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The genetic structure of boreo-montane and arctic-alpine
Lepidoptera in Europe – revisited through mt-DNA barcodes

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1. Abstract

To date, few studies have addressed the genetic consequences of disjunct distribution patterns in Europe across larger numbers of species. The arctic-alpine pattern (as seen among many cold-adapted organisms) can be explained by post-glacial range re-arrangement in organisms bound to former glacial steppes and tundra. A similar, but less strongly disjunct distribution pattern is shown by boreo-montane organisms restricted to coniferous forests in montane and subalpine regions in south or central Europe and in the boreal zone, respectively. Existing studies have been limited to either case studies on selected focal species, theoretical reviews, or macroecological studies at a coarse level. This thesis aims to investigate the genetic consequences of disjunct distribution patterns among European lepidopterans. Specifically, the hypothesis that intraspecific genetic differentiation between regions is on average higher among arctic-alpine than in boreo-montane species was tested. 36 arctic-alpine and 78 boreo-montane species from Europe were identified using published literature and Cytochrome Oxidase Subunit 1 (CO1) sequences of the selected species were obtained from the BOLD database. Intraspecific divergences were assessed using Kimura-2 parameter pairwise distances. As expected, the arctic-alpine species showed a higher mean intraspecific divergence between populations than the boreo-montane species. In addition, significant differences in intraspecific genetic distances were found between both northern and southern populations for all calculation types. Furthermore, genetic distances between northern and southern populations were found to be greater than within each population. In 18 out of the 99 investigated species with arctic-alpine and boreo-montane distribution, the average intraspecific genetic distance between northern and southern populations was found to exceed 0.02, indicating as yet unrecognized cryptic diversity in these species.

Keywords: arctic-alpine, boreal-montane, disjunct distributions, intraspecific variation, species delimitation, cryptic diversity

2. Introduction

2.1. Causes and consequences of disjunct distribution patterns

A growing number of studies focus on the impact of abiotic and biotic factors on species distributions. Climate variables such as temperature, precipitation, and wind strongly influence the distribution of many taxa globally (Berggren et al., 2009). These climate-driven changes in distribution have occurred throughout Earth's history, including during the Pleistocene cold periods and Holocene warming (Hewitt, 1996; Parmesan et al., 1999). The Pleistocene glaciations caused significant shifts in species ranges, shaping the current distribution of European flora and fauna (Schmitt, 2007). In present-day Europe, various biogeographical patterns are observed concerning species ranges. Lepidoptera, including butterflies and moths, are temperature-sensitive and show pronounced range shifts in response to climatic changes (Ehl et al., 2020; Kirichenko et al., 2014). These species exhibit different distribution types, including Mediterranean, transcontinental Eurasian, and disjunct arctic-alpine distribution patterns. This arctic-alpine disjunction can be explained by two evolutionary phenomena: the classic arctic-alpine pattern (seen among many cold-adapted organisms from tundra-like habitats) and the pattern caused by the dryness of former glacial steppes. The classic arctic-alpine pattern can be defined by the wide distribution of some species in the glacial steppes (Schmitt, 2007; Schmitt, 2009). Ancestral distributions of these organisms presumably ranged from the northern ice shield to the glaciers in the southern mountains and became only disconnected by the postglacial retraction of ice shields and immigration of forest biota into regions at mid-latitudes. This led to the separation of populations that inhabit island-like non-forest ecosystems in different high mountain systems (predominantly the Alps, Pyrenees, and the Carpathian Mountains, above the tree line) and the arctic region (tundra biome). Thereby, arctic-alpine disjunct species or populations originated which still show close genetic relations to each other like in the burnet moth *Zygaena exulans* (Schmitt, 2007; Schmitt, 2009).

Other species have accumulated much larger differentiations between populations, most likely because they were subject to disjunct distribution patterns already during earlier glacial and interglacial phases. Due to their adaptation to cold environments, which may include changes in metabolism and physiology to withstand lower temperatures and other related mechanisms, many cold-adapted species were not well suited to the dry conditions of glacial steppes. As a result, these species migrated towards more humid areas in proximity to glaciated mountain systems. This led to

the arctic-alpine pattern caused by the dryness of glacial steppes as opposed to the 'classic' arctic-alpine pattern (Schmitt, 2007).

The arctic-alpine distribution spans a northern range that is circumpolar, including species found in northern Europe, North Siberia, and even across Beringia to North America, including Greenland. The southern part comprises species from Europe (Alps, Carpathians, Apennines, Pyrenees), northern and central Asia (Himalaya, Altai Mountains, Tian Shan range, Pamir Mountains), and high mountains of North America (Mutanen et al., 2012; Stevanović et al., 2009). Those species with arctic-alpine disjunctive patterns should not be mistaken with boreo-montane species, which show similar but distinct distributions. Organisms showing this boreo-montane pattern occurring in the montane and subalpine forests in the mountain ranges of southern and central Europe as well as in the vast boreal coniferous forest zone in the North (Schmitt, 2017). These species were probably widely distributed throughout Europe during the last glacial period and survived in multiple refugia (Ehl et al., 2020; Habel et al., 2010; Maresova et al., 2019; Schmitt, 2020). The geographical disjunctions between these refugia can be explained by species-poor periglacial steppes north of the Alps and the Carpathians or the presence of trees beyond the classic mid-range refugia (Ehl et al., 2020; Schmitt, 2020). The ranges of boreo-montane organisms, like arctic-alpine species, can be divided into southern (mountain ranges) and northern (boreal) distribution areas (Ehl et al., 2020). The northern range extends below the polar forest boundaries and can have a circumpolar distribution around the Arctic, spanning from Norway to Kamchatka in Eurasia and from Alaska to Newfoundland in North America (Pfadenhauer and Klötzli, 2015a). On the other hand, the southern range is primarily limited to the mountains of central and southern Europe, including the Balkan-boreal subregion (Vukojičić et al., 2014). Additionally, there are rarer cases of postglacial expansion from the southern Urals into Europe, observed in taiga forest species (Ehl et al., 2020; Maresova et al., 2019; Kramp et al., 2016; Schmitt, 2020). Unlike arctic-alpine species, which occur above the tree line (typically between 2000-3000 m elevation), boreo-montane species inhabit the montane forests of southern and central Europe (around 1000-2000 m elevation) as well as the boreal coniferous forests in the north (Pfadenhauer and Klötzli, 2015a).

Both arctic-alpine and boreo-montane taxa have experienced range shifts during climatic warming, leading to reductions in their distribution areas and complex disjunctive biogeographic patterns (Habel et al., 2010; Ehl et al., 2020; Mutanen et al., 2012).

Glacial maxima affected genetic differentiation, with southern mountain chains now exhibiting high genetic diversity due to cold-adapted species surviving in these refugia (Dincă et al., 2021; Schmitt,

2007). Spatial separation of refugia can disrupt gene flow, potentially leading to species divergence. For example, *Monopis laevigella* showed a split in its mitochondrial DNA barcode sequence, accompanied by ecological and distributional differences, resulting in the recognition of the arctic-alpine species *Monopis jussii* separate from the boreo-montane *M. laevigella* (Mutanen et al., 2020). However, in most cases it remains to be assessed how genetically different the populations are in the northern and southern (mountain) regions today, respectively. In the taxonomically well-known European Lepidoptera, these populations have been variously treated either as distinct species, subspecies, or just as clinal variants, depending on the views of individual taxonomists (Ehl et al., 2020; Mutanen et al. 2012; Mutanen et al., 2020). But a coherent multi-species study into these genetic differentiations across a wide range of species with disjunctive distributions is lacking.

2.2. *Species delimitation*

Species identification is crucial in biology (Luo et al., 2018). However, it can be complex and subjective when dealing with species that have limited differences. Contemporary biologists use multiple species concepts, such as the biological species concept and the phylogenetic species concept (Zachos, 2016). The biological species concept is based on reproductive isolation, while in the phylogenetic species concept focuses on reciprocal monophyly (Baum and Shaw, 1995; Descimon et al., 2009; Hey et al., 2005; Luo et al., 2018; Mayr, 1942). Molecular methods, like comparing genetic distances, have become additionally valuable for species identification (Hebert et al., 2003; Luo et al., 2018). This genetic divergence can increase with geographic distance between populations (Gaytán et al., 2020). While geographic distance generally has little impact on identification, exceptions exist where broader coverage reduces success (Mutanen et al., 2012).

In animals, the mitochondrial cytochrome oxidase subunit 1 (CO1) gene is commonly used for species identification (Gaytán et al., 2020; Hebert et al., 2003; Huemer et al., 2014; Marín et al., 2021; Mutanen et al., 2012; Scalercio et al., 2021). A 2% distance threshold has proven particularly useful when screening for unrecognized taxa (Gibbs, 2017; Mutanen et al., 2012; Strutzenberger et al., 2011). Along this line, Barcode Index Numbers (BINs) have been developed to categorize DNA barcode sequence fragments into operational taxonomic units (OTU) based on their divergences (Gibbs, 2017; Ratnasingham and Herbert, 2013; Scalercio et al., 2021).

In Europe, arctic-alpine species often have isolated populations in various mountainous regions and southern glacial refugia. Several studies show that some isolated populations belong to the same

taxonomic unit (Huemer et al., 2018), while others identify new lineages that were previously unrecognized (i.e. cryptic diversity) (Dincă et al., 2021; Mutanen et al., 2020; Scalercio et al., 2021). The lack of universally accepted criteria for species delimitation poses challenges in distinguishing these lineages. The existence of cryptic species (morphologically indistinguishable but sexually incompatible species) has significant implications for evolutionary processes, ecosystem functioning, and biodiversity metrics (Marín et al., 2021). DNA barcodes, combined with morphology or ecological data, can confirm the presence of multiple species within a single taxon. For example, Kirichenko et al. (2015) confirmed two distinct lineages in the gracillariid leaf-miner moth previously known as *Callisto coffeella*, and one of them was described as a new species, *C. basistrigella*, indicating allopatric isolation mainly caused by the last glacial period.

On the other hand, populations in the arctic and alpine regions often show close genetic relatedness, despite large gaps in their geographic distribution (Ehl et al., 2020). Ehl et al. (2020) also identified subtle genetic differences in three population groups of *Boloria napaea* (western Alps, eastern Alps, and the Arctic). Similar disjunctive distribution patterns were observed in other Lepidoptera taxa occurring in the alpine mountain and boreal forest zones. Although such patterns are well-documented in the published literature, there is still a limited number of studies exploring the general prevalence and nature of these disjunctive patterns.

2.3. Conservation aspect

The term biodiversity covers various levels of life, it encompasses ecosystems, species, and genes (Gugerli et al., 2008). An important part of conservation biology is the protection and assessment of biological diversity. To preserve biodiversity, the protection of habitats has become a conservation strategy (area-based conservation: Maxwell et al. 2020). In this case, species richness and the amount of endemism in designated reserve areas are important metrics when it comes to the prevention of habitat loss and prioritizing habitats for conservation (Bickford et al., 2007; Marín et al., 2021). Proper species identification and conservation status are crucial for conservation efforts and policy-making (Tobias et al., 2010). Uncovering cryptic species and recognizing multiple species within a single taxon can reveal cases of endemism and significantly impact habitat biodiversity (Bickford et al., 2007; Fišer et al., 2018; Marín et al., 2021). Accurate species delimitation and identification of evolutionarily significant units are important essential for effective conservation (Crandall et al., 2000; Funk et al., 2012). Knowledge of life history, morphology, and genetic variability is

vital for species identification and biodiversity assessments (Sheth and Thaker, 2017). Estimating the distributional range size, specifically the extent of occurrence (EOO), is important for evaluating a species' conservation status (de Castro Pena et al., 2013; IUCN Standards and Petitions Committee, 2022). Taxonomic rearrangements can significantly impact the EOO, leading to changes in species distribution and potential alterations in conservation status and protected habitat designations, particularly for species with disjunctive distributions (de Castro Pena et al., 2013). Accepted species splits or the recognition of new species can also influence conservation status (Mace and Mace, 2004; New, 2013; Vogel Ely et al., 2017). Climate change poses risks for species distribution and the decline of narrowly endemic populations (Parmesan, 2006). Conservation biology anticipates future changes in biodiversity patterns and species responses to environmental conditions (Fuller et al., 2011). Conservation biogeography aims to create predictive models for species distribution but relies on accurate knowledge of current species distribution and delimitation for meaningful predictions (Landler and Whittaker, 2011). Understanding the genetic differentiation observed in species like *B. napaea*, caused by past glacial separation (Ehl et al., 2020), is crucial in conservation biogeography for designing effective protected area networks.

2.4. Aim of this study

To date, few studies investigated the genetic signature of disjunctive distribution patterns in European Lepidoptera. Existing studies were either limited to case studies on selected focal species, or theoretical reviews (Schmitt 2009), or coarse-scaled macroecological studies (Dincă et al., 2021). This thesis aims to investigate the genetic consequences of disjunctive distribution patterns among a broad range of European Lepidoptera species. For most of these insects, geographic distributions are fortunately well known. In addition, mtDNA barcode data exist for almost all of them, often also covering various regions in Europe (and abroad) with a substantial number of replicate sequences.

I will address the following questions:

1. Is there a detectable intraspecific genetic differentiation between the northern and southern populations? If so, how strong is the genetic differentiation in species of Lepidoptera with arctic-alpine or boreo-montane distributions in Europe?
2. Can these populations still be considered as forming one species, or should they be separated into two or more taxonomic entities?

3. Does the genetic divergence within the northern populations differ from genetic divergence within southern populations?

Hypotheses:

1. I predict that the geographic disjunction between and within northern and southern populations has left a genetic signature.
2. I predict genetic differentiation between northern and southern populations to be higher among arctic-alpine than boreo-montane species.
3. I expect greater genetic intraspecific north-south differentiation of Lepidopterans sharing eco-morphological traits normally associated with low dispersal capacity (e.g. high wing load, bulky abdomens, host-plant specialists, or capital breeders with reduced adult mouthparts).

3. Materials and Methods

3.1. Collecting and assembling data

For this study, Lepidoptera species from Europe with either a disjunctive arctic-alpine or a boreo-montane distribution were identified using published literature (Table 1 in Appendix, p.44). The geographic circumscription of Europe was used here as in 'The Geometridae of Europe' monograph series (Hausmann, 2001; Hausmann, 2004; Mironov and Hausmann, 2003; Hausmann and Viidalepp, 2012; Skou, Sihvonen, and Hausmann, 2015; Müller et al., 2019). Species with disjunctive geographic distribution in Europe are described in these books as Holarctic, Palearctic, or Eurasian in the boreo-montane or arctic-alpine zone. These areas may range from Iceland, the British Isles across Fennoscandia and northern Europe, to the south-central mountain chains: the Alps, Carpathians, and the Pyrenees. The eastern border of the region considered was given by the Ural Mountains, Belarus, i.e. the huge parts of Russia situated east of the Ural Mountains were excluded since documentation of species distributions becomes very sparse there.

In contrast to most other studies, I aimed to cover a broad range of clades across the entire phylogenetic tree of the Lepidoptera. Altogether I initially identified 45 species with arctic-alpine distribution belonging to 16 families and 106 species with boreo-montane distribution belonging to 20 families, all showing pronounced north-south disjunctions in their geographical distributions.

