 2003). North America was connected with Asia during periods of climate cooling, when the region of Beringia was above see level. Biogeography and speciation of cold-dwelling butterflies was affected by the emergence of II. Beringian Bridge (Sanmartin et al. 2001). This land bridge existed from the Miocene to the late Pliocene (14 – 3.5 Ma) and butterfly dispersion across the land bridge and subsequent allopatric speciation caused differentiation of representatives of a number of recent Holarctic butterfly genera (e.g. Mullen 2006, Kodandaramaiah and Wahlberg 2009, Simonsen et al. 2010). Arctic habitats emerged during the Pliocene (Zachos et al. 2001) and Beringia served as the largest refugium of arctic species during glacial ages of Pleistocene.

Pleistocene and its consequences

Cyclic climatic changes in the Pleistocene (2.6 Ma - recent) with alternating glacial and interglacial periods moulded the distribution of arctic (Eidesen et al. 2013) and alpine (Hewitt 2004, Schmitt et al. 2006) biota. For example, origin of nowadays alpine plant species of the highest European ranges can be dated to this period (Comes and Kadereit 2003, Nagy and Grabherr 2009). Reconstruction of biogeography of alpine and arctic biota during this period is a challenging topic, with current progress driven by novel approaches and computational tools (cf. Todisco et al. 2012, Eidesen et al. 2013, Schorr et al. 2013). How biota coped with glaciation is heatedly discussed. There is evidence that some taxa survived in isolated areas of suitable habitats surrounded by glaciers (e.g. Stewart and Lister 2001, Schmitt 2007, Schmitt 2009, Rull 2009, Schorr et al. 2013), while others retracted their range southwards during the glacial period and then returned to uncovered areas during the interglacial (Eidesen et al. 2013, Todisco et al. 2012). Asia and North America were interconnected by the III. Beringian Bridge (1.5 – 1Ma) during the Pleistocene (Sanmartin et al. 2001). Beringia provided a refuge for arctic organisms during this period. Species populations that became disconnected after the submersion of the land bridge underwent a period of differentiation and they are often distinguished as separate taxonomic units in North America and in Asia. However, taxonomic status of these divergent populations/species is often unresolved (Lukhtanov and Lukhtanov 1994, Layberry et al 1998, Todisco et al. 2012), which complicates the resolution of species distribution and their ecological requirements.

The interplay of evolutionary and ecological processes

The history of cold-dwelling biota was shaped by two evolutionary processes, first by purely geographic (neutral speciation) and, second, by ecological speciation, which works by ecological divergence in sympatry. Although they are probably frequent in nature, the interactions of ecological and biogeographical speciation are rarely studied (e.g. Vila et al.

2011, Condamine et al. 2012). Studies of purely geographic (e.g. Imanda et al. 2011) or ecological speciation (e.g. Jiggins 2008) serve as models for understanding evolutionary processes. Ecological speciation works in butterflies via species traits such as colour pattern preference (Jiggins 2008), host plant use (Nylin and Wahlberg 2008, Simonsen et al. 2010), thermal limits (Vila et al. 2011) or probably habitat affiliation (cf. Willmott et al. 2001). Integration of molecular phylogenies, biogeography and evolution of ecological traits is necessary to solve the relative contribution of ecological and biogeographical processes for the origin of species diversity and for better understanding of the effect of climatic changes on evolution, survival and extinctions of butterfly species in dependence on their ecological traits.

Conservation of mountain biota in human-altered environment

Effective targeting of conservation activities is necessary, because of limited financial resources for nature conservation and because of the increasing need to exploit natural resources by humans. In relation to conservation of temperate mountain habitats, we can ask two basic questions. First, what is the conservation status of the mountains compared to lowland habitats and, second, how to conserve mountain habitats most effectively. Mountain organisms sensitively respond to ongoing climate (Konvicka et al. 2003, Wilson et al. 2005, Chen et al. 2011, Baur and Baur 2013) and management changes (Groot de et al. 2009, Mottet et al. 2006, Dieker et al. 2011). They are considered to be in risk of extinctions mainly because of uphill retractions of their ranges (e.g. Baur and Baur 2013, Wilson et al. 2005). However, extinction threat can be still lower in mountains than in super-intensively managed lowlands where organisms suffer by climate and management changes too. The lower extinction probability of mountain organisms is supported by high spatial heterogeneity of mountain environment, which guarantees continual presence of suitable conditions for their inhabitants (Scherrer and Korner 2011) and by lower intensity of management (Mottet et al. 2006). Next, mountain organisms should be evolutionarily adapted for survival in a changing environment contrary to lowland ones (cf. Karl et al. 2011). Thus, lower effort may be sufficient for effective conservation of mountain biota compared to conservation of lowland habitats.

Efficient conservation and optimal targeting of conservation actions in mountains should be based on knowledge about factors demarcating species altitudinal ranges. Still, our knowledge of limiting biotic and abiotic factors, species perception of their range margins, and their ability to respond to novel conditions is rather fragmentary. High altitude margins are demarcated mainly by abiotic factors, while lower range margins are probably more affected by biotic interactions (Pellissier et al. 2013b). On lower margins, species face complex changes of plant composition (Holzinger et al. 2008), plant phenology (Smith et al. 2012), phenology and abundance changes of their parasitoids (Leingärtner et al. 2014), probably also newly incoming predators and parasitoids expanding from lowland areas, and finally changes of their own phenology (Altermatt 2010a, Altermatt 2010b). Potential adjustments of butterflies to these changes demand complex responses such as changes of immune system or life history traits by phenotypic plasticity or evolution (cf. Karl et al. 2011). However, immediate response to changing conditions is possible by alternation of butterfly behaviour (cf. Buckley et al. 2012, Lawson et al. 2012), which represents the most plastic response mechanism. Studies of behavioural thermoregulation can provide missing links in understanding of habitat perception in butterflies at range margins (Lawson et al. 2012, Kleckova et al. 2014). In any case, management of mountain areas should be targeted on subalpine and montane zone and it should support maximal habitat heterogeneity.

