universität wien

MASTERARBEIT | MASTER'S THESIS

Titel | Title

Spatial patterns of Species Richness and Phylogenetic Diversity of European Sterrhinae (Geometridae, Lepidoptera)

verfasst von | submitted by

Zita Roithmair BSc MSc

angestrebter akademischer Grad | in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien | Vienna, 2024

Studienkennzahl lt. Studienblatt | Degree programme code as it appears on the student record sheet:	UA 066 879
Studienrichtung lt. Studienblatt | Degree programme as it appears on the student record sheet:	Masterstudium Naturschutz und Biodiversitätsmanagement
Betreut von | Supervisor:	Univ.-Prof. Mag. Dr. Konrad Fiedler

Acknowledgements

I would like to express special thanks to my supervisors, Konrad Fiedler and Patrick Strutzenberger for their guidance and input during this study. Thank you for introducing me to the fascinating field of macroecology and particularly the topic of phylogenetic diversity! I am very happy that I could learn so many new aspects of ecological and biodiversity research and work on this project for my master's thesis.

Patrick, thank you for your help particularly when building the phylogenetic tree, and for being available for all my questions throughout my analysis and writing phase. Konrad Fiedler, thank you for your support throughout the whole project and for providing your expertise on Sterrhinae, whenever I had questions.

I would like to thank Axel Hausmann for providing unpublished barcode sequences for several Sterrhinae species for this study.

So many exciting things happened while I was working on this thesis and I want to express my gratitude to my friends and family, especially to my parents, my brother, and my partner for all your kind support!

Table of Content

Abstract

There are many ways of measuring biodiversity, besides 'simply' counting species. For example, functional and genetic diversity capture information on the ecological traits of organisms or their genetic variation and divergence. Phylogenetic diversity measures the diversity of phylogenetic lineages within a species assemblage by including information on their evolutionary history and position on the phylogenetic tree. There are different ways of calculating phylogenetic diversity (PD), for example Faith' PD is the sum of phylogenetic branch lengths present in a set of species. In this study phylogenetic diversity (Faith' PD) and structure, as well as phylogenetic endemism of European Sterrhinae (Geometridae, Lepidoptera) was investigated and described for the first time, using a grid-based approach with a spatial resolution of 50 x 50 km. Distribution data was digitized from taxonomic literature and extended with records from local literature and GBIF. For calculating the phylogeny, mitochondrial COI sequences were used, in addition with nuclear markers. In Europe, Sterrhinae are predominantly xerothermophilous, the larvae of many of which can feed on dead or decaying plant material. This distinguishes them from other geometrids. The results of this study show that PD was generally high in species rich regions, which are southwestern Europe and parts of the Balkans, however highlighting additional areas such as the entire Mediterranean coast and adjacent areas of Southern Europe as hotspots for PD. Not only was PD correlated with species richness, but also with latitude, while the positive relationship with mean annual temperature was not significant after correcting for spatial autocorrelation. Further metrics, such as net relatedness index and nearest taxon index indicated, that the diverse regions in Southern Europe host clusters of evolutionary older lineages, while recent phylogenetic clustering occurred mainly in Northern Europe. Hotspots of phylogenetic endemism were identified in the Iberian Peninsula, the Mediterranean Islands, southern France and Italy, and Greece. Using the CANAPE approach those areas were found to host both neo- and paleo-endemism and in some parts super-endemism. When looking at ecological traits, such as diet breadth, voltinism and range size, a latitudinal gradient was detected: diet breadth and restriction to a single generation per year increased with higher latitudes, possibly due to harsher environments. Range size of European Sterrhinae was generally larger in higher latitudes. While species richness was following a rather clear latitudinal gradient, patterns of PD appeared more fine-structured, showing for example intermediate – high diversity in the temperate regions of Central Europe. The results of this thesis suggest that the incorporation of different diversity metrics adds important information to biodiversity studies.