A list for each distribution type was then created including the currently accepted species names as well as their Barcode Index Numbers (BINs) from the BOLD database, relevant synonyms of the species names, and the references from which the information was obtained. Most of the information was obtained from scientific literature like 'The Geometridae of Europe' or journal articles (Table 1 in Appendix, p.44) and BINs or barcode records available on GBIF (The Global Biodiversity Information Facility) (GBIF.org, 2022) or BOLD (Barcode of Life Data) (BOLD, 2023) (Table 1 in Appendix, p.44).

3.2. Data editing

The Cytochrome Oxidase 1 (CO1) sequence data of the selected target species were searched and downloaded from BOLD by BINs and/or using the species' accepted names or their synonyms according to the nomenclature in Lepiforum e.V. (2021). 300bp was defined as the initial minimum length of sequences to be considered. Each sequence was associated with the species name, a

unique process ID-number, the URL in BOLD, and the distributional status of each species (arctic-alpine or boreo-montane). For easier handling during calculations, a few cases of recently recognized species complexes and pairs of sister species were operationally combined under one name (Table 1). For example, sequences found for the species complex of the clearwing moths *Agriades glandon/aquilo* were further processed under the species name *A. glandon*.

Table 1: Used names for species complexes to facilitate handling during calculations.

Species name complexes	Used species name
<i>Agriades glandon/aquilo</i>	<i>Agriades glandon</i>
<i>Erebia medusa/polaris</i>	<i>Erebia medusa</i>
<i>Chelis puengeleri/cervini</i>	<i>Holoarctia puengeleri</i>
<i>Nemapogon wolffiella/koenigi</i>	<i>Nemapogon koenigi</i>

With the program QGIS (2022) and using the coastline map (version 4.1.0) (Natural Earth, 2022) the collection point of each sequence was visualized and data from outside the defined geographical area (like occurrences in east Russia or North America) were deleted. Likewise, all sequence entries with insufficient or missing locality data (coordinates, country, state, province, region) were discarded. Samples without precise coordinates, but with textual locality data were geo-referenced by hand as far as possible. Sequences were then grouped by region into occurrences in the North or South of Europe, for both distributional types of species (arctic-alpine and boreo-montane taxa). In total, for arctic-alpine Lepidoptera in Europe 1463 all CO1 sequences representing 36 species belonging to 15 families, and for boreo-montane species 2637 sequences from 78 species belonging to 18 families were finally retained and examined (Table 1 in Appendix, p.43).

3.3. Sequence analysis

Sequence alignment was done with MAFFT version 7 (Katoh et al., 2019). Data were prepared for analysis using BioEdit 7.0.5.3 (Hall, 1999). All other analyses were done with R Studio 1.4.1103 (R-Studio, 2021), R v4.0.4 (R Core Team, 2021), and Microsoft Excel (2020).

Intraspecific genetic distances were evaluated through the Kimura-2-parameter (Kimura, 1980) distance, which is a commonly used distance metric for such analyses and is included in the R package ape (command dist.dna) (Paradis and Schliep, 2019). Because DNA barcode data often show a pro-

nounced geographic bias, like when several individuals have been sampled at exactly the same location, I attempted three ways of correction to compensate for these biases. Within each distribution type (arctic-alpine and boreo-montane) I first excluded all duplicate sequences (named: *No duplicates*) by using just one sequence per haplotype. To achieve that goal, sequences were filtered with the program ALTER (Alignment Transformation Environment) (Glez-Peña et al., 2010). Through this procedure, the number of sequences was reduced from 1463 sequences to 449 sequences for the arctic-alpine taxa, and from 2637 sequences to 821 sequences for the boreo-montane species. During the second analysis, only one individual per site per species was used (named: *One per site*). Therefore, a list with the coordinates of each collected individual of each sequence was prepared. To obtain the sequences for this second analysis, the full list of accepted sequences was filtered using the duplicate function in R Studio 1.4.1103 (R-Studio, 2021). For this calculation, 863 sequences for the arctic-alpine species and 1135 for the boreo-montane species were used. For the third analysis, neither duplicate sequences nor multiple individuals per site and species were excluded, i.e. the originally found sequence number of 1463 for the arctic-alpine and 2637 for the boreo-montane species were used (named: *All*).

After calculating all intraspecific pairwise Kimura-2 parameter distances for each computational type (*All*, *One per site*, and *No duplicates*), the sequences of each species were divided into two groups. For example, the sequences available for the boreo-montane geometrid moth *Macaria carbonaria* were distinguished into a boreal (northern) group and a montane (southern) group to obtain the maximum, mean, and minimum of pairwise genetic distances within and between these two groups. For the mean of pairwise genetic distance calculations the R packages ape (Paradis and Schliep, 2019), dplyr (Wickham et al., 2022), insect (Wilkinson et al., 2018), and reshape2 (Wickham, 2007) were used.

The calculated mean distances of each computational type (*All*, *One per site*, and *No duplicates*) of each species and their distribution were summarized in a list. The frequency of sequences was calculated for each species in R Studio 1.4.1103 (R Studio, 2021). For further statistical analysis in R Studio 1.4.1103 (R Studio, 2021), only species with no less than four sequences per species were considered.

3.4. Statistical analysis

The statistical analyses were performed for all corrections of geographic bias (*All*, *One per site*, and *No duplicates*) in R Studio (2011). Principal coordinates analyses (PCoA) were done to visualize differences in mean pairwise distances between and within northern and southern populations (distN and distS) of the arctic-alpine and boreo-montane distribution. For showing this function I used pcoa (Gower, 1966), which is included in the ape package of R Studio (2011). For each distance calculation (between, distN and distS) only one centroid was mapped, but in the background of the ordination analysis (= PCoA) all species used for the respective distance calculations are included. To test the hypothesis if the genetic differentiation between northern and southern populations is higher among arctic-alpine species than boreo-montane species, I performed a Mann-Whitney U-test. Since data were not normally distributed and showed heterogeneous variances, I used the mean of intraspecific divergence between the northern and southern populations as the response variable in the Mann-Whitney-U-test. As categorical grouping variable I used the distribution type (arctic-alpine vs. boreo-montane).

Another analysis was done by addressing the question if the genetic divergence within northern populations differs from genetic divergence within southern populations. To address this question a Wilcoxon's matched-pairs signed-ranks test was applied with no differentiation between arctic-alpine and boreo-montane species. As data for this analysis were not normally distributed and showed heterogeneous variances the mean of pairwise distances were used within the northern (dist_N) and southern regions (dist_S) as response variable and the species accounted as the units for the analysis. Mean of pairwise distances within regions was also calculated in R Studio (2011) by using Kimura-2-parameter (Kimura, 1980) distances. Violin plots were created using the ggplot2 package (Wickham, 2016) and gridExtra (Baptiste, 2015) in R-studio 1.4.1103 (R-Studio, 2021).

3.5. Species traits with putative relevance to dispersal

Data on eco-morphological species traits that might be related to dispersal capacity of moths, and therefore with putative relevance for gene flow between populations and regions, were extracted from literature to determine if there is a contingency between these traits and the mean intraspecific pairwise genetic distance between the North and the South, for the calculation type *No Duplicates* with correction of the sampling bias by using just one sequence per haplotype. These traits were: forewing length in mm, the occurrence of a functional proboscis, larval host plant growth

form, and larval host specificity. Data were assembled from additional literature and online sources (Guariento et al., 2020; Hausmann, 2001; Hausmann, 2004; Hausmann and Viidalepp, 2012; Kimber, 2023; Lepiforum, 2021; Mironov and Hausmann, 2003; Müller et al., 2019; Skou, Sihvonen, and Hausmann, 2015). Forewing length was measured with the program Image J (Schneider et al., 2012) using the instruction of García-Barros (2015). Therefore, scaled photographs were searched on BOLD, the Lepiforum (2021), or GBIF (2022). Forewing length (in mm) was measured from the insertion of the wing at the thorax along its costal margin to its apex including the fimbriae (García-Barros, 2015). Larval host plants were categorized according to their growth forms into grasses, herbs, woody plants, and diverse plants. With regard to larval food niche breadth, a distinction was made on whether the caterpillars feed only on plant species within one genus (monophagous) or only on plants of one family (oligophagous), or whether they feed on plant species in several families (polyphagous). A Spearman correlation for continuous variables such as for example forewing length was applied. Kruskal-Wallis ANOVAs for all categorical traits as predictors were performed separately for each trait. No distinction was made between the species distribution types. I used the genetic intraspecific distance between northern and southern populations as response variable and the species as units of analysis.

4. Results

After editing the data, I identified more species with boreo-montane distribution ($n=78$) with suitable CO1 sequence data than species with an arctic-alpine distribution ($n=36$). Also, fewer sequences were found for the species of the arctic-alpine distribution ($n= 1463$) than for those with boreo-montane distributions ($n=2637$). Through the correction for geographic sampling bias, a lot of sequences including whole species were excluded from the calculations. Thus, for the calculation type with *No duplicates* sequence number was reduced to 449 sequences of species with arctic-alpine distribution and to 821 for lepidopterans with boreo-montane distribution. For the calculation type *One per Site*, whereby only one individual per site/coordinate per species was used, the sequence count of species with arctic-alpine distribution was reduced to 863 and for species with boreo-montane distribution to 1135.

4.1. *Genetic signature between and within northern and southern populations of the arctic-alpine and boreo-montane distribution types*

The study of CO1 Lepidoptera sequences revealed a clear genetic signatur resulting from spatial disjunction in all groups (Figure 1). This pattern was evident in all types of calculations. The mean of pairwise distances between the two regions are usually larger compared to those within the northern (distN) and within southern distances (distS). Conversely, the within- region distances of the arctic-alpine distribution are generally smaller across all calculation types (Figure 1). Additionally, by excluding duplicate sequences of the boreo-montane distribution, all calculated means of pairwise distances are comparatively closer to each other (Figure 1).

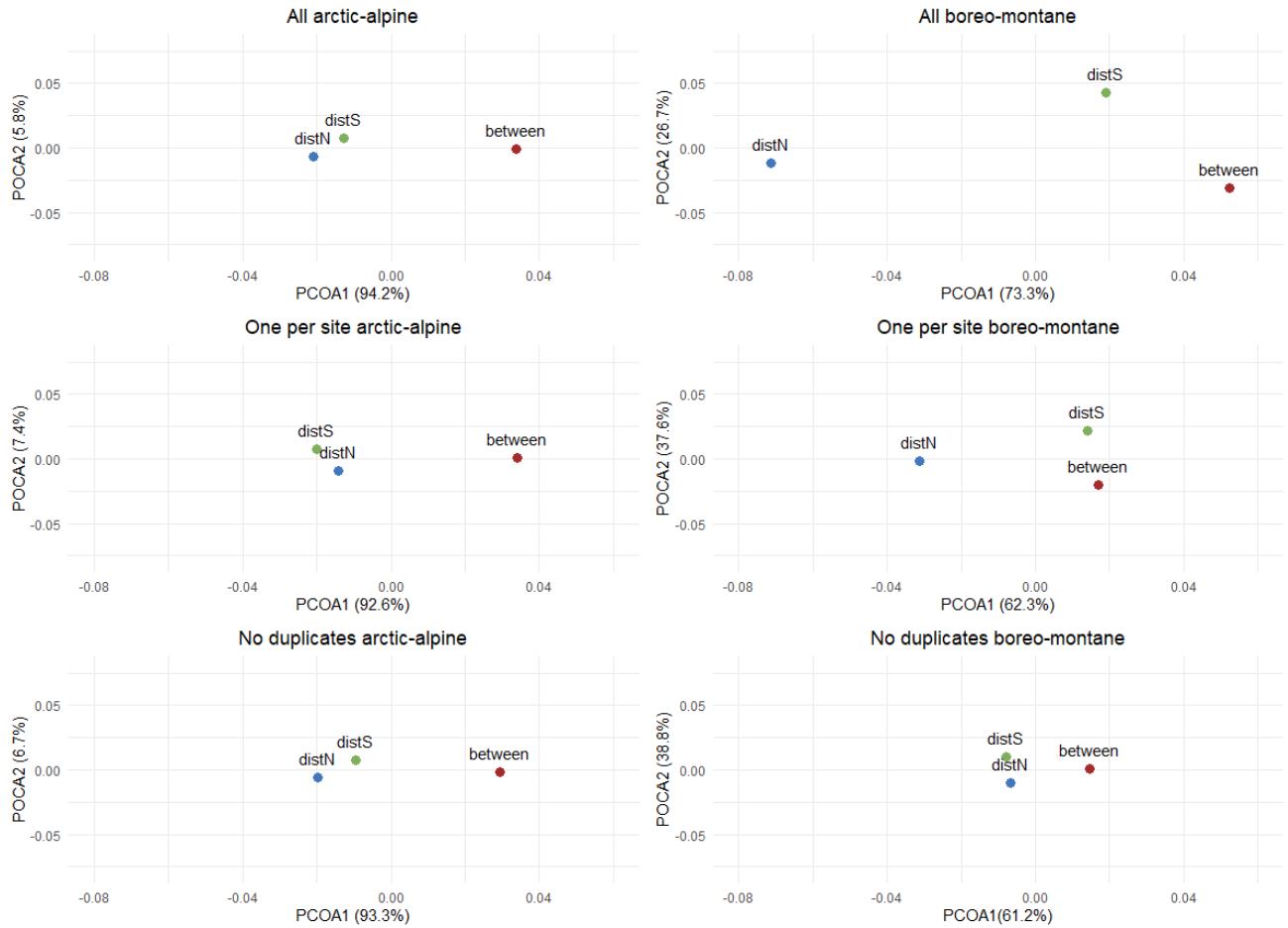


Figure 1: Principal coordinates analysis of mean pairwise distances comparing arctic-alpine and boreo-montane distribution types of all the calculation type (*All*, *One per site* and *No duplicates*):

On the left side are the mean of pairwise distance of species of the arctic-alpine distribution: between the northern (arctic) and southern (alpine) region (dark red), within distances of species of the arctic region (distN in blue) and within distances of species of the alpine region (distS in green).

On the right side are the genetic signatures of the intermediate divergences of boreo-montane species: between the northern (boreo) and southern (montane) region (dark red), within distances of species of the boreo region (distN in blue) and within distances of species of the montane region (distS in green). The percentages at the ordination axes are the relative eigenvalues of the principal coordinates analysis. The individual centroids represented the respective groups of pairwise distances. The individual species were thus combined to form a point of the different mean of pairwise distances.

4.2. Intraspecific genetic differences between the arctic-alpine and boreo-montane distribution types

Analyses comparing the mean of genetic distances between the northern and southern parts of the species distributions showed no statistically significant difference between species of the two distribution types (Figure 2), as long as duplicate sequences were included (Mann-Whitney U-test; *All*: $W = 1169.5$, $p = 0.0848$; *One per site*: $W = 445$, $p = 0.8898$). However, after excluding all duplicates (which bias the result towards low distances), genetic differentiation between northern and southern populations emerged as significantly higher among arctic-alpine than boreo-montane species (*No duplicates*: $W = 193$, $p = 0.0141$). The mean value of pairwise Kimura-2P distances ranged from 0.00 to 0.07 per species between regions among species with boreo-montane distribution, and from 0.00 to 0.03 between regions among species with arctic-alpine distribution.