Model organisms

Butterflies of the genus *Erebia* represent a suitable insect model for mountain ecology (e.g. Cizek et al. 2003, Vrba et al. 2012) and European biogeography (e.g. Schmitt et al. 2006, Schmitt and Haubrich 2008). Further, the representatives of the genus are sensitive indicators of climate change (Franco et al. 2006). The genus *Erebia* is very diverse (about 100 species) and comparative studies of habitat use, behaviour and thermal biology of different species (Vrba et al. 2012, Kleckova et al. 2014) and complete phylogeny of this genus (Peña et al. *in preparation*) can provide promising indicia of butterfly ability to cope with large-scale changes in the environment such as ongoing climate change. To get insight into the processes which shaped evolution of cold-climate specialists, I choose mountain butterflies of the genus *Oeneis* as a second model group. The genus *Oeneis* is less numerous (about 30 species) than the genus *Erebia*, thus it was more feasible to collect and analyse molecular data. These genera differ in distribution patterns, probably because of different time of their origin. The genus *Erebia* arose in the beginning of the Oligocene (ca 33 Ma), whereas the genus *Oeneis* arose much later, in the Miocene (ca 15 Ma) (Peña et al. 2011). Genus *Erebia* has two main centres of distribution in mountain ranges of Asia and Europe. Further, a smaller number of species inhabits the arctic regions of Eurasia and North America and mountains of North America (Warren 1936). Only a few representatives, such as *Erebia aethiops* (Esper, 1777) and *Erebia medusa* (Fabricius, 1787), occur in warmer lowland areas. Genus *Oeneis* has the main centre of diversity in mountain ranges of Asia (Layberry et al. 1998). European mountains are inhabited by *Oeneis glacialis* (Moll, 1785) occurring in the Alps. The rest of the species inhabit arctic and mountain ranges of North America. Both butterfly genera are feeding generalists using ubiquitous grasses as larval food plants; thus, their evolution and geographic distribution were probably affected rather by climate and habitat changes than by distribution of host plants (cf. Weingartner et al. 2006, Schweiger et al. 2008). Representatives of both genera frequently prolong their larval development to cope with adverse climatic conditions (Layberry et al. 1998, Sonderegger 2005). Overall, both *Erebia* and *Oeneis* are suitable groups for studies of evolution of ecological traits.

Objectives of the thesis

My thesis aims to extend the knowledge about evolution and ecology of cold-dwelling butterflies. I merged various methodical approaches such as behavioural observations, measurements of body temperatures in the field and molecular phylogenetic analyses to get insight into processes which shape distribution and diversity of mountain butterflies.

Chapter I examines the relative contribution of biogeography and evolution of ecological traits in mountain butterflies of the Holarctic region using genus *Oeneis* as a model group. Phylogeny of the genus was reconstructed using one mitochondrial and three nuclear genes. The phylogeny was used to infer the most likely biogeographical scenario and to conduct ancestral reconstruction of habitat use and evolution of thermal requirements. Further, Chapter I reveals phylogenetic relationships among traditional species groups of the genus based on morphology and clarifies the taxonomic position of the related genera *Paroeneis* Moore, 1893 and *Neominois* Scudder, 1875.

Chapter II describes variable synchronicity of abundance fluctuations in several populations of a mountain butterfly *Erebia euryale* in the Czech Republic and discusses possible causes of the observed pattern. Three permanent transects representing main mountains ranges in the

Czech Republic provided five year of abundance observations, which reveal differences in the presence of biennial fluctuations of population size among mountain ranges.

Chapter III and Chapter IV provide novel knowledge of the role of behaviour, habitat use and thermoregulation in butterfly perception of marginal conditions. Findings presented in these two chapters have implications for the conservation of butterflies in human altered habitats. Chapter III compares microhabitat use and thermoregulation in seven species of *Erebia* butterflies which co-occur in the Alps. Field records of body, microhabitat and air temperatures were used for tests of interspecific and intraspecific differences in thermoregulation. A major question of Chapter III is whether mountain butterflies are able to actively search for suitable microclimate within heterogeneous mountain habitats. Chapter IV describes intersexual differences in habitat use in *Erebia aethiops*, an aberrant lowland species of the genus. Mark-recapture data were used to get insight into the effects of the structure of vegetation, distribution of nectar sources and habitat management on population density and mobility of males and females.

References

Ager DV 1975. The geological evolution of Europe. Proceedings of the Geologists' Association 86: 127−154.

Albre J, Gers C, Legal L 2008. Molecular phylogeny of the *Erebia tyndarus* (Lepidoptera, Rhopalocera, Nymphalidae, Satyrinae) species group combining CoxII and ND5 mitochondrial genes: A case study of a recent radiation. Molecular phylogenetics and evolution 47: 196–210.

Altermatt F 2010a. Tell me what you eat and I'll tell you when you fly: diet can predict phenological changes in response to climate change. Ecology Letters 13: 1475 – 1484.

Altermatt F 2010b. Climatic warming increases voltinism in European butterflies and moths. Proceedings of the Royal Society of London Series B 277: 1281–1287.

Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Symrnioudis I, Watt AD, Whittaker JB 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8: 1–16.

Baur B, Baur A 2013. Snails keep the pace: shift in upper elevational limit on mountain slopes as a response to climate warming. Canadian Journal of Zoology 91: 596–599.

Berteaux D, Réale D, McAdam AG, Boutin S 2004. Keeping pace with fast climate change: can arctic life count on evolution? Integrative and Comparative Biology 44: 140–151.

Briggs JC 1995. *Global Biogeography*. Amsterdam, Elsevier Science.