1. Introduction

Biodiversity refers to the variety of life-forms on our planet, and its assessment is one of the most important tasks in conservation biology. Since E. O. Wilson spread the term widely in 1988, biodiversity research has gained more and more attention and the concept has been discussed utilizing different approaches (Wilson, 1988; Liu et al., 2011). Traditionally, biodiversity is measured as species richness, however, genetic diversity and diversity of ecosystems are commonly understood to be aspects of biodiversity as well (Haila & Kouki, 1994; Sarkar & Margules, 2002; Liu et al., 2011; Theissinger et al., 2023). Species richness is not only a well-established variable used in important early theories in biogeography (for example island biogeography; MacArthur & Wilson, 1967), it is still used in most contemporary assessments of biodiversity (e.g., Paillet et al., 2010) and remains probably the most frequently used measure for biodiversity studies and science communication (Bermudez & Lindemann-Matthies, 2020; Llorente-Culebras et al., 2023). More recent approaches also formalized those alternative measures of biodiversity in terms of functional and phylogenetic diversity (for example: Hillebrand & Matthiessen, 2009; Mishler et al., 2014; Guariento et al., 2020; Earl et al., 2021). Functional diversity aims to quantify the different phenotypic traits of organisms observed within a spatially defined set of species (Wong et al. 2019). While early studies focused mostly on the categorization into functional groups, more recent analyses utilize multivariate techniques to calculate trait diversity indices (Gagic et al., 2015). Functional diversity is particularly used to better understand and explain ecosystem functions (Cadotte et al., 2011; Gagic et al., 2015).

In contrast, phylogenetic diversity includes evolutionary information in the assessment of biodiversity, a concept which was first proposed by Vane-Wright and colleagues and further developed by Faith in the early 1990's and has been increasingly included in community ecology and biodiversity research (Vane-Wright et al., 1991; Faith, 1992; review by Cavender-Bares et al., 2009; Tucker et al., 2017). Phylogenetic diversity expresses the differences between organisms within a set of species, according to their evolutionary history (Pellens & Grandcolas, 2016). Different diversity metrics have been established, the most commonly used being Faith' phylogenetic diversity (Faith, 1992), evolutionary distinctiveness (Isaac et al., 2007), and phylogenetic endemism (Rosauer et al., 2009). There are several recently developed metrics, which can be broadly categorized into three groups, measuring (i) richness, (ii) divergence and (iii) regularity (for a review see Tucker et al., 2017). Weighted forms of these diversity metrics have been proposed as well, including for example, abundance-informed ecophylogenetics at the community level (Cadotte et al., 2010) and relative phylogenetic diversity and endemism (Mishler et al., 2014). Phylogenetic diversity can be implemented into conservation strategies and help decision makers in prioritizing conservation areas (Rosauer et al., 2009; Winter et al., 2013; Jetz et al., 2014). The importance of implementing phylogenetic diversity into conservation strategies is meanwhile broadly acknowledged and the IUCN nominated its own task force "SSC Phylogenetic Diversity Task Force (PDTF)" to include this aspect of

biodiversity heritage into conservation planning (https://www.pdtf.org/). Another interesting aspect is the integration of spatial data, usually at large scales (i.e. above the community level), into phylogenetic diversity studies (e.g., Jetz et al., 2012; Jetz et al., 2014; Gumbs et al., 2020; Earl et al., 2021).

Functional and phylogenetic diversity are important indicators of biodiversity and improve our understanding of ecosystem functions (examples: Tilman et al., 1997; Cavender-Bares et al., 2009; Mouquet et al., 2012; Gagic et al., 2015; Cadotte, 2017; Wong et al, 2019; Craven et al., 2018). Caution is advised, as differently informed diversity metrics (e.g., species richness, functional diversity, and phylogenetic diversity) can sometimes provide varying – and potentially contradictory – results (Gagic et al., 2015; Cadotte et al., 2017; Mazel et al., 2018; Guariento et al., 2020). However, it must be also considered that some metrics will not be entirely independent from each other. For example, phylogenetic diversity and functional diversity are somehow linked, since closely related species will often share more traits with each other than with distant species (Guariento et al., 2020). Certain aspects of the connection between phylogenetic traits and functional traits, however, are contested and the question remains, to what extent phylogeny can be used to predict trait similarity across species (Losos, 2008; Kelly et at., 2014). These contradictions might be explained by to-date unresolved methodological issues, as the field is relatively new (Cadotte et al. 2017). Studying various diversity metrics in concert is therefore helpful to better understand ecosystems and conduct proper conservation planning (Cadotte et al., 2010 & 2011; Craven et al., 2018; Guariento et al., 2020).