Two geometrid species (*Colostygia turbata* and *Elophos vittaria*) with boreo-montane distribution showed particularly large intraspecific pairwise between-region divergences at the calculation *All*. Yet, the number of sequences was then greatly reduced in these two species due to the correction of geographic bias, so that they had less than four sequences remaining and thus did not appear in the other calculations.

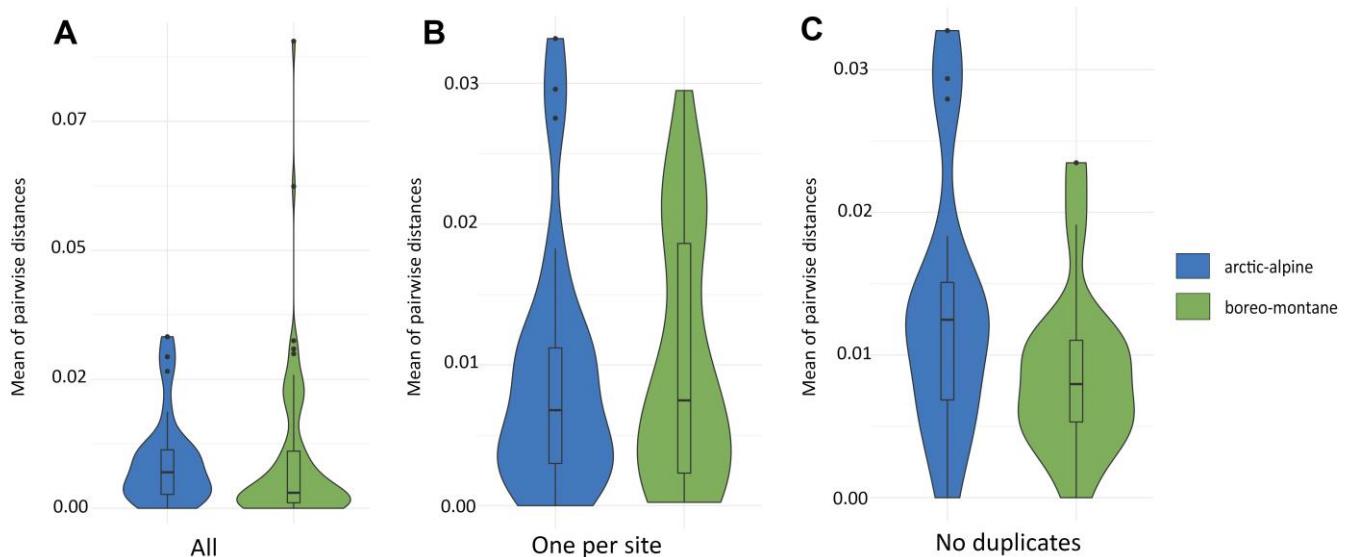


Figure 2: Comparison of the mean of intraspecific pairwise distances between northern and southern populations of arctic-alpine and boreo-montane Lepidoptera species: Mean divergences of pairwise distance comparing between arctic-alpine species (dark blue) and boreo-montane species (dark green), calculated with three different selection criteria for sequences. *All*: no sequences

were excluded (A). *One per Site*: only one individual per site and species were used (B). *No duplicates*: one sequence per haplotype were used (C).

4.3. Analyses of the influence of traits on the mean of pairwise between region divergence

For each distribution, the characteristics of the identified species were included to see if there is a correlation between the mean of the pairwise distances and the selected characteristics. For this, only the values of the calculation *No duplicates* were used.

The result of the Spearman rank correlation shows that there is no significant correlation between mean of pairwise genetic distances between northern and southern populations and forewing length (Table 2). Also, the Kruskal-Wallis-ANOVAs for all categorical traits show no significance (Table 2). Appropriate plots (Figure 3) likewise visualize that no contingencies between the studied species traits and the average intraspecific degree of genetic north-south divergence was observed.

Table 2: Results of statistical analyses of species characteristics and their possible influence on the mean pairwise genetic distances between northern and southern populations. Mean of intra-specific pairwise distances between-region in correlation to the different traits. rho= correlation coefficient according to Spearman, S= value of the test statistic, Chi²=chi-squared.

Tested species trait	Test Statistic	Degrees of Freedom (df)	Correlation Coefficient (rho)	p-value
Forewing length	S = 5867.2	N/A	rho = -0.0754	p= 0.6818
Functional proboscis	Chi ² = 0.002	df = 1	N/A	p = 0.9615
Larval host specificity	Chi ² = 1.447	df = 3	N/A	p = 0.6946
Larval host plants	Chi ² = 0.584	df = 5	N/A	p= 0.9887

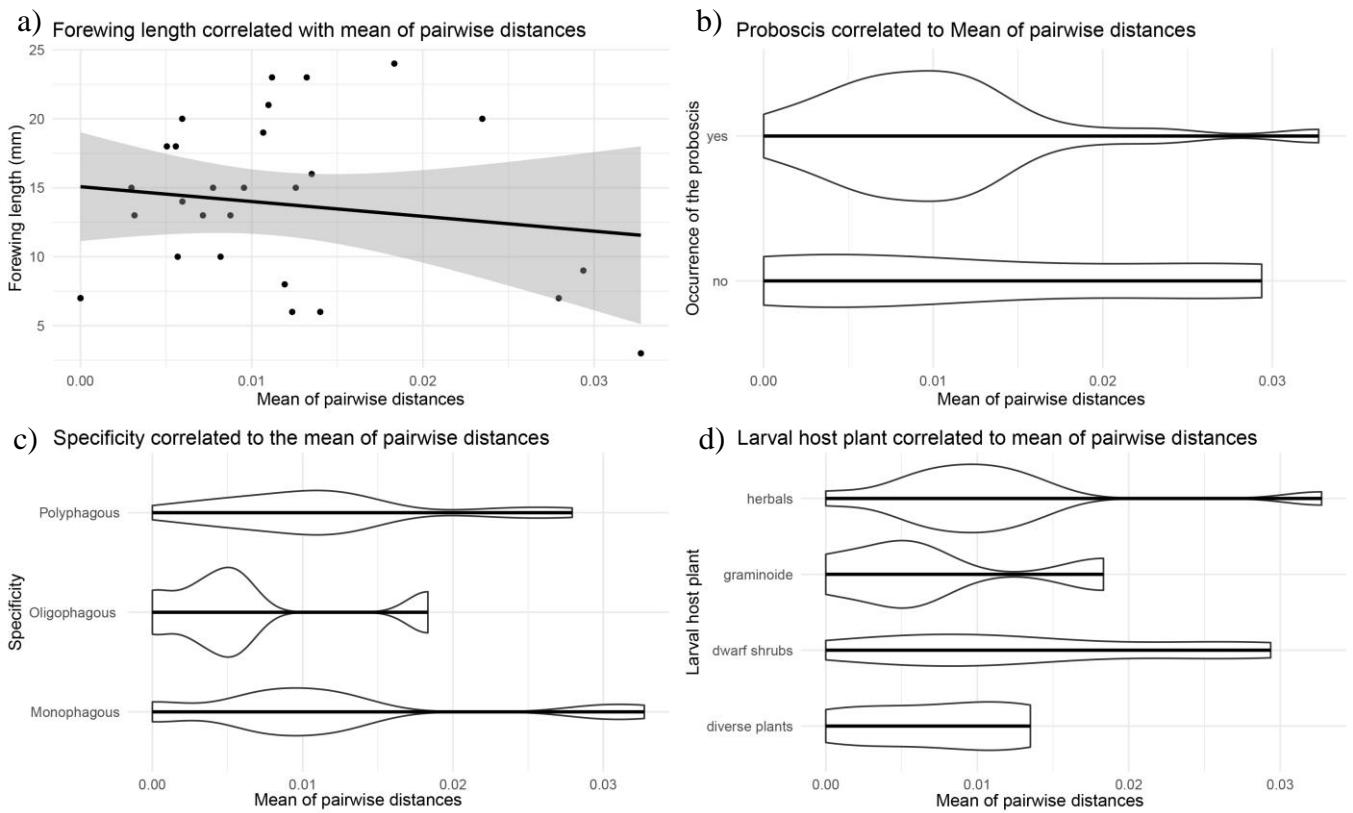


Figure 3: Mean of pairwise genetic between-region divergence in relation to the chosen species traits :

Mean of pairwise distances between-region of the calculation *No Duplicate* in relation to the different traits combined from both distribution types: a) scatterplot of the forewing length b) density plot of the occurrence of the proboscis c) boxplot of the food spectrum (monophagous, oligophagous, polyphagous) d) boxplot larval host plant (herbs, graminoids, dwarf shrubs, diverse plants).

4.4. Species with high genetic distances between the northern and southern regions of their distributions

Altogether in 18 out of 99 investigated species the mean value of intraspecific genetic distance between northern and southern populations in at least one mode of analysis was above 0.02 (Table 3). When correcting for geographic bias, many sequences had to be excluded so that for some species not all calculations were possible. In addition, the exclusion of taxa with fewer than four sequences resulted in species with too few sequences also not being included, leading to a further reduction. Therefore, some species only appear in one calculation type and not in all (Table 3).

Only three of these species have an arctic-alpine distribution type, whereas the majority occupy boreo-montane ranges. In most cases the genetic distance between northern and southern populations was in the range of 2-3%, i.e. at the margin of what is often considered as a threshold for spe-

cies delimitation in Lepidoptera. Only two boreo-montane geometrids, *Colostygia turbata* and *Elophos vittaria*, revealed a substantially larger genetic differentiation between northern and southern populations. Species complexes that are already considered as distinct species in recent taxonomy (Table 1) do not show a genetic differentiation between northern and southern "subspecies" compared to the mean of pairwise distances calculations of this work (Table 3).

Table 3: Species with intraspecific genetic distances greater than 2%, sorted alphabetically within the two distribution types: The mean of pairwise distances values of intraspecific between-region divergences of the different calculation types ordered to their distribution. Some species had no pairwise distances due to geographic sampling bias. Gray shading showed species complexes. There was no genetic difference between the northern and southern "subspecies".

Species name	No duplicates	One per site	All	distribution
<i>Agriades glandon/ aquilo</i>	0.0070	0.0063	0.0088	arctic-alpine
<i>Caryocolum pullatella</i>	0.0327	0.0331	0.0333	arctic-alpine
<i>Chelis puengeleri/ cervini</i>	0.0056	0.0053	0.0056	arctic-alpine
<i>Epinotia mercuriana</i>	0.0279	0.0275	0.0266	arctic-alpine
<i>Erebia medusa/ polaris</i>	0.0019	0.0016		arctic-alpine
<i>Incurvaria vetulella</i>	0.0294	0.0296	0.0294	arctic-alpine
<i>Acasis appensata</i>			0.0325	boreo-montane
<i>Alcis jubata</i>			0.0259	boreo-montane
<i>Aricia nicias</i>		0.0046	0.0248	boreo-montane
<i>Chionodes luctuella</i>			0.0216	boreo-montane
<i>Colias palaeno</i>		0.0272	0.0262	boreo-montane
<i>Colostygia turbata</i>			0.0906	boreo-montane
<i>Cucullia lactucae</i>		0.0224	0.0257	boreo-montane
<i>Elophos vittaria</i>			0.0624	boreo-montane
<i>Erebia ligea</i>			0.0218	boreo-montane
<i>Eudonia murana</i>			0.0220	boreo-montane
<i>Eudonia sudetica</i>			0.0309	boreo-montane
<i>Eupithecia conterminata</i>		0.0295	0.0299	boreo-montane
<i>Nemapogon wolffiella/ koenigi</i>	0.0032	0.0039		boreo-montane
<i>Parnassius apollo</i>		0.0217	0.0222	boreo-montane
<i>Rheumaptera hastata</i>		0.0208	0.0205	boreo-montane
<i>Xestia speciosa</i>	0.0235	0.0238	0.0243	boreo-montane

4.5. Mean of intraspecific pairwise distances within northern and southern regions of the two distributions

Regardless the distribution type, the southern population group show significantly higher internal genetic distances compared to the northern populations (Table 4, Figure 4). Among the three types of calculations, the *All* exhibits the highest mean intraspecific distance, ranging from 0.00 to 0.045 (Figure 4). The *One per site* calculation shows slightly higher internal distances, ranging from 0.00 to 0.034, compared to the *No duplicates* calculation, which ranges from 0.00 to 0.015.

Table 4: Results of Wilcoxon's matched-pairs signed-ranks test: Using species as units of analysis and comparing northern and southern mean pairwise distances as response variables.

Calculation type	v-statistic	p-values
<i>All</i>	1582	0.0028
<i>One per site</i>	397	0.0018
<i>No duplicates</i>	144	0.0425

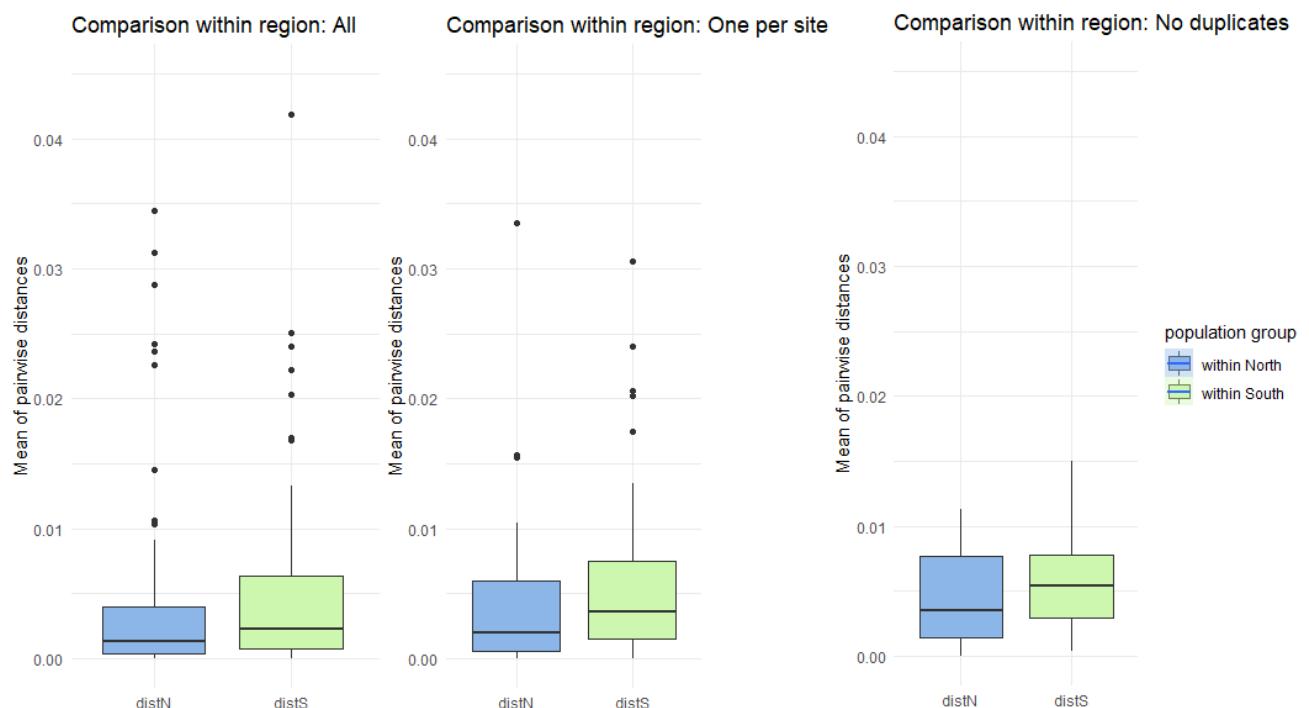


Figure 4: Comparing the pairwise distance within northern and southern regions of European Lepidopteran species with arctic-alpine and boreo-montane distributions: Mean within-region intra-specific divergences of species within northern distances (blue) and within southern distances (green) distribution.