Buckley J,Butlin RK, Bridle JR 2012.Evidence for evolutionary change associated with the recent range expansion of the British butterfly, *Aricia agestis*, in response to climate change. Molecular Ecology 21: 267–280.

Chamberlain NL, Hill RI, Kapan DD, Gilbert LE, Kronforst MR 2009. Polymorphic Butterfly Reveals the Missing Link in Ecological Speciation. Science 326: 847–850.

Chen IC, Hill JK, Ohlemuller R, Roy DB, Thomas CD 2011.Rapid range shifts of species associated with high levels of climate warming. Science 333: 1024–1026.

Cizek O, Bakesova A, Kuras T, Benes J, Konvicka M 2003. Vacant niche in alpine habitat: the case of an introduced population of the butterfly *Erebia epiphron* in the Krkonose Mountains. Acta Oecologica 24:15–23.

Comes HP, Kadereit JW 2003. Spatial and temporal patterns in the evolution of the flora of the European Alpine System. Taxon 52: 451 – 462.

Condamine FL, Sperling FAH, Wahlberg N, Rasplus JY, Kergoat GJ 2012. What causes latitudinal gradients in species diversity? Evolutionary processes and ecological constraints on swallowtail biodiversity. Ecology Letters 15: 267–277.

De Grave J, Buslov MM, Van den haute P 2007. Distant effects of India–Eurasia convergence and Mesozoic intracontinental deformation in Central Asia: Constraints from apatite fission-track thermochronology. Journal of Asian Earth Sciences 29: 188–204.

Dieker P, Drees C, Assmann T 2011. Two high-mountain burnet moth species (Lepidoptera, Zygaenidae) react differently to the global change drivers climate and land-use. Biological Conservation 144: 2810–2818.

English JM, Johnston ST 2004. The Laramide Orogeny: What Were the Driving Forces? International Geology Review 46: 833–838.

Eidesen PB, Ehrich D, Bakkestuen V, Greve Alsos I, Gilg O, Taberlet P, Brochmann C 2013. Genetic roadmap of the Arctic: plant dispersal highways, traffic barriers and capitals of diversity. New Phytol. 200: 898–910.

Fiedler K, Strutzenberger 2013. Past dynamics of speciation in Andean mountain rainforests Pp. 67-79 in: Bendix J, Beck E, Bräuning A, Makeschin F, Mosandl R, Scheu S, Wilcke W (eds.) *Ecosystem services, biodiversity and environmental change in a tropical mountain ecosystem of South Ecuador*. Ecological Studies 221, Springer, Berlin, Heidelberg, New York.

Fjeldsa J, Lovett JC 1997. Geographical patterns of old and young species in African forest biota: The significance of specific montane areas as evolutionary centres. Biodiversity and Conservation 6: 325–346.

Franco A, Hill J, Kitschke C, Collingham Y, Roy D, Fox R, Huntley B, Thomas C 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. Global Change Biology 12: 1545–1553.

Gaston KJ 2000. Global patterns in biodiversity. Nature 405: 220–227.

Groot de M, Rebeusek F, GrobelnikV, Govedic M, Salamun A, Verovnik R 2009. Distribution modelling as an approach to the conservation of a threatened alpine endemic butterfly (Lepidoptera: Satyridae). European Journal of Entomology 106: 77–84.

Hall JPV 2005. Montane speciation patterns in *Ithomiola* butterflies (Lepidoptera: Riodinidae): are they consistently moving up in the world? Proceedings of the Royal Society B 272: 2457–2466.

Hewitt GM. 2004. Genetic consequences of climatic oscillations in the Quaternary. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences 359: 183–195.

Holzinger B, Hulber K, Camenisch M, Grabherr G 2008. Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. Plant Ecology 195: 179–196.

Hörandl E, Emadzade K 2011. The evolution and biogeography of alpine species in *Ranunculus* (Ranunculaceae): A global comparison. TAXON 60: 415–426.

Hubbell SP 2001. *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*. Princeton University Press, Princeton.

Imada Y, Kawakita A, Kato M 2011. Allopatric distribution and diversification without niche shift in a bryophyte-feeding basal moth lineage (Lepidoptera: Micropterigidae). Proceedings of the Royal Society B: Biological Sciences 278: 3026–3033.

Lawson CR, Bennie JJ, Thomas CD, Hodgson JA, Wilson RJ 2012. Local and landscape management of an expanding range margin under climate change. Journal of Applied Ecology 49: 552–561

Janzen DH 1967. Why mountain passes are higher in the tropics. The American Naturalist 101: 233–249.

Jiggins CD 2008. Ecological Speciation in Mimetic Butterflies. BioScience 58: 541–548.

Kadereit JW , Licht W, Uhink CH 2008. Asian relationships of the flora of the European Alps, Plant Ecology & Diversity 1: 171–179.

Kadereit JW, Baldwin BG 2012. Western Eurasian–western North American disjunct plant taxa: The dry-adapted ends of formerly widespread north temperate mesic lineages—and examples of long-distance dispersal. Taxon 61: 3-17(15)

Kadereit JW, Greibler EM, Comes HP 2004. Quaternary diversification in European alpine plants: pattern and process. Philosophical Transactions of the Royal Society B: Biological Sciences 359:265–274.

Karl I, Stoks R, De Block M, Janowitz SA, Fischer K 2011. Temperature extremes and butterfly fitness: conflicting evidence from life history and immune function. Global Change Biology 17: 676–687.

Kimura M 1983. *The neutral theory of molecular evolution*. Cambridge

Klečková I, Konvička M, Klečka J 2014. Thermoregulation and microhabitat use in mountain butterflies of the genus Erebia: importance of fine-scale habitat heterogeneity. Journal of Thermal Biology 41: 50–58.