In this study I will focus on phylogenetic diversity using the following diversity metrics: phylogenetic diversity (Faith' PD), net relatedness index (NRI), nearest taxon index (NTI) and phylogenetic endemism (PE). Faith' PD is one of the most popular phylogenetic diversity metrics and is calculated as the sum of phylogenetic branch lengths of a set of species (Faith, 1992; Grandcolas & Pellens, 2016). NRI and NTI are used to investigate the underlying phylogenetic structures within species assemblages. They are both calculated by the difference between observed and expected mean phylogenetic distance in the phylogenetic tree (in case of NRI) or mean nearest taxon distance in the phylogenetic tree (in case of NTI) divided by their standard deviations (Manish, 2021). Phylogenetic clustering results in positive values of both NRI and NTI (assemblages consist on average of more closely related taxa than expected by chance), while negative values of NRI and NTI occur in cases of phylogenetic overdispersion (assemblage formed by distantly related taxa) (Manish, 2021). Phylogenetic endemism is a metric measuring the spatial restriction of phylogenetic diversity by weighting the results of phylogenetic diversity by the range size of each taxon within an assemblage of species (Rosauer et al., 2009). To differentiate between different types of endemism, I will utilize CANAPE (categorical analysis of neo- and paleo-endemism; Mishler et al. 2014), which compares PE values to a random null-model, identifying areas of paleo-endemism (more older evolutionary lineages than expected), neo-endemism (more younger evolutionary lineages than expected), mixed-endemism (high amount of both paleo- and neo-endemism), and super-endemism (significant results for mixed endemism in measured and expected cases) (Mishler et al. 2014; Nitta et al., 2022).

The investigation of phylogenetic diversity within a species assemblage may aid the reconstruction and interpretation of the origin of the phylogenetic structure of the assemblage. Two of the most studied mechanisms for the establishment of a species assemblage are environmental filtering and competitive interactions (Webb et al., 2002; Cavender-Bares et al., 2009; Guariento et al., 2020). Environmental filtering describes the process by which only a subset of species from a regional species pool is able to colonize a certain habitat (i.e., a set of ecological niches), due to their ecological capacities (Emmerson & Gillespie, 2008). Within the local species assemblage only those species remain that can outlast their competitors (Emmerson & Gillespie, 2008). On the other hand, species that use the same resources and are forced to compete for them will probably not be able to co-exist over ecological time (Cavender-Bares et al., 2006). The phylogenetic structure of a community can therefore be assumed to reflect large-scale macroecological patterns caused by its formation: environmental filtering resulting in phylogenetic clustering, and competitive exclusion resulting in phylogenetic overdispersion (Cavender-Bares et al., 2009). Another concept is the limiting similarity hypothesis, stating that closely related species are more likely to inhabit similar ecological niches, resulting in increased competitive exclusion among closely related species (Violle et al., 2011), again assuming that closer related species will show higher similarity in their traits (Guariento et al., 2020). The phylogenetic structure of a community can also be influenced by other mechanisms, such as predation (Vamosi & Vamosi, 2007) or disturbances (Verdu & Pausas, 2007). Furthermore, the environmental filter model has been criticised due to its simplicity, ignoring more complex interactions between biota and their environment (Cadotte & Tucker, 2017). Still, this new interdisciplinary approach of combining phylogeny and ecology is a great opportunity to investigate the impact of evolutionary history on community ecology (Ricklefs, 2006; Webb et al., 2006; Mouquet et al., 2012).

In contrast to species richness, where presence-absence data are usually sufficient, the study of phylogenetic diversity requires additional information about the taxon of interest (Guariento et al., 2020). Phylogenetic diversity can only be calculated for relatively well investigated species groups, because the distribution of each species as well as phylogenetic data in the form of a phylogenetic tree are required. This is the reason, why most previous phylogenetic diversity studies focused on well-studied taxa such as vascular plants (e.g., Mishler et al., 2014; Cubino et al., 2021), birds (e.g., Jetz et al., 2014), mammals (e.g., Rosauer et al., 2017), and butterflies (e.g., Earl et al., 2021).