5. Discussion

5.1. The intraspecific genetic distance between populations in the northern and southern regions of the two distribution types

Few studies have thus far more broadly examined the genetic dimension of European disjunctive distribution patterns in insects (Ehl et al., 2020; Maresova et al., 2019; Schmitt, 2007; Schmitt, 2009; Schmitt, 2020). In this thesis, the genetic consequences of disjunctive distribution patterns among European Lepidoptera of arctic-alpine and boreo-montane distribution have been investigated in a comparative framework.

Since arctic-alpine and boreo-montane distributions have different histories of origin and can be clearly separated despite their similarities (Schmitt, 2020), the question arose whether there is a difference between the two distribution types in terms of genetic differences between the regional populations and how pronounced these are.

Indeed, I observed differences between the intraspecific genetic distances, of both between and within the northern and southern populations in all calculation types. Further, genetic distances between the northern and southern populations are higher than within those populations. Furthermore, as expected the mean intraspecific divergence between populations inhabiting both regions is greater for arctic-alpine species than for the boreo-montane ones (Figure 2). However, this rather small difference could only be retrieved after excluding all biases resulting from multiple records per site, since these cases of 'pseudo-replication' obscured any patterns in the other two analytical approaches.

Higher genetic differentiation among arctic-alpine species compared to boreo-montane species can be attributed to a combination of different factors such as geographic barriers, historical processes, and ecological conditions (Ehl et al., 2020; Habel et al., 2010; Schmitt, 2020). Species with arctic-alpine distribution often inhabit extreme environments (like very low temperatures) at high latitudes or elevations, where they may be subject to strong environmental gradients and limited gene flow (Schmitt, 2020). In addition to the isolation of populations due to habitat fragmentation with different geographic regions, the challenging environmental conditions they are exposed to also lead to increased genetic differentiation between northern and southern populations (Pellissier et al. 2013; Schmitt, 2020). This genetic differentiation can also be seen in both animal and plant species in arctic-alpine environment, including wolf spiders of the *Pardosa saltuaria* group, which have a mtDNA lineage that occurs in the Alps, the Tatra Mountains, the low mountain ranges of the Ba-

varian Forest, the Krkonoše Mountains and in Scandinavia. However, in addition to this line, own genetic lineages for the Pyrenees as well as for the Eastern Balkan high mountains could be identified (Muster and Berendonk, 2006). The study by Alvarez et al. (2012) investigated the genetic structure of the snow Gentian (*Gentiana nivalis*) and revealed the presence of four distinct genetic lineages. Notably, one of these lineages exhibited a widespread distribution across different regions in Europe, including the Pyrenees, Jura, Carpathian arc, Scandinavia, and Iceland. This genetic differentiation and distribution pattern indicate possible differentiation and adaptation to various northern and southern populations. The presence of multiple genetic lineages suggests that the snow Gentian experienced limited gene flow and possibly underwent historical range shifts, resulting in unique genetic clusters across its distribution range (Alvarez et al., 2012).

In contrast, boreo-montane species usually inhabit more contiguous areas within the boreal forest biome. Their distribution of these species is influenced by environmental gradients at high latitudes or altitudes than by latitudinal gradients (Harbel et al., 2010; Schmitt, 2020). Although genetic differentiation has been observed in certain boreo-montane species, such as Lepidoptera species like *Lycaena helle*, and plant species like *Polygonatum verticillatum*, they are still underrepresented in the existing literature (Kramp et al., 2009; Maresova et al., 2019).

These differences in representation can contribute to lower levels of genetic differentiation between northern and southern populations of boreo-montane species compared to arctic-alpine species. The unique environmental conditions and fragmented habitats of arctic-alpine regions often result in greater isolation and increased genetic differentiation.

In general, greater genetic diversity is observed in the southern sub-areas than in the north, suggesting that more genotypes might have survived in the glacial refugia and became impoverished during the postglacial recolonization of the northern parts of the area (Schmitt et al. 2010; Schmitt, 2020). This pattern is supported by the results of the current study, where despite the distribution type the southern population group has significantly higher internal genetic distances than northern populations (Figure 4, Table 4).

However, one should not generalize these trends to all species as there could be exceptions depending on the species and its evolutionary history. Factors such as dispersal ability, historical range shifts, and local adaptations may also play a role in influencing genetic differentiation between populations of both boreo-montane and arctic-alpine species (Jermakowicz et al., 2015; Schmitt, 2020). Detailed genetic studies of species are needed for a better understanding of population structure and genetic differences.

5.2. Correlation of species traits and the intraspecific pairwise distances

According to my results, no significant patterns were observed (Table 4). As can be seen in Figure 4 the scatter of the pairwise between-region distances is broad for most traits, which could be a reason why no clear patterns were noticeable. Such intraspecific genetic variation in mtDNA is not easy to be explained by different species traits, which could be caused by the non-neutral nature of mtDNA variation, the erratic mutation rate, and strong fluctuations in population sizes in historical times, affecting mtDNA polymorphism (Dapporto et al., 2019).

5.3. Species with high genetic differentiation

Most species with a boreo-montane or arctic-alpine distribution have a low intraspecific divergence between regions, as expected if these populations are considered being conspecific. In only 18 out of 95 species substantial intraspecific distances around or above the 2% threshold were found. One of those is the arctic-alpine and circumpolar species *Caryocolum pullatella* (Table 3). In all different calculations, my results showed over 2% intraspecific genetic distance between northern and southern populations. This correlates the study of Huemer et al. (2018), who identified two DNA barcode clusters with allopatric distributions between central/south-eastern Europe compared to northern Europe/southern Siberia. Other studies also showed that this species has an extraordinary genetic variation across its Holarctic range (Huemer and Karsholt, 2020; Mutanen et al. 2012).

Rheumaptera subhastata shows also a high intraspecific genetic distance that can be explained by the existence of two major intraspecific clusters (Hausmann and Viidalepp, 2012; Mutanen et al., 2012). As mentioned by Mutanen et al. (2012) *R. subhastata* may indeed rather represent two distinct cryptic species. In this case, for the Nordic populations the taxon name *R. moestata* is available, whereas the nominotypical *R. subhastata* comes from Central Europe (Hausmann and Viidalepp, 2012).

Earlier analyses of the boreo-montane Holarctic species *Colias palaeno* have already shown that there is genetic differentiation among their European population, even if this differentiation is moderately low for the mtDNA data (Kramp et al., 2016). The mitochondrial haplotype network indicates a recent range expansion reflecting a moderate differentiation. This can be interpreted as the result of the existence of a continuous Würm glacial distribution in Central Europe with a secondary separation during this Last Glacial Maximum into a southwestern and a northeastern frag-

ment, which brought a subsequent moderate differentiation (Kramp et al., 2016). This rather weak differentiation can also be recognized in the results of this thesis (Table 3).

Although, some of my results corroborate those of other studies, there are also discrepancies in some species. Among others, there are taxa that have already been taxonomically separated into distinct species and recognized as such, but at least do not yet show these differences between the northern and southern regions of the arctic-alpine and boreo-montane distribution. For example, in this work no such separation into northern and southern populations was found in the species complex of *Erebia medusa* and *E. polaris*. In this particular species complex, the main species is *E. medusa*, which belongs to the so-called *medusa* group. Through the analysis of CO1 sequences, it was discovered that *E. medusa* exhibits significant variability and contains distinct lineages specific to different geographic regions (Mutanen et al. 2012; Šemeláková et al., 2013).

To obtain a clear species delimitation, specific in-depth analyzes of each case using a larger number of sequences and genes would be necessary. This could also explain why high intraspecific sequence divergence occurs in these species. Among other things, it could be evidence of Wolbachia infection (which can cause selective spreading of the mitochondrial genome) or an indication of taxonomic problems such as misidentified specimens in data repositories or overlooked cryptic taxa (Huemer et al., 2014; Huemer and Karsholt, 2018). Anyhow, depending on the method of molecular species delimitation as well as the taxonomic classification, according to the taxonomist's opinion (such as "splitters" vs. "lumpers"), some will conclude that the mentioned taxa can be separated into different species or alternatively should still be seen as populations within the same species (Luo et al., 2018; Matos-Maraví et al., 2019; Zachos, 2016). Not all species considered in this thesis had a high intraspecific divergence between regions. Many species had a low number of haplotypes, which is evident from the significantly reduced sequence count in the calculation without duplicates since only one sequence per haplotype was used in this form of calculation. A low number of haplotypes can have a negative effect on delimitation efficiency (Magoga et al., 2021). Even if, through haplotypes, the genetic variation will be better represented, it can blur the differences between species (Magoga et al., 2021). However, a clear delimitation of species is essential for many field in biology, including ecology and conservation science and practice (Petit and Excoffier, 2009).

5.4. Conclusion and conservational aspects

Knowledge of species delimitation and understanding of changes in biogeographic patterns are important components for determining effective conservation measures (Kramp et al., 2016). Recent climate-driven changes are considered to be responsible for species distribution shifts (Habel et al., 2010). Such climate-driven changes are also noticeable in cold-adapted organisms. For example, various species with arctic-alpine and boreo-montane distribution patterns have migrated from lower to higher elevations due to global temperature increases (Habel et al., 2010, Minter et al., 2020; Parmesan, 2006). Especially cold-adapted species of the highest elevations may eventually reach the elevation limits and cannot respond any further to the continuous temperature increases (Habel et al., 2010). However, some of them will not be able to adapt as quickly as others and become extinct because of these rapid environmental changes. Despite some species being resilient to changing environmental conditions, it is likely that there will still be a considerable loss of such species alongside the ongoing climate change (Schmitt, 2020). Therefore, maintaining intraspecific genetic variation is an important goal for biodiversity conservation. In this thesis, it was shown that arctic-alpine species have significantly higher mean pairwise distances between northern and southern regions than boreo-montane species, at least when only one sequence per haplotype is used. Which in turn has an influence on the species delimitation as has been shown at least in a few species with high intraspecific differences, which may lead to a reduction in the ability of individuals to use local resources and tolerate environmental stress (Dincă et al., 2018). Furthermore, the count and conservation status of species are of great significance to conservationists and policy-makers. Species play a crucial role in prioritizing conservation actions and shaping national and international laws, particularly in terms of habitat protection (Tobias et al., 2010). Preserving habitats is a valuable conservation strategy that has been recognized by experts in the field (Bickford et al., 2007; Marín et al., 2021). The observation of genetic variation of species in combination with changes in distribution patterns is an important part of conservation. However, more research is needed to clarify changes in the disjunct arctic-alpine and boreo-montane distribution.

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7. Appendix

7.1. Zusammenfassung

Bislang haben sich nur wenige Studien mit den genetischen Folgen disjunkter Verbreitungsmuster in Europa über eine größere Zahl von Arten hinweg befasst. Das arktisch-alpine Muster (das bei vielen kälteangepassten Organismen zu beobachten ist) lässt sich durch die postglaziale Verbreitung von Organismen erklären, die an ehemalige eiszeitliche Steppen und Tundren gebunden sind. Ein ähnliches, aber weniger stark disjunktes Verbreitungsbild weisen boreo-montane Organismen auf, die auf Nadelwälder in montanen und subalpinen Regionen in Mittel- oder Südeuropa sowie in der borealen Zone beschränkt sind. Vorhandene Studien beschränken sich entweder auf Fallstudien zu ausgewählten Schwerpunktarten, auf theoretische Übersichten oder auf makroökologische Vergleiche auf grober Skala. Ziel dieser Arbeit ist es, die genetischen Folgen der disjunktten Verbreitungsmuster europäischer Lepidopteren zu untersuchen. Für diese Studie wurde die Hypothese getestet, dass die intraspezifische genetische Differenzierung zwischen nördlichen und südlichen Populationen bei arktisch-alpinen Arten im Durchschnitt stärker ausgeprägt ist als bei boreo-montanen Arten. 36 arktisch-alpine und 78 boreo-montane Arten aus Europa wurden anhand der veröffentlichten Literatur identifiziert. Sequenzen der Cytochromoxidase-Untereinheit 1 (CO1) der ausgewählten Arten wurden aus der BOLD-Datenbank bezogen. Intraspezifische Divergenzen wurden anhand der paarweisen Kimura-2-Parameter-Distanzen bewertet. Wie erwartet wiesen die arktisch-alpinen Arten eine höhere mittlere intraspezifische Divergenz zwischen den Populationen auf als die boreo-montanen Arten. Darüber hinaus wurden für alle Berechnungstypen signifikante Unterschiede in den intraspezifischen genetischen Abständen zwischen den nördlichen und südlichen Populationen festgestellt. Außerdem wurde festgestellt, dass die genetischen Abstände zwischen den nördlichen und südlichen Populationen größer sind als innerhalb der Populationen. Bei 18 der 99 untersuchten Arten mit arktisch-alpiner und boreo-montaner Verbreitung betrug der durchschnittliche intraspezifische genetische Abstand zwischen nördlichen und südlichen Populationen mehr als 0,02, was auf eine noch nicht erkannte kryptische Vielfalt bei diesen Arten hinweist.

Schlüsselwörter: arktisch-alpine, boreo-montane, disjunkte Verbreitung, intraspezifische Variabilität, Artabgrenzung, kryptische Diversität

Table 1: Lepidoptera species from Europe with a disjunctive arctic-alpine and boreo-montane distribution. List of species with suitable sequence data for the two distribution types, the synonyms of each species, and the reference to each species confirming the distribution allocation.

Family	Genusname	Speciesname	BIN-URI	Synonyms	distribution type	Literatur
Tortricidae	<i>Aethes</i>	<i>deutschiana</i>	BOLD:AAB4419 BOLD:AAB4420, BOLD:ACE5515 BOLD:ACE5553 BOLD:ACE5554 BOLD:ACJ1175	<i>Troxis deutschiana</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214 .
Lycaenidae	<i>Agriades</i>	<i>glandon</i>	BOLD:AAA5321	<i>Agrioades aquilo</i> , <i>Plebejus glandon</i> , <i>Agriades glandon</i> subsp. <i>aquilina</i> , <i>Agriades glandon</i> subsp. <i>bavarica</i> , <i>Agriades glandon</i> subsp. <i>dealbata</i> , <i>Agriades glandon</i> subsp. <i>gigantalpina</i> , <i>Agriades glandon</i> subsp. <i>glandon</i> , <i>Agriades glandon</i> . <i>magnaglandon</i> , <i>Agriades glandon</i> subsp. <i>marlene</i> , <i>Agriades glandon</i> subsp. <i>oberthuri</i> , <i>Agriades glandon</i> subsp. <i>orbitulinus</i> , <i>Lycaena nevadensis</i> , <i>Lycaena orbitulus</i> , <i>Lycaena orbitulus</i> subsp. <i>aquilina</i> , <i>Lycaena orbitulus</i> subsp. <i>bavarica</i> , <i>Lycaena orbitulus</i> subsp. <i>dardanus</i> , <i>Lycaena orbitulus</i> subsp. <i>jaloka</i> , <i>Lycaena orbitulus</i> subsp. <i>rebeli</i> , <i>Lycaena orbitulus</i> subsp. <i>tartarus</i> , <i>Lycaena orbitulus</i> subsp. <i>walli</i> , <i>Papilio glandon</i> , <i>Papilio orbitulus</i> , <i>Plebeius glandon</i> , <i>Polyommatus glandon</i>	arctic-alpine	Varga, Z. S., and Schmitt, T., (2008). Types of oreal and oreotundral disjunctions in the western Palearctic. Biological Journal of the Linnean Society, 93(2), 415-430. https://doi.org/10.1111/j.1095-8312.2007.00934.x
Noctuidae	<i>Agrotis</i>	<i>fatidica</i>	BOLD:AAA1629	<i>Noctua fatidica</i>	arctic-alpine	Wiesmair, B.J., (2015). Die Artenvielfalt der Ordnung der Lepidoptera der subalpinen und alpinen Zone des Dobratsch: mit zusätzlichen Untersuchungen der Populationsgenetik ausgewählter Arten. MSc thesis, Univ. Graz (Austria).