Konvicka M, Benes J, Kuras T 2002. Microdistribution and diurnal behaviour of two sympatric mountainous butterflies (*Erebia epiphron* and *E. euryale*): relations to vegetation and weather. Biologia 57: 221–233.

Konvicka M, Benes J, Schmitt T 2009. Ecological limits vis a vis changing climate: relic *Erebia* butterflies in insular Sudetan mountains. In: Habel JC, Assmann T (eds.) *Survival on Changing Climate – Phylogeography and Conservation of Relict Species.* Springer, Heidelberg.

Konvicka M, Maradova M, Benes J, Fric Z, Kepka P 2003. Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale**.** Global Ecology and Biogeography 12: 403–410.

Konvička M, Mihaly CV, Rákosy L, Beneš J, Schmitt T 2014. Survival of cold-adapted species in isolated mountains: the population genetics of the Sudeten ringlet, *Erebia sudetica sudetica*, in the Jeseník Mts., Czech Republic. Journal of Insect Conservation, *in press*.

Kodandaramaiah U, Wahlberg N 2009. Phylogeny and biogeography of *Coenonympha* butterflies (Nymphalidae: Satyrinae) - patterns of colonization in the Holarctic. Systematic Entomology 34:315–323.

Kuras T, Benes J, Fric Z, Konvicka M 2003. Dispersal patterns of endemic alpine butterflies with contrasting population structures: *Erebia epiphron* and *E. sudetica*. Population Ecology 45: 115–123.

Layberry RA, Hall PW, Lafontaine JD 1998. *The Butterflies of Canada.* University of Toronto Press, Toronto.

Leingärtner A, Krauss J, Steffan-Dewenter I 2014. Elevation and experimental snowmelt manipulation affect emergence phenology and abundance of soil-hibernating arthropods. Ecological Entomology *in press*

Leneveu J, Chichvarkhin A, Wahlberg N 2009. Varying rates of diversification in the genus *Melitaea* (Lepidoptera: Nymphalidae) during the past 20 million years. Biological Journal of the Linnean Society 97: 346–361.

Lukhtanov V, Lukhtanov A, 1994. *Die Tagfalter Nordwestasiens*. Herbipoliana 3, Marktleuthen, Verlag Dr. Ulf Eitschberger.

MacArthur RH, Wilson EO 1967. *The theory of island biogeography*. Princeton University Press, New Jersey.

MacArthur RH, Pianka ER 1966. On optimal use of a patchy environment. The American Naturalist 100: 603–609.

Machac A, Janda M, Dunn RR, Sanders NJ 2011. Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. Ecography 34: 364 – 371.

Matos Maravi PF, Peña C, Willmott KR, Freitas AVL, Wahlberg N 2013. Systematics and evolutionary history of butteflies in the "*Taygetis* clade" (Nymphalidae: Satyrinae: Euptychiina): towards a better understanding of Neotropical biogeography. Molecular Phylogenetics and Evolution 66: 54–68.

Moores EM, Fairbridge RW (Eds) 1998. *Encyclopedia of European and Asian Regional Geology.* Encyclopedia of Earth Sciences Series, London.

Mottet A, Ladet S, Coque N, Gibon A 2006. Agricultural land-use change and its drivers in mountain landscapes: a case study in the Pyrenees. Agriculture, Ecosystems & Environment 114: 296–310.

Mullen SP 2006. Wing pattern evolution and the origins of mimicry among North American admiral butterflies (Nymphalidae: *Limenitis*). Molecular Phylogenetics and Evolution 39: 747–758.

Nagy L, Grabherr G 2009. *The Biology of Alpine Habitats*. Oxford University Press.

Nylin S, Wahlberg N 2008. Does plasticity drive speciation? Host plant shifts and diversification in nymphaline butterflies (Lepidoptera: Nymphalidae) during the tertiary. Biological Journal of the Linnean Society 94: 115–130.

Parmesan C 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37: 637–669.

Pellissier L, Alvarez N, Espíndola A, Pottier J, Dubuis A, Pradervand JN, Guisan A, 2013a. Phylogenetic alpha and beta diversities of butterfly communities correlate with climate in the western Swiss Alps. Ecography 36: 541 – 550.

Pellissier L, Bråthen KA, Vittoz PA, Yoccoz NG, Dubuis A, Meier AS, Zimmermann NE, Randin CF, Thuiller W, Garraud L, Van Es J, Guisan A 2013b. Thermal niches are more conserved at cold than warm limits in arctic-alpine plant species. Global Ecology and Biogeography 22**:** 933–941.

Peña C, Nylin S, Wahlberg N 2011. The radiation of Satyrini butterflies (Nymphalidae: Satyrinae): a challenge for phylogenetic methods. Zoological Journal of the Linnean Society 161: 64–87.

Peña C, Wahlberg N 2008. Prehistorical climate change increased diversification of a group of butterflies. Biology Letters 4: 274–278.

Peña C, Witthauer H, Kleckova I, Faltynek Fric Z,Wahlberg N (*in preparation*). Adaptive radiations in butterflies: evolutionary history of the genus *Erebia* (Nymphalidae: Satyrinae).

Pierce NE, Braby MF, Heath A, Lohman DJ, Mathew J, Rand DB, Travassos MA 2002. The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annual Review of Entomology 47: 733–771.

Retallack GJ 2001. Cenozoic expansion of grasslands and climatic cooling. The Journal of Geology 109: 407–426.

Rull V 2009. Microrefugia. Journal of Biogeography 36: 481–484.

Rundle HD, Nosil P 2005. Ecological speciation. Ecology Letters 8: 336–352

Schorr G, Pearman PB, Guisan A, Kadereit JW 2013. Combining palaeodistribution modelling and phylogeographical approaches for identifying glacial refugia in Alpine *Primula*. Journal of Biogeography 40: 1947–1960.

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.