This study investigates the phylogenetic diversity of European Sterrhinae, one of the nine currently recognized subfamilies of the species-rich moth family Geometridae (Murillo-Ramos et al., 2023). Sterrhinae are according to recent phylogenetic reconstruction the sister group to all other geometrid subfamilies (Õunap et al., 2024). While the non-Sterrhinae geometrids have been focus of previous macroecological studies, Sterrhinae have received less attention (e.g., Seifert et al., 2022a; Seifert et al., 2022b; Seifert et al., 2023). The subfamily shows an almost worldwide distribution and about 3,000 species are currently described (Sihvonen et al., 2020). Their species richness is highest at lower latitudes and elevations, reaching their maximum in the tropics (Brehm & Fiedler, 2003; Sihvonen et al., 2020). In Europe, Sterrhinae are represented with approximately 200 species, which makes them the third largest geometrid subfamily (Hausmann, 2004;

Hausmann et al., 2019). The group (monophyletic, when the genera *Ergavia* Walker, 1866, *Ametris* Hübner, 1822 and *Macrotes* Westwood, 1841 are included) comprises eight tribes within two major lineages: "Timandrini lineage" (including Timandrini, Rhodometrini, Cosymbiini and Lythriini) and "Scopulini lineage" (including Rhodostrophiini, Cyllopodini, Scopulini and Sterrhini), both showing morphological and molecular support (Sihvonen & Kaila, 2004; Murillo-Ramos et al. 2019; Sihvonen et al., 2020). Sterrhinae are rather small in body size compared to other geometrid moths and usually show cryptic, wavy wing patterns (Hausmann, 2004; Sihvonen & Kaila, 2004). In the Neotropics, however, there are also a few cases of aposematic coloration. The adult moths are frequently sexually dimorphic, with males showing secondary sexual characters like hair tufts and tibial modifications (Hausmann, 2004; Sihvonen et al., 2020). In Europe there are univoltine and plurivoltine species, all of which hibernate as larvae, except for species of the tribe Cosymbiini and Lythriini, which hibernate as pupa (Hausmann, 2004; Hausmann & Viidalepp, 2012). The period of highest activity for most species is at dusk, but certain species are active during the day instead (Hausmann, 2004). Sterrhinae larvae feed on vascular plants and/or dead plant material, and species can be poly- or monophagous (Hausmann, 2004). Particularly species from the tribe Sterrhini are known to feed primarily on decaying leaves, making them rather detritivores, than herbivores, which is unique for this group within Geometridae (Hausmann, 2004). Some species are known as minor pests of crop plants, most prominently on tobacco (Hausmann, 2004; Sihvonen et al., 2020). In some South-east Asian *Scopula* species adults are known to be zoophilous, feeding on secretions (blood, sweat and tears) of mammals (Bänzinger & Fletcher, 1985). Most species of Sterrhinae in Europe prefer xerothermic habitats and open landscapes (Hausmann, 2004). Accordingly, within Europe they are primarily found in the central to southern parts, being largely absent from the boreal zone (Hausmann, 2004). While some are included in local red lists (e.g., in Germany) that include geometrid moths (see for example Werno, 2020), there is no current estimation of threats to Sterrhinae diversity for Europe. Likewise, there is also no comprehensive collection of data about their biogeography and phylogenetic diversity in Europe.

The goal of the current study is to provide such a compilation, which aims to give insights into the biogeography of the subfamily, analysing their distribution patterns, phylogenetic structure and identify regions with high phylogenetic diversity and/or endemism. The identification of such regions may provide important information useful for conservation purposes.