Noctuidae	<i>Anarta</i>	<i>melanopa</i>	BOLD:AAF8108	<i>Noctua melanopa</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214 . Wiesmair, B.J. (2015). Die Artenvielfalt der Ordnung der Lepidoptera der subalpinen und alpinen Zone des Dobratsch : mit zusätzlichen Untersuchungen der Populationsgenetik ausgewählter Arten. MSc thesis, Univ. Graz (Austria). Skou, P. (1991). Nordens Ugler. Handbog over de i Danmark, Norge, Sverige, Finland og Island forekommende arter af Herminiiidae og Noctuidae (Lepidoptera). Stenstrup: Apollo Books. https://doi.org/10.1002/mmnd.19920390128
Noctuidae	<i>Apamea</i>	<i>maillardi</i>	BOLD:ACE5998 BOLD:AAA5797	<i>Hadena maillardi, Noctua maillardi</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214 .
Tortricidae	<i>Argyroploce</i>	<i>noricana</i>	BOLD:AAD8744	<i>Troxis noricana, Paedisca noricana, Olethreuts noricana</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214 . Razowski, J., (2003): Tortricidae (Lepidoptera) of Europe 2 Olethreutinae (1.st ed.). Bratislava: Slamka.
Nymphalidae	<i>Boloria</i>	<i>napaea</i>	BOLD:AAA9406	<i>Argynnis isis, Argynnis napaea, Argynnis pales subsp. brogotarus, Boloria atroviolacea, Boloria atroviridis, Boloria frigida, Boloria napaea subsp. brogotarus, Boloria napaea subsp. napaea, Papilio dirphya, Papilio isis, Papilio napaea</i>	arctic-alpine	Varga, Z. S., and Schmitt, T., (2008). Types of oreal and oreotundral disjunctions in the western Palearctic. Biological Journal of the Linnean Society, 93(2), 415-430. https://doi.org/10.1111/j.1095-8312.2007.00934.x Tshikolovets, V. (2011). Butterflies of Europe & the mediterranean area. Pardubice: Tshikolovets. 415–430. DOI: 10.1111/j.1095-8312.2007.00934.x.
Gracillariidae	<i>Callisto</i>	<i>coffeella</i>	BOLD:AAE0738	<i>Oecophora interruptella, Annickia alpicola Gibeaux</i>	arctic-alpine	Buszko, J., and Barniak, E. (1988). Studies on the mining Lepidoptera of Poland, III., Species of the genus Callisto STEPH. (Gracillariidae), Polskie pismo entomologiczne, 57(4), 783-786.
Gelechiidae	<i>Caryocolum</i>	<i>petrophila</i>	BOLD:AAO3809	<i>Gelechia petrophila, Phthorimaea kemnerella</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214 . Huemer, P., and Karsholt, O. (1999). Microlepidoptera of Europe 3 Gelechiidae I (Gelechiinae: Teleiodini, Gelechiini). Leiden: Apollo Books Brill.

Gelechiidae	<i>Caryocolum</i>	<i>pullatella</i>	BOLD:AAC1597 BOLD:AAC1598 BOLD:AAC1599 BOLD:AAH4284 BOLD:AAH6281 BOLD:ACI5465	<i>Gelechia agricolaris</i> , <i>Gelechia pullatella</i> , <i>Gelechia subtractella</i> , <i>Phthorimaea livoniella</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214 .
Tortricidae	<i>Epinotia</i>	<i>mercuriana</i>	BOLD:AAE1186 BOLD:AAE1187	<i>Troxis mercuriana</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214 .
Nymphalidae	<i>Erebia</i>	<i>medusa</i>	BOLD:AAB1340 (<i>Erebia me-dusa</i>)	<i>Erebia polaris</i> , <i>Erebia alpestris</i> , <i>Erebia brigobanna</i> , <i>Erebia grisea</i> , <i>Erebia infrabosparsa</i> , <i>Erebia macromata</i> , <i>Erebia manchurica</i> , <i>Erebia masculine</i> , <i>Erebia medusa</i> subsp. <i>brigobanna</i> , <i>Erebia medusa</i> subsp. <i>Hippomedusa</i> , <i>Erebia medusa</i> subsp. <i>hyperapennina</i> , <i>Erebia medusa</i> subsp. <i>medusa</i> , <i>Erebia paradoxa</i> , <i>Erebia parumgenerosa</i> , <i>Erebia pulchrappennina</i> , <i>Erebia sylvatica</i> , <i>Hipparchia hippomedusa</i> , <i>Hipparchia medusa</i> subsp. <i>Hippomedusa</i> , <i>Papilio medusa</i> , <i>Papilio mergus</i> , <i>Papilio psodea</i>	arctic-alpine	Schmitt, T., and Seitz, A. (2001). Intraspecific allozymatic differentiation reveals the glacial refugia and the postglacial expansions of European <i>Erebia medusa</i> (Lepidoptera, Nymphalidae). Biological Journal of the Linnean Society, 74(4), 429–458. DOI: https://doi.org/10.1006/bijl.2001.0584
Nymphalidae	<i>Erebia</i>	<i>pandrose</i>	BOLD:AAB3454, BOLD:ADR3010	<i>Papilio pandrose</i>	arctic-alpine	Varga, Z. S., and Schmitt, T., (2008). Types of oreal and oreo-tundral disjunctions in the western Palearctic. Biological Journal of the Linnean Society, 93(2), 415-430. https://doi.org/10.1111/j.1095-8312.2007.00934.x Tshikolovets, V. (2011). Butterflies of Europe & the mediterranean area. Pardubice: Tshikolovets. 415–430. doi: 10.1111/j.1095-8312.2007.00934.x.
Lasiocampidae	<i>Eriogaster</i>	<i>arbusculae</i>	BOLD:AAE2337	<i>Gastropacha arbusculae</i>	arctic-alpine	Aarvik, Leif, Lars Ove, Hansen, and Kononenko, V. (2009) Norges sommerfugler, Håndbok over Norges dagsommerfugler og nattsvermere. Norsk entomologisk forening og Naturhistorisk museum, Oslo
Erebidae	<i>Apantesis</i>	<i>quenseli</i>	BOLD:AAB2979, BOLD:AAA4398, BOLD:ABZ6253, BOLD:ACF3388	<i>Bombyx quenseli</i> , <i>Bombyx qvenseli</i> , <i>Grammia qvenseli</i> , <i>Orodemnias quenseli</i> , <i>Apantesis quenseli</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214 . Varga, Z. S., and Schmitt, T., (2008). Types of oreal and oreo-tundral disjunctions in the western Palearctic. Biological Journal of the Linnean Society, 93(2), 415-430. https://doi.org/10.1111/j.1095-8312.2007.00934.x

Tortricidae	<i>Grapholita</i>	<i>aureolana</i>	BOLD:AAE7252	<i>Cydia aureolana</i> , <i>Grapholitha aureolana</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214 .
Erebidae	<i>Chelis</i>	<i>puengeleri</i>	BOLD:AAE5387	<i>Holoarctica cervini</i> , <i>Chelis puengeleri</i> , <i>Orodemnias fridolini</i> , <i>Orodemnias puengeleri</i> , <i>Chelis cervine</i> , <i>Chelis cervini</i> subsp. <i>cervine</i> , <i>Holoarctia cervini</i> subsp. <i>cervine</i> , <i>Nemeophila cervine</i> , <i>Orodemnias cervini</i> subsp. <i>Scriniensis</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214 .
Incurvariidae	<i>Incurvaria</i>	<i>vetuella</i>	BOLD:AAD4279 BOLD:AAP5641 BOLD:ACI3470	<i>Adela vetuella</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214 .
Geometridae	<i>Macaria</i>	<i>fusca</i>	BOLD:AAC7749	<i>Bombyx fusca</i> , <i>Geometra fusca</i>	arctic-alpine	Skou, P., Sihvonen, P. and Hausmann, A. (2015). The geometrid moths of Europe: Volume 5, Subfamily Ennominae I (Abraxini, Apeirini, Baptini, Caberini, Campaeini, Cassymini, Colotoini, Ennomini, Epionini, Gnophini (part), Hypochrosini, Lithinini, Macariini, Prosopolophini, Theriiini and 34 species of uncertain tribus association) (The Geometrid Moths of Europe). Leiden: Brill.
Crambidae	<i>Metaxmeste</i>	<i>phrygialis</i>	BOLD:AAE7685	<i>Hercyna rupicolalis</i> , <i>Pyralis phrygialis</i>	arctic-alpine	Slamka, F., (2006). Pyraloidea of Europe: identification, distribution, habitat, biology = Pyraloidea Europas (Lepidoptera). Bratislava: Slamka.
Pterophoridae	<i>Oidaematophorus</i>	<i>rogenhoferi</i>	BOLD:AAE5830	<i>Pterophorus rogenhoferi</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214
Lycaenidae	<i>Agriades</i>	<i>orbitulus</i>	BOLD:AAE5039	<i>Agriades orbitulus</i>	arctic-alpine	Tshikolovets, V., (2011). Butterflies of Europe & the mediterranean area. Pardubice: Tshikolovets.
Geometridae	<i>Psodos</i>	<i>coracina</i>	BOLD:AAD3142	<i>Phalaena hirtata</i> , <i>Psodos chaonaria</i> , <i>Psodos hirtata</i> , <i>Glacies coracina</i>	arctic-alpine	Müller, B., Erlacher, S., Hausmann, A., Rajaei, H., Sihvonen, P. and Skou, P., (2019). The geometrid moths of Europe: Volume 6, Part, 1. Subfamily Ennominae: II (Boarmiini, Gnophini, additions to previous volumes), Netherlands: Brill.
Hesperiidae	<i>Pyrgus</i>	<i>andromedae</i>	BOLD:ACE9283	<i>Hesperia andromedae</i> , <i>Hesperia perseus</i> , <i>Hesperia striata</i> , <i>Pyrgus manca</i> , <i>Syrichthus andromedae</i> , <i>Syrichthus borealis</i> , <i>Syrichthus andromedae</i>	arctic-alpine	Willner, W., (2017). Taschenlexikon der Schmetterlinge Europas: Alle Tagfalter im Porträt, Wiebelsheim: Quelle & Meyer Verlag

Pterophoridae	<i>Stenoptilia</i>	<i>islandicus</i>	BOLD:AAF3619	<i>Pterophorus borealis</i> , <i>Pterophorus islandicus</i> , <i>Pterophorus pelidnodactylus</i> subsp. <i>Borealis</i> , <i>Pterophorus pelidnodactylus</i> var. <i>borealis</i> , <i>Stenoptilia pelidnodactylus</i> subsp. <i>alpinalis</i>	arctic-alpine	Huemer, P., and Wiesmair, B. (2016). Schmetterlinge (Lepidoptera) des Altai-Gebirges (Südsibirien, Russland). Eindrücke einer internationalen Expedition im Spätsommer 2016.
Noctuidae	<i>Syngrapha</i>	<i>hochenwarthi</i>	BOLD:ABX4966	<i>Calophasia hochenwarthi</i> , <i>Phalaena hochenwarthi</i> , <i>Plusia hochenwarthi</i> , <i>Syngrapha hochenwarthi</i>	arctic-alpine	Varga, Z. S., and Schmitt, T., (2008). Types of oreal and oreo-tundral disjunctions in the western Palearctic. Biological Journal of the Linnean Society, 93(2), 415-430. https://doi.org/10.1111/j.1095-8312.2007.00934.x
Noctuidae	<i>Xestia</i>	<i>alpicola</i>	BOLD:ABZ1718	<i>Hadena alpicola</i>	arctic-alpine	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214
Zygaenidae	<i>Zygaena</i>	<i>exulans</i>	BOLD:AAD7474	<i>phinx exulans</i> , <i>Zygaena analiconfluens</i> , <i>Zygaena analielongata</i> , <i>Zygaena apicaliconfluens</i> , <i>Zygaena apicalielongata</i> , <i>Zygaena clara</i> , <i>Zygaena confluens</i> , <i>Zygaena costaliconfluens</i> , <i>Zygaena costalielongata</i> , <i>Zygaena crassimaculata</i> , <i>Zygaena exilioides</i> , <i>Zygaena flavidornis</i> , <i>Zygaena fulva</i>	arctic-alpine	Varga, Z. S., and Schmitt, T., (2008). Types of oreal and oreo-tundral disjunctions in the western Palearctic. Biological Journal of the Linnean Society, 93(2), 415-430. https://doi.org/10.1111/j.1095-8312.2007.00934.x
Geometridae	<i>Acasis</i>	<i>appensata</i>	BOLD:ABX5594 BOLD:ACE4671	<i>Acidalia appensata</i>	boreo-montane	Hausmann, A., and Viidalepp, J., (2012). The geometrid moths of Europe Volume 3, Subfamily: Larentiinae I (Cataclysmini, Xanthorhoini, Euphyiini, Larentiini, Hydriomenini, Stamnodini, Cidariini, Operophterini, Astenini, Phileremini, Rheumapterini, Solitaneini, Melanthiini, Chesladini, Trichopterygini): Subfamily Sterrhinae (II) (Lythriini), Vester Skerninge: Apollo Books.
Tortricidae	<i>Acleris</i>	<i>maccana</i>	BOLD:AAA8391	<i>Teras maccana</i>	boreo-montane	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214
Noctuidae	<i>Acronicta</i>	<i>cinerea</i>	BOLD:AAC6993	<i>Acronicta euphorbiae</i> , <i>Acronicta euphorbiae</i> , <i>Acronicta myricae</i> , <i>Phalaena cinerea</i>	boreo-montane	Rákosy, L., and Giesenleitner, F., (1996): Die Noctuiden Rumäniens: (Lepidoptera noctuidae). Linz: Land Oberösterreich, OÖ. Landesmuseum.
Geometridae	<i>Alcis</i>	<i>jubata</i>	BOLD:AAD8767	<i>Phalaena jubata</i>	boreo-montane	Müller, B., Erlacher, S., Hausmann, A., Rajaei, H., Sihvonen ,P., and Skou, P., (2019): The geometrid moths of Europe. : Volume 6, Part 1, Subfamily Ennominae II (Boarmiini, Gnophini, additions to previous volumes), Netherlands: Brill.