Scotese CR 2001. *Atlas of Earth History*. PALEOMAP Project, Arlington, TX.

Sanmartín I, Ronquist F 2004. Southern Hemisphere biogeography analyzed with event-based models: Plant versus animal patterns. Systematic Biology 53: 216–243.

Sanmartin I, Enghoff H, Ronquist F 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. Biological Journal of the Linnean Society 73: 345–390.

Scherrer D, Korner C 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. Journal of Biogeography38: 406–416.

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, 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 GM, Muller P 2006. Disjunct distributions during glacial and interglacial periods in mountain butterflies: *Erebia epiphron* as an example. Journal of Evolutionary Biology 19: 108–113.

Simonsen TJ , Wahlberg N, Warren AD, Sperling FAH 2010. The evolutionary history of *Boloria* (Lepidoptera: Nymphalidae): phylogeny, zoogeography and larval-foodplant relationships. Systematics and Biodiversity 8: 513–529.

Sonderegger P 2005. Die Erebien der Schweiz (Lepidoptera:Satyrinae, Genus *Erebia*). Verlag Peter Sonderegger, Brüggbei Biel.

Smith JG, Sconiers W, Spasojevic MJ, Ashton IW, Suding KN. 2012. Phenological changes in alpine plants in response to increased snowpack, temperature, and nitrogen. Arctic, Antarctic, and Alpine Research 44: 135–142.

Stewart JR, Lister AM 2001. Cryptic northern refugia and the origins of the modern biota. Trends in Ecology & Evolution 16: 608–613.

Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, Conradt L 2006. Ecological and evolutionary processes at expanding range margins. Nature 411: 577–581.

Todisco V, Gratton P, Wheat C, Zakharov E, Sbordoni V, Sperling F 2012. Mitochondrial phylogeography of the Holarctic *Parnassius phoebus* complex supports a recent refugial model for alpine butterflies. Journal of Biogeography 39: 1058–1072

Valdiya KS 2002. Emergence and evolution of Himalaya: Reconstructing history in the light of recent studies. Progress in Physical Geography 26: 360–399.

Vila R, Bell CD, Macniven R, Goldman-Huertas B, Ree RH, Marshall CR, Bálint Z, Johnson K, Benyamini D Pierce NE 2011. Phylogeny and palaeoecology of *Polyommatus* blue butterflies show Beringia was a climate-regulated gateway to the New World. Proceedings of the Royal Society B: Biological Sciences 278: 2737–2744.

Vrba P, Konvicka M, Nedved O 2012. Reverse altitudinal cline in cold hardiness among *Erebia* butterflies. CryoLetters 33: 251–258.

Wahlberg N, Leneveu J, Kodandaramaiah U, Peña C, Nylin S, Freitas AVL, Brower AVZ 2009. Nymphalid butterflies diversify following near demise at the Cretaceous/Tertiary boundary. Proceedings of the Royal Society Series B Biological Sciences 276: 4295–4302.

Wang YJ, Li XJ, Hao G, Liu JQ 2004. Molecular phylogeny and biogeography of *Androsace* (Primulaceae) and the convergent evolution of cushion morphology. Acta Phytotaxonomica Sinica 42: 481–499.

Warren BCS 1936. *Monograph of the Genus Erebia*. Adlard and Son, London.

Weber WA 2003. The Middle Asian element in the southern Rocky Mountain flora of the western United States: a critical biogeographic review. Journal of Biogeography 30:649–685.

Weingartner E, Wahlberg N, Nylin S 2006. Dynamics of host plant use and species diversity: a phylogenetic investigation in *Polygonia* butterflies (Nymphalidae). Journal of Evolutionary Biology 19: 483–491.

Willmott KR, Hall JPW, Lamas G 2001. Systematics of *Hypanartia (*Lepidoptera*:* Nymphalidae*:* Nymphalinae), with a test for geographic speciation mechanisms in the Andes. Systematic Entomology 26: 369–399.

Wilson RJ, Gutierrez D, Gutierrez J, Martinez D, Agudo R, Monserrat VJ 2005. Changes to the elevational limits and extent of species ranges associated with climate change. Ecology Letters 8: 1138–1146.

Wing SL 1987. Eocene and Oligocene floras and vegetation of the Rocky Mountains. Annals of the Missouri Botanical Garden 74: 748–784.

Zachos J, Pagani M, Sloan L, Thomas E, Billups K 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686–693.

CHAPTER I.

Phylogeny of a mountain butterfly genus *Oeneis*: biogeographical and ecological speciation processes interact during evolution of Holarctic diversity

Irena Klečková*, Loic Pellissier, Martin Česánek, Martin Konvička, Zdeněk Faltýnek Fric

Manuscript

*author for correspondence (irena.slamova@gmail.com)

Abstract

We studied historical biogeography and evolution of ecological traits in Holarctic arcto-alpine butterfly genus *Oeneis* (Lepidoptera: Satyrinae), based on phylogenetic hypothesis inferred from four genes. Our results show that the genus originated in mountains of central Asia and further dispersed to North America and the Arctic at least five times independently. Geographic (neutral) speciation was a primary mode of speciation. Habitat affiliations to wet/dry, open/woodland habitats and climatic requirements displayed convergent pattern of evolution. However, ecological speciation probably contributed to the speciation of the arctic representatives of the genus, where sister species occur in sympatry. We also clarify several taxonomical issues. First, the genus *Oeneis* is paraphyletic with respect to *Neominois* (syn. n.) and thus, we synonymize the latter one with *Oeneis*. Within the genus, we detected five main species groups corresponding to the traditional division of the genus. We suggest that subgenus Protoeneis should not be further divided in species groups. Finally, *Oeneis aktashi*, which was previouslys assumed to be closely related to *O. mulla* and *O. elwesi*, is a sister species of *O. melissa*.