Noctuidae	<i>Amphyipyra</i>	<i>perflua</i>	BOLD:AAD2299	<i>Noctua perflua</i>	boreo-montane	Skou, P. (1991). Nordens Ugler. Handbog over de i Danmark, Norge, Sverige, Finland og Island forekommende arter af Herminiidae og Noctuidae (Lepidoptera). Stenstrup: Apollo Books. https://doi.org/10.1002/mmnd.19920390128 Kanarskyi, Y., Geryak, Y., and Lyashenko, E., (2011), Ecogeographic structure of the moth fauna (Lepidoptera, Drepanoidea, Bombycoidea, Noctuoidea) in upper Tisa river basin and adjacent areas (Ukraine). Transylvanian Review of Systematical and Ecological Research 11. 143.
Tortricidae	<i>Ancylis</i>	<i>myrtillana</i>	BOLD:ABZ7857 BOLD:ACE7743	<i>Ancylis vacciniana, Leptia myrtillana, Phoxopteris myrtillana, Phoxopterix myrtillana, Phoxopteryx dentana</i>	boreo-montane	Karisch T., (2014). Die Schmetterlinge (Lepidoptera) im Hochharz Sachsen-Anhalts: unter besonderer Berücksichtigung der kennzeichnenden Arten der Fauna-Flora-Habitat-Lebensraumtypen, Universitäts-und Landesbibliothek Sachsen-Anhalt.
Noctuidae	<i>Apamea</i>	<i>furva</i>	BOLD:AAC7157	<i>Abromias furva, Hadena furva, Noctua furva</i>	boreo-montane	Skou, P. (1991). Nordens Ugler. Handbog over de i Danmark, Norge, Sverige, Finland og Island forekommende arter af Herminiidae og Noctuidae (Lepidoptera). Stenstrup: Apollo Books. https://doi.org/10.1002/mmnd.19920390128 Kanarskyi, Y., Geryak, Y., and Lyashenko, E., (2011), Ecogeographic structure of the moth fauna (Lepidoptera, Drepanoidea, Bombycoidea, Noctuoidea) in upper Tisa river basin and adjacent areas (Ukraine). Transylvanian Review of Systematical and Ecological Research 11. 143.
Noctuidae	<i>Apamea</i>	<i>rubrirena</i>	BOLD:ACE5999	<i>Abromias rubrirena, Apamea marginipicta, Hadena rubrirena, Mamestra rubrirena</i>	boreo-montane	Karisch, T., (1998). Zur Schmetterlingsfauna der Moore des Brockengebietes (Insecta: Lepidoptera), Hercynia NF (Halle), 31, 229-268.
Tortricidae	<i>Argyroploce</i>	<i>arbutella</i>	BOLD:AAF6741	<i>Troxis arbutella, Stictea arbutella</i>	boreo-montane	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214
Lycaenidae	<i>Aricia</i>	<i>nicias</i>	BOLD:ABY4540 BOLD:ABZ0886	<i>Argus donzelii, Aricia donzelii, Aricia nicias, Aricia nicias, Aricia nicias, Aricia nicias, Lycaena donzelii, Plebeius donzeli, Plebejus donzelii, Polyommatus nicias, Pseudoaricia nicias Pseudoaricia nicias, Pseudoaricia nicias, Pseudoaricia nicias, Pseudoaricia nicias</i>	boreo-montane	Willner W., (2017). Taschenlexikon der Schmetterlinge Europas : Alle Tagfalter im Porträt, Wiebelsheim: Quelle & Meyer Verlag
Noctuidae	<i>Autographa</i>	<i>bractea</i>	BOLD:AAD2827	<i>Noctua bractea, Plusia bractea</i>	boreo-montane	Skou, P. (1991). Nordens Ugler. Handbog over de i Danmark, Norge, Sverige, Finland og Island forekommende arter af Herminiidae og Noctuidae (Lepidoptera). Stenstrup: Apollo Books. https://doi.org/10.1002/mmnd.19920390128 Kanarskyi, Y., Geryak, Y., and Lyashenko, E. (2011): Ecogeographic structure of the moth fauna (Lepidoptera, Drepanoidea,

						Bombycoidea, Noctuoidea) in upper Tisa river basin and adjacent areas (Ukraine). Transylvanian Review of Systematical and Ecological Research 11, 143.
Noctuidae	<i>Autographa</i>	<i>buraetica</i>	BOLD:AAA3990	<i>Plusia buraetica</i>	boreo-montane	Skou, P. (1991). Nordens Ugler. Handbog over de i Danmark, Norge, Sverige, Finland og Island forekommende arter af Hesperiidae og Noctuidae (Lepidoptera). Stenstrup: Apollo Books. https://doi.org/10.1002/mmnd.19920390128 Kanarskyi, Y., Geryak, Y., and Lyashenko, E., (2011), Ecogeographic structure of the moth fauna (Lepidoptera, Drepanoidea, Bombycoidea, Noctuoidea) in upper Tisa river basin and adjacent areas (Ukraine). Transylvanian Review of Systematical and Ecological Research 11: 143.
Nymphalidae	<i>Boloria</i>	<i>eunomia</i>	BOLD:ACB3899	<i>Boloria eunomia, Proclossiana eunomia</i>	boreo-montane	Habel, J. C., Schmitt, T., Meyer, M., Finger, A., Roedder, D., Assmann, T., and Zachos, F. E., (2010). Biogeography meets conservation: the genetic structure of the endangered lycaenid butterfly <i>Lycaena helle</i> (Denis & Schiffermüller, 1775), Biological Journal of the Linnean Society, 101(1), 155-168. https://doi.org/10.1111/j.1095-8312.2010.01471.x
Nymphalidae	<i>Boloria</i>	<i>thore</i>	BOLD:AAC1422 BOLD:ABZ5868	<i>Papilio thore, Argynnis thore, Brenthis thore, Clossiana thore</i>	boreo-montane	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214
Noctuidae	<i>Brachionycha</i>	<i>nubeculosa</i>	BOLD:AAE0860	<i>Asteroscopus nubeculosa, Bombyx nubeculosa, Phalaena nubeculosa</i>	boreo-montane	Rákosy, L., and Gusenleitner, F., (1996). Die Noctuiden Rumäniens: (Lepidoptera noctuidae), Linz: Land Oberösterreich, OÖ. Landesmuseum.
Geometridae	<i>Carsia</i>	<i>sororiata</i>	BOLD:AAC1640	<i>Carsia paludata, Geometra sororiata, Phalaena paludata</i>	boreo-montane	Hausmann, A., and Viidalepp, J., (2012). The geometrid moths of Europe: Volume 3, Subfamily Larentiinae I (Cataclysmini, Xanthorhoini, Euphyiini, Larentiini, Hydriomenini, Stamnodini, Cidariini, Operophterini, Asthenini, Phileremini, Rheumapterini, Solitaneini, Melanthiini, Chesladini, Trichopterygini): Subfamily Sterrhinae (II) (Lythriini), Vester Skerninge: Apollo Books.
Pyralidae	<i>Catastia</i>	<i>marginea</i>	BOLD:AAE9528	<i>Noctua marginata, Phalaena marginata</i>	boreo-montane	Slamka, F., (2019). Pyraloidea of Europe: identification, distribution, habitat, biology 4. Phycitinea, Part 1, 1. ed., Bratislava: Slamka.
Gelechiidae	<i>Chionodes</i>	<i>luctuella</i>	BOLD:AAD2579 BOLD:ABY8068	<i>Gelechia sauteriella, Phalaena luctuella</i>	boreo-montane	Huemer, P., and Karsholt, O. (1999). Microlepidoptera of Europe 3 Gelechiidae I (Gelechiinae: Teleiodini, Gelechiini). Leiden Apollo Books Brill.
Gelechiidae	<i>Chionodes</i>	<i>viduella</i>	BOLD:AAJ0096 BOLD:AAJ0121 BOLD:ACF2998 BOLD:ACF2999	<i>Gelechia labradoriella, Gelechia luctiferella, Tinea viduella, Tinea leucomella, Tinea viduella</i>	boreo-montane	Huemer, P., and Karsholt, O. (1999). Microlepidoptera of Europe u3 Gelechiidae I (Gelechiinae: Teleiodini, Gelechiini). Leiden Apollo Books Brill.

Pieridae	<i>Colias</i>	<i>palaeno</i>	BOLD:ABY4460	<i>Colias europomene</i> , <i>Colias palaeno</i> subsp. <i>Europome</i> , <i>Colias palaeno</i> subsp. <i>Jurassica</i> , <i>Colias palaeno</i> subsp. <i>Poktussani</i> , <i>Papilio europome</i> , <i>Papilio palaeno</i>	boreo-montane	Habel, J. C., Schmitt, T., Meyer, M., Finger, A., Roedder, D., Assmann, T., and Zachos, F. E., (2010). Biogeography meets conservation: the genetic structure of the endangered lycaenid butterfly <i>Lycaena helle</i> (Denis & Schiffermüller, 1775), Biological Journal of the Linnean Society, 101(1), 155-168. https://doi.org/10.1111/j.1095-8312.2010.01471.x
Geometridae	<i>Colostygia</i>	<i>turbata</i>	BOLD:AAC0785	<i>Cidaria turbaria</i> , <i>Geometra turbata</i> , <i>Larentia turbata</i> , <i>Melanippe turbaria</i>	boreo-montane	Hausmann, A., and Viidalepp, J., (2012). The geometrid moths of Europe Volume 3, Subfamily: Larentiinae I (Cataclysmini, Xanthorhoini, Euphyiini, Larentiini, Hydriomenini, Stamnodini, Cidariini, Operophterini, Asthenini, Phileremini, Rheumapterini, Solitaneini, Melanthiini, Chesladini, Trichopterygini): Subfamily Sterrhinae (II) (Lythriini), Vester Skerninge : Apollo Books.
Noctuidae	<i>Coranarta</i>	<i>cordigera</i>	BOLD:AAF1113	<i>Noctua cordigera</i>	boreo-montane	Yela, J., (2002). The internal genitalia as a taxonomic tool: description of the relict endemic moth, <i>Coranarta restricta</i> sp. n., from the Iberian Peninsula (Lepidoptera: Noctuidae: Hadeninae). Entomologica Fennica, 13(1), 1-12.
Crambidae	<i>Crambus</i>	<i>alienellus</i>	BOLD:AAB6451 BOLD:AAB6452	<i>Chilo zinckenellus</i> , <i>Crambus tigurinellus</i> , <i>Chilo ocellellus</i>	boreo-montane	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214
Noctuidae	<i>Cucullia</i>	<i>lactucae</i>	BOLD:AAF1930	<i>Noctua lactucae</i>	boreo-montane	Skou, P. (1991). Nordens Ugler. Handbog over de i Danmark, Norge, Sverige, Finland og Island forekommende arter af Herminiidae og Noctuidae (Lepidoptera). Stenstrup: Apollo Books. https://doi.org/10.1002/mmnd.19920390128 Kanarskyi, Y., Geryak, Y., and Lyashenko, E., (2011). Ecogeographic structure of the moth fauna (Lepidoptera, Drepanoidea, Bombycoidea, Noctuoidea) in upper Tisa river basin and adjacent areas (Ukraine). Transylvanian Review of Systematical and Ecological Research, (11), 143.
Elachistidae	<i>Elachista</i>	<i>albidella</i>	BOLD:AAE9972 BOLD:AAH4947 BOLD:ABX6815	<i>Biselachista albidella</i> , <i>Biselachista rhynchosporaella</i> , <i>Elachista rhynchosporaella</i>	boreo-montane	Karisch, T., (2014). Die Schmetterlinge (Lepidoptera) im Hochharz Sachsen-Anhalts: unter besonderer Berücksichtigung der kennzeichnenden Arten der Fauna-Flora-Habitat-Lebensraumtypen, Universitäts-und Landesbibliothek Sachsen-Anhalt.
Geometridae	<i>Entephria</i>	<i>nobilioria</i>	BOLD:AAB5559 BOLD:ABZ6762 BOLD:ACF5603	<i>Larentia nobiliaria</i>	boreo-montane	Müller, B., Erlacher, S., Hausmann, A., Rajaei, H., Sihvonen, P. and Skou, P., (2019). The geometrid moths of Europe: Volume 6, Part 1, Subfamily Ennominae II (Boarmiini, Gnophini, additions to previous volumes), Brill.

Geometridae	<i>Entephria</i>	<i>caesiata</i>	BOLD:AAB9028	<i>Geometra caesiata</i> , <i>Larentia caesiaria</i> , <i>Phaesylloides caesiaria</i>	boreo-montane	Hausmann, A., and Viidalepp, J., (2012). The geometrid moths of Europe: Volume 3, Subfamily: Larentiinae I (Cataclysmini, Xanthorhoini, Euphyiini, Larentiini, Hydriomenini, Stamnodini, Cidariini, Operophterini, Asthenini, Phileremini, Rheumapterini, Solitaneini, Melantheini, Chesladini, Trichopterygini): Subfamily Sterrhinae (II) (Lythriini), Vester Skerninge: Apollo Books.
Geometridae	<i>Entephria</i>	<i>flavicinctata</i>	BOLD:AAC5436	<i>Geometra flavicinctata</i> , <i>Larentia flavicincta</i> , <i>Larentia flavicinctaria</i> , <i>Phaesylloides flavicinctaria</i>	boreo-montane	Hausmann, A., and Viidalepp, J., (2012). The geometrid moths of Europe: Volume 3, Subfamily Larentiinae I (Cataclysmini, Xanthorhoini, Euphyiini, Larentiini, Hydriomenini, Stamnodini, Cidariini, Operophterini, Asthenini, Phileremini, Rheumapterini, Solitaneini, Melantheini, Chesladini, Trichopterygini): Subfamily Sterrhinae (II) (Lythriini), Vester Skerninge : Apollo Books.
Noctuidae	<i>Epipsilia</i>	<i>grisescens</i>	BOLD:AAF4729	<i>Agrotis grisescens</i> , <i>Noctua grisescens</i> , <i>Rhyacia grisescens</i>	boreo-montane	Steiner, A., and Ebert, G., (1998). Die Schmetterlinge Baden-Württembergs 7, Nachtfalter, 5. Allgemeiner Teil: Benutzerhinweise, Ergebnisse. Spezieller Teil: Noctuidae (Schluß). Stuttgart: Ulmer.
Nymphalidae	<i>Erebia</i>	<i>ligea</i>	BOLD:AAA8264	<i>Erebia albofasciata</i> , <i>Erebia altaica</i> , <i>Erebia apupillata</i> , <i>Erebia bieneri</i> , <i>Erebia czekelii</i> , <i>Erebia dovrensis</i> , <i>Erebia euryaloides</i> , <i>Erebia ligea</i> subsp. <i>carthusianorum</i> <i>Erebia macroscia</i> , <i>Erebia minuta</i> , <i>Erebia murasei</i> , <i>Erebia tenuifasciata</i> , <i>Erebia tenuifasciata</i> , <i>Erebia violaceofasciata</i> , <i>Papilio ligea</i> , <i>Satyrus ligea</i>	boreo-montane	Zapp, A., (2010). Montane Tagfalter im Rückzug: zur Chorologie und Ökologie von <i>Erebia ligea</i> (LINNAEUS, 1758) und <i>Lycaena virgaureae</i> (LINNAEUS, 1758) im Hunsrück (Rheinland-Pfalz, Saarland). Aus Natur und Landschaft im Saarland, Abh. DELATTINIA, 35(36), 455-485.
Noctuidae	<i>Eriopygodes</i>	<i>imbecilla</i>	BOLD:AAE1902		boreo-montane	Varga, Z. and Rákosy, L., (2007). Biodiversität der Karstgebiete im Karpatenbecken am Beispiel der Gross-Schmetterlingsfauna der Turzii-Schlucht bzw. des Aggteleker Karstgebietes. Entomol Rom, 12, 15-29; Skou, P. (1991). Nordens Ugler. Handbog over de i Danmark, Norge, Sverige, Finland og Island forekommende arter af Herminiidae og Noctuidae (Lepidoptera). Stenstrup: Apollo Books. https://doi.org/10.1002/mmnd.19920390128
Crambidae	<i>Eudonia</i>	<i>sudetica</i>	BOLD:AAB9089 BOLD:AAO2586	<i>Eudorea sudetica</i> , <i>Eudorea sudeticalis</i>	boreo-montane	Huemer, P., and Karsholt, O. (1999). Microlepidoptera of Europe 3 Gelechiidae I: (Gelechiinae: Teleiodini, Gelechiini). Leiden Apollo Books Brill.
Crambidae	<i>Eudonia</i>	<i>murana</i>	BOLD:AAB9086 BOLD:AAB9087 BOLD:ACI957	<i>Eudorea murana</i> , <i>Scoparia pseudomurana</i> , <i>Scoparia ranica</i>	boreo-montane	Huemer, P., and Karsholt, O. (1999). Microlepidoptera of Europe 3 Gelechiidae I : (Gelechiinae: Teleiodini, Gelechiini). Leiden Apollo Books Brill.
Yponomeutidae	<i>Euhyonomeutoides</i>	<i>albithoracellus</i>	BOLD:AAF7153	<i>Tinea rufella</i> , <i>Kesseleria rufella</i> , <i>Argyresthia rufella</i>	boreo-montane	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214