CHAPTER II.

Quantitative evidence for biennial life cycle and its spatial variation in the mountain butterfly *Erebia euryale* in the Czech Republic

Irena Kleckova, Pavel Vrba, Martin Konvicka*

(*in revision, European Journal of Entomology)*

*author for correspondence (konva333@gmail.com)

Abstract

Erebia euryale (Esper, 1805) is a montane-belt representative of the Palaearctic butterfly genus with prominent alpine radiation, endemic to the mountains of temperate Europe. As in many mountain insects, it has prolonged biennial larval development, which can be synchronised across mountains, resulting in profound biennial peaks of adult emergence. However, the existing reports are often contradictory, suggesting a variation in this synchronicity among populations. We present here the first quantitative assessment of the situation in the Czech Republic, based on five years of transect monitoring in three areas, representing the major mountain systems in the country. We detected two-orders of magnitude in biennial adult abundance fluctuations, peaking in even years (i.e. 2010, 2012) in the Šumava Mts. (Southwest Czech Republic). We found less distinct odd year (i.e. 2009, 2011, 2013) peaks in the Hrubý Jeseník Mts. (Northeast) and no fluctuations in the Krkonoše Mts. (North). Although the mechanisms behind these patterns remain unknown, we hypothesise that rugged terrain desynchronises the abundance fluctuations within mountain ranges and that the different synchronicity in individual mountain ranges may reflect different postglacial histories of respective populations.

CHAPTER III.

Thermoregulation and microhabitat use in mountain butterflies of the genus *Erebia*: Importance of fine-scale habitat heterogeneity

Irena Klečková*, Martin Konvička, Jan Klečka

Journal of Thermal Biology

*author for correspondence (irena.slamova@gmail.com)

Abstract

Mountain butterflies have evolved efficient thermoregulation strategies enabling their survival in marginal conditions with short flight season and unstable weather. Understanding the importance of their behavioural thermoregulation by habitat use can provide novel information for predicting the fate of alpine Lepidoptera and other insects under ongoing climate change. We studied the link between microhabitat use and thermoregulation in adults of seven species of a butterfly genus *Erebia* co-occurring in the Austrian Alps. We captured individuals in the field and measured their body temperature in relation to microhabitat and air temperature. We asked whether closely related species regulate their body temperature differently, and if so, what is the effect of behaviour, species traits and individual traits on body to air and body to microhabitat temperature differences. Co-occurring species differed in mean body temperature. These differences were driven by active microhabitat selection by individuals and also by species-specific habitat preferences. Species inhabiting grasslands and rocks utilised warmer microclimates to maintain higher body temperature than woodland species. Under low air temperatures, species of rocky habitats heated up more effectively than species of grasslands and woodlands which allowed them to stay active in colder weather. Species morphology and individual traits play rather minor roles in the thermoregulatory differences; although large species and young individuals maintained higher body temperature. We conclude that diverse microhabitat conditions at small spatial scales probably contribute to sympatric occurrence of closely related species with different thermal demands and that preserving heterogeneous conditions in alpine landscapes might mitigate detrimental consequences of predicted climate change.

CHAPTER IV.

Woodland and grassland mosaic from a butterfly perspective: habitat use by *Erebia aethiops* (Lepidoptera: Satyridae)

Irena Slámová*, Jan Klečka, Martin Konvička

Insect Conservation and Diversity

*author for correspondence (irena.slamova@gmail.com)

Abstract

1. We studied the habitat requirements of a vulnerable butterfly, *Erebia aethiops*, in a grassland-forest mosaic within a nature reserve. This species inhabits seemingly abundant habitats such as forest edges, but it is declining in many parts of Europe.
2. We analysed mark-recapture data, focusing on the effects of distinct vegetation structures, nectar sources and management regimes on population density and mobility.
3. Adult *E. aethiops* preferred abandoned grasslands and small open enclaves surrounded by forest; i.e. highly heterogeneous habitats. Male densities were higher in sparse woodlots, female densities at grassland patches. These intersexual differences in habitat use emphasise the need for heterogeneous vegetation.
4. Like other inhabitants of traditional woodlands, *E. aethiops* suffers from canopy closure, leading to its retreat to transitional structures such as forest edges or abandoned grasslands. Such preferences are in conflict with regular grassland management, necessary for conserving many other grassland organisms. Therefore, sparse woodlands containing forest free enclaves should be restored to protect this and other woodland organisms.

SUMMARY

The thesis extends general knowledge of history and speciation processes in mountain and arctic biota, behavioural thermoregulation and habitat use in butterflies. A common topic of all chapters in my thesis is the importance of environment heterogeneity for speciation and survival of species in the long term (chapter I), differentiation of development length among populations of one species (chapter II), coexistence of several closely related species (chapter III), and finally, for survival of individual species under ongoing changes of landscape structure and climate (chapter III and chapter IV). The conclusions of the studies presented in the thesis are applied in the context of effective conservation of cold-dwelling butterflies in human altered environments.

Chapter I describes biogeography of Holarctic mountain butterflies of the genus *Oeneis*. The genus originated in mountains of Asia and spread to North America independently in different lineages across Beringian land bridges. The Arctic was colonized also several times by a few independent lineages. Geographic (neutral) speciation was a primary mode of speciation, but also ecological speciation caused divergence of *Oeneis* species. Ecological speciation was convergent in different developmental lineages. The chapter highlights importance of mountains for conservation of species diversity during climatic changes of the Quaternary period and importance of the Beringia region for survival of arctic biota during cold periods of the Pleistocene. Last, we established that the name *Neominois* (syn. n.) should be a synonymum of the name *Oeneis* on the generic level.

In chapter II we described the geographic pattern in biennial abundance fluctuations in adults of a mountain butterfly *Erebia euryale* in three main mountain ranges of the Czech Republic. We hypothesise that rugged terrain desynchronises the abundance fluctuations within mountain ranges and that the different synchronicity in individual mountain ranges may reflect different postglacial histories of respective populations.

Chapter III describes differences in thermoregulation of seven sympatric species of the genus *Erebia*, which co-occur in the Alps. These differences were driven by active microhabitat selection of individuals and also by species–specific habitat preferences. We conclude that diverse microhabitat conditions at small spatial scales probably contribute to the sympatric occurrence of closely related species with different thermal demands and that preserving heterogeneous conditions in alpine landscapes might mitigate detrimental consequences of on-going climate change.

Finally, chapter IV illustrates the importance of structurally heterogeneous forest steppe habitats for an aberrant lowland representative of the genus, *Erebia aethiops*. Males preferred shady habitats of open woodlands, whereas females occurred in more open habitats, i.e. grassland patches within the matrix created by open woodlands. Thus, presence of both habitat types in the close vicinity is necessary to satisfy habitat demands of both sexes.

FUTURE PERSPECTIVES

The thesis presents several topics from ecology and evolution, with an attempt to integrate ecology into evolutionary framework in Chapter I. Thus, I see future perspectives in merging of both disciplines and testing the role of species traits (ecology, morphology) in evolution. Knowledge about the role of species traits is applicable for predicting of consequences of ongoing habitat and climate changes. The integration of species traits into phylogenies demands application of novel approaches and computational tools (e.g. integration of species distribution models or food web concepts to phylogenies). Particularly interesting are studies across complete taxonomics units and large spatial scales or studies comparing the effect of species traits on evolution of higher number of co-occurring species. Next, extension of our knowledge about limiting factors demarcating species distributions is necessary for effective conservation especially of mountain assemblages. Specific topics and questions, which came out from the thesis are:

I) Biogeography of cold-dwelling biota of the Holarctic region
Asian mountains are the centre of speciation and long term refugium of alpine species, but the knowledge about this centre and its biogeographic relationships to other mountain ranges is still low for butterflies (higher for plants and birds), which represent a model group for organisms with medium mobility. Thus, extension of the scope of future studies to large groups (e.g. all cold-dwelling representatives of the whole Satyrini butterflies, which is a group with already well known phylogeny), and reconstruction of their biogeography, detection of species traits facilitating settlement of mountain areas and further, description of speciation processes in this environment promise to provide novel information.
Another refugium and probably also speciation centre of cold-dwelling biota is the Beringia region. Similarly as above, the role of Beringia for emergence of "old" species can be detected for lager taxonomical groups. On population level, we can ask on the distribution of genetic diversity across the whole range of species (similarly as had been already done for *Parnassius phoebus* complex) and compare patterns among species with different ecological traits.

II) Altitudinal limits of mountain butterflies
Exploring the lower elevation limits of species occurrence seems to be a challenge for further studies. Specifically, the role of behavioural adaptation to marginal conditions and the effect of marginal conditions on insect immune systems and the role of parasitoids is largely unexplored.

III) Mechanisms of survival of Pleistocene climatic changes
The phylogeny of the genus *Erebia* is under reconstruction. But, one question remains – what mechanisms enabled *Erebia* butterflies to conserve their extraordinary diversity in European mountain rages. The answers could be provided by an integration of species distribution and niche modelling into the phylogenetic reconstruction.

IV) Competition among related polyphagous butterflies
Is competition for nectar enhanced among related butterflies occurring in sympatry? Competition is generally considered to be a driver of sympatric speciation, but for example in polyfagous species of butterflies, it is not easy to imagine resources for which species compete. Most likely, nectar might be a subject of competition. Testing this possibility could be a fruitful topic for future studies.

V) Last, a meta-analysis of already published studies could provide an insight into the role of ecological and neutral speciation and its frequency in tropical and Holarctic mountain systems of similar age.

APPENDIX: CURRICULUM VITAE

Irena Klečková (maiden name Slámová) - Curriculum Vitae

Address

Laboratory of Temperate Biodiversity
Biology Centre of the Academy of Sciences of the Czech Republic, v.v.i.
Institute of Entomology
Branišovská 31
České Budějovice
Czech Republic
37005

*13.4.1984 Planá u Mariánských Lázní, Czech Republic

Research interests

- Major question of my current research is how species biogeography and ecology shape species evolution. In particular, I have been studying the relative contribution of biogeography, habitat use and thermal requirements for the evolution of mountain butterflies of the Holarctic region.
- I gained detailed knowledge of butterfly habitat requirements by studying their behaviour, habitat use at different spatial scales and thermoregulation and I am using this information to guide effective conservation of butterflies in human altered habitats. With my colleagues, I am working on projects documenting phenology and abundance changes of mountain butterflies under climate change.
- Recently, I started to collaborate on a project on plant-pollinator interactions, focusing on the role of species traits on flower choice by pollinators and the temporal variation of plant-pollinator networks.
- I have been routinely using various methods of statistical data analysis to find answers to questions of interest using specialized software, such as R, Canoco, Statistica, Bioedit, TNT, MrBayes, Beast and RASP.