Eeometridae	<i>Eupithecia</i>	<i>cauchiata</i>	BOLD:AAD8535	<i>Larentia cauchiata</i>	boreo-montane	Hausmann, A., and Viidalepp, J., (2012). The geometrid moths of Europe: Volume 3, Subfamily: Larentiinae I (Cataclysmini, Xanthorhoini, Euphyiini, Larentiini, Hydriomenini, Stamnodini, Cidariini, Operophterini, Asthenini, Phileremini, Rheumapterini, Solitaneini, Melanthiini, Chesladini, Trichopterygini): Subfamily Sterrhinae (II) (Lythriini), Vester Skerninge : Apollo Books.
Geometridae	<i>Eupithecia</i>	<i>conterminata</i>	BOLD:AAD4722 BOLD:AAD4723 BOLD:ACV0190 BOLD:ADB8427 BOLD:ADF1792	<i>Larentia conterminata</i>	boreo-montane	Weidlich, M., (2008). Beitrag zur Lepidopteren-Fauna des Notia Pindos (Tringia-Massiv, Lákmos-Gebirge und Athamáno-Gebirge) in Griechenland mit Beschreibung von zwei neuen Arten sowie Angaben zur Köcherfliegen-(Trichoptera) und Schnakenfauna (Diptera: Tipulidae). Entomofauna, 29(27), 469-504. Mironov, V., and Hausmann, A., (2003). The geometrid moths of Europe: Vol. 4 Larentiinae 2: (Perizomini and Eupitheciini). Stenstrup: Apollo Books.
Noctuidae	<i>Euxoa</i>	<i>recussa</i>	BOLD:ACE9579	<i>Agrotis recussa</i> , <i>Agrotis telifera</i> Donzel, <i>Noctua recussa</i>	boreo-montane	Steiner, A., and Ebert, G., (1998). Die Schmetterlinge Baden-Württembergs 7, Nachtfalter, 5 Allgemeiner Teil: Benutzerhinweise, Ergebnisse. Spezieller Teil: Noctuidae (Schluß). Stuttgart: Ulmer.
Depressariidae	<i>Exaeretia</i>	<i>ciniflonella</i>	BOLD:AAD5010	<i>Depressaria ciniflonella</i> , <i>Depressaria smolandiae</i> , <i>Martyrhilda isa</i>	boreo-montane	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214
Geometridae	<i>Gnophos</i>	<i>obfuscata</i>	BOLD:ACE7309 BOLD:AAB8516 BOLD:AAB8517 BOLD:ABZ5475 BOLD:ACC5028	<i>Geometra limosaria</i> , <i>Geometra obfuscata</i> , <i>Gnophos myrtillata</i> , <i>Gnophos obfuscaria</i> , <i>Phalaena myrtillata</i>	boreo-montane	Müller, B., Erlacher, S., Hausmann, A., Rajaei, H., Sihvonen, P. and Skou, P., (2019). The geometrid moths of Europe: Volume 6, Part 1, Subfamily Ennominae II (Boarmiini, Gnophini, additions to previous volumes), Netherlands: Brill.
Geometridae	<i>Hydriomena</i>	<i>ruberata</i>	BOLD:AAA2035 BOLD:AAB6494	<i>Acidalia ruberata</i> , <i>Hydriomena ruberaria</i>	boreo-montane	Hausmann, A., and Viidalepp, J., (2012). The geometrid moths of Europe Volume 3, Subfamily: Larentiinae I (Cataclysmini, Xanthorhoini, Euphyiini, Larentiini, Hydriomenini, Stamnodini, Cidariini, Operophterini, Asthenini, Phileremini, Rheumapterini, Solitaneini, Melanthiini, Chesladini, Trichopterygini): Subfamily Sterrhinae (II) (Lythriini), Vester Skerninge: Apollo Books.
Noctuidae	<i>Hyppa</i>	<i>rectilinea</i>	BOLD:ABZ5210	<i>Phalaena rectilinea</i>	boreo-montane	Rákosi, L., and Gusenleitner, F., (1996). Die Noctuinen Rumäniens: (Lepidoptera noctuidae). Linz: Land Oberösterreich, OÖ. Landesmuseum.
Yponomeutidae	<i>Kessleria</i>	<i>fasciapennella</i>	BOLD:AAF3317	<i>Zelleria fasciapennella</i> , <i>Hofmannia fasciapennella</i>	boreo-montane	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214.

							https://doi.org/10.1371/journal.pone.0047214
Nymphalidae	<i>Lasiommata</i>	<i>petropolitana</i>	BOLD:AAC3112	<i>Lasiommata hiera</i>	boreo-montane	Tshikolovets, V., (2011). Butterflies of Europe & the mediterranean area. Pardubice: Tshikolovets.	
Noctuidae	<i>Lithophane</i>	<i>consocia</i>	BOLD:AAD9908	<i>Phalaena consocia</i>	boreo-montane	Rákosy, L. and Giesenleitner, F. (1996). Die Noctuiden Rumäniens: (Lepidoptera noctuidae) Linz: Land Oberösterreich, OÖ. Landesmuseum.	
Lycaenidae	<i>Lycaena</i>	<i>helle</i>	BOLD:AAB5175	<i>Polyommatus amphidamas, Papilio helle, Papilio amphidamas, Helleia helle</i>	boreo-montane	Louy D., (2016). Molecular biogeography of alpine-disjunct species: the genus Erebia as model taxon	
Geometridae	<i>Macaria</i>	<i>carbonaria</i>	BOLD:AAF6678	<i>Itame carbonaria, Phalaena carbonaria, Semiothisa carbonaria</i>	boreo-montane	Skou, P., Sihvonen, P., and Hausmann, A., (2015). The geometrid moths of Europe. Volume 5, Subfamily: Ennominae I (Abraxini, Apeirini, Baptini, Caberini, Campaeini, Cassymini, Colotoini, Ennomini, Epionini, Gnophini (part), Hypochrosini, Lithinini, Macariini, Prosopolophini, Theriiini and 34 species of uncertain tribus association) (The Geometrid Moths of Europe). Leiden: Brill.	
Geometridae	<i>Martania</i>	<i>taeniata</i>	BOLD:AAE9770	<i>Cidaria arctata, Cidaria taeniata, Emmelesia taenia-ta, Perizoma taeniata</i>	boreo-montane	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214	
Crambidae	<i>Metaxmeste</i>	<i>schränkiana</i>	BOLD:AAE7792	<i>Hercyna holosericalis, Phalaena schrankiana</i>	boreo-montane	Slamka, F., (2006). Pyraloidea of Europe: identification, distribution, habitat, biology = Pyraloidea Europas (Lepidoptera). Bratislava: Slamka.	
Noctuidae	<i>Mniotype</i>	<i>adusta</i>	BOLD:AAD5982	<i>Hadena adusta, Hadena sommeri, Hadena valida, Mniotype sommeri, Phalaena adusta, Blepharita adusta</i>	boreo-montane	Rákosy, L., and Giesenleitner, F., (1996). Die Noctuiden Rumäniens: (Lepidoptera noctuidae). Linz: Land Oberösterreich, OÖ. Landesmuseum.	
Tineidae	<i>Nemapogon</i>	<i>koenigi</i>	BOLD:AAD6594	<i>Nemapogon wolffiiella, Nemapogon albipunctellus, Tinea albipunctella</i>	boreo-montane	Gaedike, Nuss, M., Karsholt, O., and Mutanen, M., (2015). Tineidae I. (Dryadaulinae, Hapsiferinae, Eupocaninae, Scardiinae, Nemapogoninae and Meessiinae) Microlepidoptera of Europe 2017, Brill. Richard Gaedike Brill -Verlag, Petersen G., and Gaedike, R., (1985). Beitrag zur Kleinschmetterlingsfauna Österreichs und der angrenzenden Gebiete (Lepidoptera: Tineidae, Epermeniidae, Acrolepiidae, Douglasiidae), Mitt. Abt. Zool. Landesmus. Joanneum, Heft 36, p. 1-48	
Gelechiidae	<i>Neofaculta</i>	<i>infernella</i>	BOLD:AAC1363	<i>Gelechia infernella</i>	boreo-montane	Karisch, T., (2014). Die Schmetterlinge (Lepidoptera) im Hochharz Sachsen-Anhalts: unter besonderer Berücksichtigung der kennzeichnenden Arten der Fauna-Flora-Habitat-Lebensraumtypen, Universitäts-und Landesbibliothek Sachsen-Anhalt.	

Noctuidae	<i>Papestra</i>	<i>biren</i>	BOLD:AAA9849	<i>Mamestra glauca</i> , <i>Papestra bombycina</i> , <i>Papestra glauca</i> , <i>Phalaena biren</i> , <i>Polia frustrata</i>	boreo-montane	Spitzer, K., and Danks, H. V., (2006). Insect biodiversity of boreal peat bogs. <i>Annu. Rev. Entomol.</i> , 51, 137-161.
Papilionidae	<i>Parnassius</i>	<i>apollo</i>	BOLD:ABZ7543 BOLD:ACE6682 BOLD:ACF6579	<i>Papilio apollo</i> , <i>Parnassius apollo</i> var. <i>alba</i> , <i>Parnassius apollo</i> var. <i>brittingeri</i> , <i>Parnassius apollo</i> var. <i>carpathicus</i> , <i>Parnassius apollo</i> var. <i>dubius</i> , <i>Parnassius apollo</i> var. <i>hoglandicus</i> , <i>Parnassius apollo</i> var. <i>laufferi</i> , <i>Parnassius apollo</i> var. <i>lilburnicus</i> , <i>Parnassius apollo</i> var. <i>minerva</i> , <i>Parnassius apollo</i> var. <i>minor</i> , <i>Parnassius apollo</i> var. <i>sojoticus</i> , <i>Parnassius apollo</i> var. <i>suaneticus</i> , <i>Parnassius apollo</i> var. <i>transsylvanicus</i>	boreo-montane	Stettmer, C. (2007). Die Tagfalter Bayerns und Österreichs. 2., überarb. Aufl. Laufen: ANL, Bayer. Akad. für Naturschutz und Landschaftspflege.
Geometridae	<i>Perizoma</i>	<i>minorata</i>	BOLD:AAD4210	<i>Cidaria minorata</i> , <i>Emmelesia minorata</i>	boreo-montane	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. <i>PLoS ONE</i> , 7, e47214. https://doi.org/10.1371/journal.pone.0047214
Tortricidae	<i>Phiaris</i>	<i>schulziana</i>	BOLD:ACF5701	<i>Pyralis schulziana</i>	boreo-montane	Karisch, T., (2014). Die Schmetterlinge (Lepidoptera) im Hochharz Sachsen-Anhalts: unter besonderer Berücksichtigung der kennzeichnenden Arten der Fauna-Flora-Habitat-Lebensraumtypen, Universitäts- und Landesbibliothek Sachsen-Anhalt.
Gelechiidae	<i>Prolita</i>	<i>sexpunctella</i>	BOLD:AAB2663 BOLD:ABZ5400	<i>Gelechia alpicolo</i> , <i>Gelechia alternatella</i> , <i>Gelechia histrionella</i> , <i>Gelechia longicornella</i> , <i>Gelechia longicornis</i> , <i>Gelechia melanica</i> , <i>Gelechia petulans</i> , <i>Gelechia virgella</i> , <i>Gelechia zebrella</i> , <i>Lita histrionella</i> , <i>Lita sexpunctella</i> , <i>Lita virgella</i> , <i>Prolita longicornis</i> , <i>Prolita virgella</i> , <i>Tinea histrionella</i> , <i>Tinea sexpunctella</i> , <i>Tinea virgella</i>	boreo-montane	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. <i>PLoS ONE</i> , 7, e47214. https://doi.org/10.1371/journal.pone.0047214
Noctuidae	<i>Protolampra</i>	<i>sobrina</i>	BOLD:AAE8181	<i>Agrotis sobrina</i> , <i>Noctua sobrina</i> , <i>Paradiarsia sobrina</i>	boreo-montane	Steiner, A., and Ebert, G., (1998). Die Schmetterlinge Baden-Württembergs: [im Rahmen des Artenschutzprogrammes Baden-Württemberg] 7, Nachtfalter, 5 Allgemeiner Teil: Benutzerhinweise, Ergebnisse. Spezieller Teil: Noctuidae (Schluß). Stuttgart: Ulmer.
Geometridae	<i>Rheumaptera</i>	<i>subhastata</i>	BOLD:AAA5435 BOLD:AAA5436	<i>Cidaria subhastata</i> , <i>Larentia digitata</i> , <i>Rheumaptera sagittifera</i>	boreo-montane	Hausmann, A., and Viidalepp, J., (2012). The geometrid moths of Europe: Volume 3, Subfamily: Larentiinae I (Cataclysmi, Xanthorhoini, Euphyiini, Larentiini, Hydriomenini, Stamnodes, Cidariini, Operophterini, Aethenini, Phileremini, Rheumapterini, Solitaneini, Melantheini, Chesladini, Trichopterygini): Subfamily Sterrhinae (II) (Lythriini), Vester Skerninge: Apollo Books.
Gelechiidae	<i>Scrobipalpa</i>	<i>murinella</i>	BOLD:AAH9720 BOLD:ACY8255	<i>Lita murinella</i>	boreo-montane	Wiesmair, B.J., (2015). Die Artenvielfalt der Ordnung der Lepidoptera der subalpinen und alpinen Zone des Dobratsch: mit zusätzlichen Untersuchungen der Populationsgenetik ausgewählter Arten.

Noctuidae	<i>Standfussiana</i>	<i>lucernea</i>	BOLD:AAE9254	<i>Agrotis lucernea</i>	boreo-montane	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214
Psychidae	<i>Sterrhopterix</i>	<i>standfussi</i>	BOLD:AAI0085 BOLD:ACE9284	<i>Psyche standfussi, Sterrhopterix kurenzovi</i>	boreo-montane	Arnscheid, W. R. and Weidlich, M., (2017): Psychidae. Boston: Brill.
Noctuidae	<i>Syngrapha</i>	<i>interrogationis</i>	BOLD:AAB3481	<i>Phalaena interrogationis, Plusia interrogationis</i>	boreo-montane	Spitzer, K., and Danks, H. V., (2006): Insect biodiversity of boreal peat bogs. Annu. Rev. Entomol., 51, 137-161.
Geometridae	<i>Thera</i>	<i>cognata</i>	BOLD:AAB9686	<i>Cidaria similaria, Corythea similaria, Corythea simularia, Geometra cognata, Phalaena cognata, Thera coniferata, Thera simulata</i>	boreo-montane	Hausmann, A., and Viidalepp, J., (2012): The geometrid moths of Europe. Volume 3, Subfamily Larentiinae I (Cataclysmi, Xanthorhoini, Euphyiini, Larentiini, Hydriomenini, Stamnodini, Cidariini, Operophterini, Asthenini, Phileremini, Rheumapterini, Solitaneini, Melanthiini, Chesladini, Trichopterygini): Subfamily Sterrhinae (II) (Lythriini), Vester Skerninge : Apollo Books.
Crambidae	<i>Udea</i>	<i>inquinalis</i>	BOLD:AAB9747	<i>Pionea albinalis, Scopula inquinatalis</i>	boreo-montane	Slamka, F., (2013): Pyraloidea of Europe: identification, distribution, habitat, biology: 3. Pyraustinea and Spilomelinae, 1. ed., Bratislava: Slamka.
Crambidae	<i>Udea</i>	<i>nebulalis</i>	BOLD:AAD5509 BOLD:ACP5764	<i>Pyralis nebulalis</i>	boreo-montane	Slamka, F., (2013): Pyraloidea of Europe: identification, distribution, habitat, biology: 3. Pyraustinea and Spilomelinae, 1. ed., Bratislava: Slamka.
Crambidae	<i>Udea</i>	<i>decrepitalis</i>	BOLD:ABY5633 BOLD:AAC7950	<i>Botys decrepitalis</i>	boreo-montane	Mally, R., and Nuss, M., (2011): Molecular and morphological phylogeny of European Udea moths (Insecta: Lepidoptera: Pyraloidea), Arthropod systematics & phylogeny, 69(1), pp. 55–71.
Geometridae	<i>Venusia</i>	<i>cambrica</i>	BOLD:AAA1585 BOLD:AAA1586	<i>Hydrelia cambricata, Tephrosia scitularia, Venusia cambricaria</i>	boreo-montane	Hausmann, A., and Viidalepp, J., (2012): The geometrid moths of Europe Volume 3, Subfamily: Larentiinae I (Cataclysmi, Xanthorhoini, Euphyiini, Larentiini, Hydriomenini, Stamnodini, Cidariini, Operophterini, Asthenini, Phileremini, Rheumapterini, Solitaneini, Melanthiini, Chesladini, Trichopterygini): Subfamily Sterrhinae (II) (Lythriini), Vester Skerninge: Apollo Books.
Geometridae	<i>Xanthorhoe</i>	<i>decoloraria</i>	BOLD:AAA5318	<i>Geometra munitata, Phalaena decoloraria, Xanthorhoe decoloraria</i>	boreo-montane	Hausmann, A., and Viidalepp, J., (2012): The geometrid moths of Europe Volume 3, Subfamily Larentiinae I (Cataclysmi, Xanthorhoini, Euphyiini, Larentiini, Hydriomenini, Stamnodini, Cidariini, Operophterini, Asthenini, Phileremini, Rheumapterini, Solitaneini, Melanthiini, Chesladini, Trichopterygini): Subfamily Sterrhinae (II) (Lythriini), Vester Skerninge: Apollo Books.
Geometridae	<i>Xanthorhoe</i>	<i>incursata</i>	BOLD:AAB5059	<i>Geometra incurvata, Larentia incurvata</i>	boreo-montane	Mutanen, M., Hausmann, A., Hebert, P.D.N., Landry, J.F., de Waard, J., and Huemer, P. (2012). Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE, 7, e47214. https://doi.org/10.1371/journal.pone.0047214

Noctuidae	<i>Xestia</i>	<i>sincera</i>	BOLD:AAF0680	<i>Agrotis sincera, Anomogyna sincera</i>	boreo-montane	Steiner, A., and Ebert, G., (1998): Die Schmetterlinge Baden-Württembergs 7, Nachtfalter, 5 Allgemeiner Teil: Benutzerhinweise, Ergebnisse. Spezieller Teil: Noctuidae (Schluß). Stuttgart: Ulmer.
Noctuidae	<i>Xestia</i>	<i>collina</i>	BOLD:AAE1853	<i>Agrotis collina, Amathes collina, Noctua collina</i>	boreo-montane	Steiner, A., and Ebert, G., (1998): Die Schmetterlinge Baden-Württembergs 7, Nachtfalter, 5 Allgemeiner Teil: Benutzerhinweise, Ergebnisse. Spezieller Teil: Noctuidae (Schluß). Stuttgart: Ulmer.
Noctuidae	<i>Xestia</i>	<i>speciosa</i>	BOLD:AAA2273 BOLD:ACE4665 BOLD:ACE4666 BOLD:ACF2639 BOLD:ACF2698	<i>Agrotis speciosa, Amathes speciosa, Anomogyna speciosa, Aplecta speciosa, Noctua speciosa</i>	boreo-montane	Steiner, A., and Ebert, G., (1998): Die Schmetterlinge Baden-Württembergs 7, Nachtfalter, 5 Allgemeiner Teil: Benutzerhinweise, Ergebnisse. Spezieller Teil: Noctuidae (Schluß). Stuttgart: Ulmer.
Geometridae	<i>Yezognophos</i>	<i>vittaria</i>	BOLD:AAD3010 BOLD:AAD3009	<i>Elophos vittaria</i>	boreo-montane	Müller B., Erlacher S., Hausmann A., Rajaei H., Sihvonen P. and Skou P., (2019), The geometrid moths of Europe.: Volume 6, Part 1, Subfamily Ennominae. II (Boarmiini, Gnophini, additions to previous volumes), Netherlands: Brill.

Table 2: Intraspecific genetic distances of used species, sorted alphabetically within the two distribution types: The mean intraspecific between-region divergences of the different calculation types ordered to their distribution (MPD = Mean of pairwise distance). Not all species delivered pairwise distances for each calculation type because of the geographic sampling bias in available sequences.

Speciesname	between MPD All	between MPD <i>One per site</i>	between MPD <i>No duplicates</i>	distribution type
<i>Aethes deutschiana</i>	0.0035			arctic-alpine
<i>Agriades glandon</i>	0.0070	0.0063	0.0088	arctic-alpine
<i>Agriades orbitula</i>	0.0027			arctic-alpine
<i>Agrotis fatidica</i>	0.0019	0.0019		arctic-alpine
<i>Anarta melanopa</i>	0.0024	0.0023	0.0032	arctic-alpine
<i>Apamea maillardi</i>	0.0187	0.0183	0.0183	arctic-alpine
<i>Apantesis quenseli</i>	0.0157	0.0157		arctic-alpine
<i>Argyroploce noricana</i>	0	0	0	arctic-alpine
<i>Boloria napaea</i>	0.0108	0.0109	0.0132	arctic-alpine
<i>Callisto coffeella</i>	0.0092	0.0090	0.0124	arctic-alpine
<i>Caryocolum petrophila</i>	0.0103	0.0109		arctic-alpine
<i>Caryocolum pullatella</i>	0.0333	0.0332	0.0327	arctic-alpine
<i>Chelis puengeleri</i>	0.0056	0.0053	0.0056	arctic-alpine
<i>Epinotia mercuriana</i>	0.0266	0.0275	0.0279	arctic-alpine
<i>Erebia medusa</i>	0.0019	0.0016		arctic-alpine
<i>Erebia pandrose</i>	0.0053	0.0047	0.0059	arctic-alpine
<i>Eriogaster arbusculae</i>	0.0113	0.0113	0.0126	arctic-alpine
<i>Grapholita aureolana</i>	0.0042	0.0041		arctic-alpine
<i>Incurvaria vetulella</i>	0.0294	0.0296	0.0294	arctic-alpine
<i>Macaria fusca</i>	0.0099	0.0097	0.0119	arctic-alpine
<i>Oidaematophorus rogenhoferi</i>	0.0055	0.0050	0.0060	arctic-alpine
<i>Psodos coracina</i>	0.0074	0.0073	0.0072	arctic-alpine
<i>Pyrgus andromedae</i>	0.0118	0.0109	0.0140	arctic-alpine
<i>Sparganothis praecana</i>	0.0034	0.0027		arctic-alpine
<i>Stenoptilia islandicus</i>	0.0031	0.0036		arctic-alpine
<i>Synanthedon aurivillii</i>	0.0583	0.0528	0.0561	arctic-alpine
<i>Syngrapha hochenwarthi</i>	0.0025	0.0025		arctic-alpine
<i>Xestia alpicola</i>	0.0002	0.0002		arctic-alpine
<i>Zygaena exulans</i>	0.0127	0.0127	0.0135	arctic-alpine
<i>Acasis appensata</i>	0.0325			boreo-montane
<i>Acleris maccana</i>	0.0002			boreo-montane
<i>Acronicta cinerea</i>	0.0015	0.0010		boreo-montane
<i>Acronicta menyanthidis</i>	0.00081			boreo-montane
<i>Alcis jubata</i>	0.0259			boreo-montane
<i>Amphipyra perflua</i>	0.0012			boreo-montane

<i>Ancylis myrtillana</i>	0.0016	0.0016		boreo-montane
<i>Apamea furva</i>	0.0048	0.0047	0.0050	boreo-montane
<i>Apamea rubrirena</i>	0.0028	0.0021		boreo-montane
<i>Argyroploce arbutella</i>	0.0033			boreo-montane
<i>Aricia nicias</i>	0.0248	0.0226		boreo-montane
<i>Autographa bractea</i>	0			boreo-montane
<i>Autographa buraetica</i>	0.0006	0.0002		boreo-montane
<i>Boloria eunomia</i>	0.0087	0.0102	0.0110	boreo-montane
<i>Boloria thore</i>	0.0059	0.0080	0.0112	boreo-montane
<i>Brachionycha nubeculosa</i>	0.0099			boreo-montane
<i>Carsia sororiata</i>	0.0061	0.0051	0.0077	boreo-montane
<i>Catastia marginea</i>	0.0016			boreo-montane
<i>Chionodes luctuella</i>	0.0216			boreo-montane
<i>Chionodes viduella</i>	0.0117	0.0123		boreo-montane
<i>Colias palaeno</i>	0.0262	0.0272		boreo-montane
<i>Colostygia turbata</i>	0.0906			boreo-montane
<i>Coranarta cordigera</i>	0.0022			boreo-montane
<i>Crambus alienellus</i>	0.0005			boreo-montane
<i>Cucullia lactucae</i>	0.0257	0.0224		boreo-montane
<i>Elachista albidella</i>	0.0166	0.0218		boreo-montane
<i>Elophos vittaria</i>	0.0624			boreo-montane
<i>Entephria caesiata</i>	0.0095	0.0082	0.0107	boreo-montane
<i>Entephria flavidinctata</i>	0.0076	0.0071		boreo-montane
<i>Entephria nobiliaria</i>	0.0023	0.0021		boreo-montane
<i>Epipsilia grisescens</i>	0.0012			boreo-montane
<i>Erebia ligea</i>	0.0218	0.0062		boreo-montane
<i>Eudonia murana</i>	0.0220	0.0192		boreo-montane
<i>Eudonia sudetica</i>	0.0309	0.0180	0.0191	boreo-montane
<i>Euhypomeutoides albithoracellus</i>	0.0112		0.0117	boreo-montane
<i>Eupithecia cauchiata</i>	0.0016			boreo-montane
<i>Eupithecia conterminata</i>	0.0300	0.0295		boreo-montane
<i>Euxoa recussa</i>	0.0013	0.0016		boreo-montane
<i>Exaeretia ciniflonella</i>	0.0011			boreo-montane
<i>Gnophos obfuscata</i>	0.0110	0.0175		boreo-montane
<i>Hydraecia petasitis</i>	0.0006			boreo-montane
<i>Hydriomena ruberata</i>	0.0053		0.0054	boreo-montane
<i>Hyppa rectilinea</i>	0.0127			boreo-montane
<i>Kessleria fasciapennella</i>	0.0003			boreo-montane
<i>Lampropteryx otregiata</i>	0.0002			boreo-montane
<i>Lasiommata petropolitana</i>	0.0007			boreo-montane
<i>Lithophane consocia</i>	0			boreo-montane
<i>Lycaena helle</i>	0.0011			boreo-montane
<i>Lygephila viciae</i>	0.0005			boreo-montane
<i>Martania taeniata</i>	0.0023	0.0038	0.0038	boreo-montane

<i>Metaxmeste phrygialis</i>	0.0041	0.0051u		boreo-montane
<i>Metaxmeste schrankiana</i>	0.0042	0.0044	0.0057	boreo-montane
<i>Mniotype adusta</i>	0.0023	0.0024	0.0056	boreo-montane
<i>Nemapogon koenigi</i>	0.0032	0.0039		boreo-montane
<i>Neofaculta infernella</i>	0.0050	0.0111		boreo-montane
<i>Papestra biren</i>	0.0015	0.0022		boreo-montane
<i>Parnassius apollo</i>	0.0222	0.0217		boreo-montane
<i>Perizoma minorata</i>	0.0011			boreo-montane
<i>Phiaris schulziana</i>	0.0051			boreo-montane
<i>Prolita sexpunctella</i>	0.0014	0.0004		boreo-montane
<i>Protolampra sobrina</i>	0.0003			boreo-montane
<i>Rheumaptera subhastata</i>	0.0205	0.0208		boreo-montane
<i>Scrobipalpa murinella</i>	0.0066			boreo-montane
<i>Spargania luctuata</i>	0.0009			boreo-montane
<i>Sterrhopterix standfussi</i>	0.0007			boreo-montane
<i>Syngrapha interrogationis</i>	0.0006	0.0010		boreo-montane
<i>Thera cognata</i>	0			boreo-montane
<i>Udea decrepitalis</i>	0.0060	0.0079	0.0082	boreo-montane
<i>Udea inquinatalis</i>	0.0022		0.0030	boreo-montane
<i>Udea nebulalis</i>	0.0190	0.0075	0.0095	boreo-montane
<i>Venusia cambrica</i>	0.0009			boreo-montane
<i>Xanthorhoe decoloraria</i>	0.0076			boreo-montane
<i>Xestia collina</i>	0.0023	0.0025		boreo-montane
<i>Xestia sincera</i>	0.0012			boreo-montane
<i>Xestia speciosa</i>	0.0243	0.0238	0.0235	boreo-montane
<i>Xylena solidaginis</i>	0.0010			boreo-montane