Employment history

- Since 2009, Biology Centre of the Academy of Sciences of the Czech Republic, v. v. i., České Budějovice, Czech Republic
- 2010–2011, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic

Education

- 2012 RNDr., Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic; Thesis: "Diurnal behavior and habitat preferences of *Erebia aethiops*, an aberrant lowland species of a mountain butterfly clade"
- 2009 MSc. (with a teaching certificate), Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic; Thesis: "Bionomics, diurnal behaviour and habitat selection of a vulnerable butterfly *Erebia aethiops*", supervised by Dr. Martin Konvička
- 2007 BSc. Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic; Thesis: "Seasonal and spatial dynamics of sexual generation of *Daphnia galeata* in Římov reservoir", supervised by Dr. Jiří Macháček

Stays abroad

- 2010 (three months), ERASMUS scholarship at the University of Turku, Finnland; Faculty of Mathematics and Natural Sciences, Laboratory of Genetics, The Nymphalidae Systematics Group. Project: "Reconstruction of phylogenies of the butterfly genera *Neptis* and *Erebia*", supervised by Niklas Wahlberg.
- 2008 (1 month), Field Course of Tropical Ecology: Papua New Guinea (organized by Faculty of Science, University of South Bohemia, České Budějovice, New Guinea Binatang Research Centre, Madang and PNG Institute of Biological Research, Goroka)

Membership in scientific societies

- Since 2011, Czech Society for Ecology

Grants

- 2010, Grant Agency of the University of South Bohemia, Project: "Habitat preferences and diurnal behaviour of mountain satyrid butterflies along an altitudinal gradient"

Reviewing

I have served as reviewer for Journal of Insect Conservation and Biodiversity.

Publications

- Papers in international peer reviewed journals:

In preparation

Klečková I., Pellissier L., Česánek M., Faltynek Fric Z., Konvicka M. (in preparation) Phylogeny of a mountain butterfly genus *Oeneis*: biogeographical and ecological speciation processes interact during evolution of Holarctic diversity.

Konvička M., Čížek O., Kuras T., Beneš J., Klečková I. (in preparation) Abundance changes of endemic alpine butterfly *Erebia epiphron silesiana* during 18 years – effect of climate and management changes.

Peña C., Witthauer H., Klečková I., Faltynek Fric Z.,Wahlberg N. (in preparation). Adaptive radiations in butterflies: evolutionary history of the genus *Erebia* (Nymphalidae: Satyrinae).

Published or submitted

Klečková I., Vrba P., Konvička M. (in revision) Quantitative evidence for biennial life cycle and its spatial variation in the mountain butterfly *Erebia euryale* in the Czech Republic. *European Journal of Entomology*

Klečková I., Konvička M., Klečka J. (2014) Thermoregulation and microhabitat use in mountain butterflies of the genus *Erebia*: importance of fine-scale habitat heterogeneity. *Journal of Thermal Biology* 41: 50–58.

Slámová I., Klečka J., Konvička M. (2013) Woodland and grassland mosaic from a butterfly perspective: habitat use by *Erebia aethiops* (Lepidoptera: Satyridae). *Insect Conservation and Diversity* 6: 243-254.

Slámová I., Klečka J., Konvička M. (2011) Diurnal behavior and habitat preferences of *Erebia aethiops*, an aberrant lowland species of a mountain butterfly clade. *Journal of Insect Behavior* 24: 230-246.

Zimmermann K., Blažková P., Čížek O., Fric Z., Hůla V., Kepka P., Novotný D., Slámová I., Konvička M. (2011) Demography of adults of the Marsh fritillary butterfly, *Euphydras aurinia* (Lepidoptera: Nymphalidae) in the Czech Republic: Patterns across sites and seasons. *European Journal of Entomology* 108: 243-254.

- Papers in Czech:

Slámová I., Konvička M. (2012) Naši velehorští okáči [Our mountain satyrids]. *Krkonoše - Jizerské hory* 2012: (7) 4-8. (popular)

Slámová I., Vrba P., Konvička M. (2012) Příběh vzácného motýla, který se stal na Šumavě obyčejným aneb co k životu potřebuje perleťovec mokřadní. [The story of a declining butterfly *Boloria eunomia* in Sumava Mts.]. *Šumava* 2012: 16-17. (popular)

Slámová I., Spitzer L., Konvicka M. (2010) Kde u nás přežívá okáč kluběnkový? Význam stanovištní mozaiky pro ustupujícího motýla [Where does *Erebia aethiops* survive in our country? An importance of habitat mosaic for survival of a vulnerable butterfly]. *Živa* 2010: 32-34. (popular)

Conferences

Only conferences where I personally presented the results of my research are included.

- February 2013, Zoological Days 2013, Brno, Czech Republic. Poster: Phylogeny of the genus *Oeneis* and biogeography of mountain fauna of Holarctic region (in Czech).
- January 2013, VII. Lepidopterological Colloquium, Olomouc, Czech Republic. Poster: Variable development length in *Erebia euryale* across mountain ranges of the Czech Republic (in Czech).
- March 2012, International Symposium: Future of Butterflies in Europe III, Dutch Butterfly Conservation (De Vlinderstichting), Wageningen, Netherlands. Oral presentation: Thermoregulation and microhabitat use in cold-dwelling butterflies: comparative analysis of the genus *Erebia*.
- February 2012, Zoological Days 2012, Olomouc, Czech Republic. Oral presentation: Habitat use and thermal niche in butterflies of the genus *Erebia* (in Czech).
- October 2011, Conference of the Czech Society for Ecology, Kostelec nad Černými lesy, Czech Republic. Poster: Thermoregulation and habitat use in butterflies: comparison of mountain and lowland representatives of the genus *Erebia* (in Czech).
- September 2011, VI. Lepidopterological Colloquium, Košice, Slovakia. Oral presentation: Phylogeny of the mountain butterfly genus *Erebia* (in Czech).
- April 2008, International Symposium: Future of Butterflies in Europe II, Dutch Butterfly Conservation (De Vlinderstichting), WICC Congress Centre, Wageningen, Netherlands. Poster: Habitat preferences of a vulnerable butterfly *Erebia aethiops.*
- February 2008, Zoological Days 2008, České Budějovice, Czech Republic. Poster: Habitat preferences of a vulnerable butterfly *Erebia aethiops* (in Czech).
- January 2008, III. Lepidopterological Colloquium. Mendel University, Brno, Czech Republic. Poster: Habitat preferences of a vulnerable butterfly *Erebia aethiops* (in Czech).