Besides the descriptive aspect of this study in which the phylogenetic structure and hotspots of phylogenetic diversity and endemism will be investigated, the following hypothesis shall be tested:

A) Phylogenetic diversity is positively correlated with species richness and mean annual temperature, which might reflect a latitudinal gradient

This assumption is based on three ideas:

1. Sterrhinae are known to prefer a warmer climate, like in the Mediterranean area, where they also show the highest species richness, and to be almost absent from boreal or even subarctic regions (Hausmann, 2004, Seifert et al. 2022a).
2. Previous studies have suggested, that species richness and phylogenetic diversity are often correlated, especially if species assemblages contain several anciently diverged lineages and randomly accumulated species (Tucker & Cadotte, 2013; Tucker et al., 2017). I would assume that warm and dry habitats (which are known to be species rich regions for Sterrhinae) attracted and accumulated many evolutionary lineages and therefore expect, that phylogenetic diversity is higher in species rich-regions than in species-poor regions.
3. As climate is expected to change to the colder with increasing latitude in Europe, it is expected that diversity patterns of Sterrhinae are similar between climate and latitude as predictor.

B) Endemic hotspots of Sterrhinae in Europe mainly occur in isolated areas (e.g., islands) in warmer climates and are associated with phylogenetic distinctiveness of the respective taxa

This assumption is based on two ideas:

1. Endemism is usually found in areas that were or still are isolated (MacArthur and Wilson, 1967; Hamilton & Rubinoff, 1967). In Europe this would concern islands, glacial refugia like the Mediterranean region and regions of postglacial re-immigration like mountains (see for example Kenyeres et al. 2009; Jetz et al., 2014; Menchetti et al., 2021).
2. Taxa that lived in isolated refugia during glaciation had less opportunities for genetical exchange and can therefore be expected to show higher evolutionary distinctiveness and the region where they live now should have increased paleo-endemism (Stebbins & Major 1965; Hewitt, 1996; Tribsch & Schoenswetter, 2003).

C) Food specialization, voltinism and range size are correlated with climate and latitude

Three assumptions are made:

1. Rapoport's rule suggests that species living at higher latitudes have increased range sizes (Stevens, 1989), which was already found to be true for geometrid moths excluding Sterrhinae (Seifert et al. 2022a).

2. Finer resource partitioning in low latitudes, where higher diversity occurs (and therefore probably higher competition prevails) was found among European non-Sterrhinae geometrid moths (Seifert et al., 2022a). However, Sterrhinae are different in their ability to also feed on dead or decaying plant material (Hausmann, 2004) and therefore might show different patterns.

3. Insects are known to adapt their reproductive period to the climate, and it was frequently found that populations living in warmer climates could complete more life cycles within one year than their conspecifics living in colder climates (Hausmann, 2004; Välimäki et al., 2013; Kroschel et al., 2013; Rao et al., 2014; Seifert et al., 2023).

2. Material and Methods

2.1. Material

This study takes into account all 207 currently described and recognized European Sterrhinae species (see Appendix table A1), following the taxonomy according to Hausmann et al. (2019). Synonyms were checked using Hausmann et al., 2004; Hausmann & Viidalepp, 2012; Hausmann et al., 2019; GBIF (GBIF.org) and Lepiforum (lepiforum.org).

2.1.1. Distribution data

The distribution data were primarily extracted from Volume 2, 3 and 6 of the monograph series „Geometrid Moths of Europe“ (GMoE) (Hausmann, 2004; Hausmann & Viidalepp, 2012; Hausmann et al., 2019) and supplemented with records from GBIF. GBIF records were downloaded via R and RStudio (R version 4.2.1.) using the package “rgbif” version 3.7.7’ (Chamberlain & Boettiger, 2017; Chamberlain et al., 2023) and the GBIF "species-key" of all 207 species as one geopackage (point geometry). Additional more recent literature was included for the Iberian Peninsula (Redondo et al., 2009), the United Kingdom (Randle et al., 2019), and Norway (Aarvik et al., 2009).

Geographical data on distribution were digitized in QGIS (QGIS 3.22.4. Białowieża). For European shorelines and administrative boundaries, the shapefile “EEA coastline – Polygon” provided by the European Environment Agency, EEA, (https://www.eea.europa.eu/data-and-maps/data/eea-coastline-for-analysis-2/gis-data/eea-coastline-polygon) was used. The borders were adapted according to the Hausmann et al. (2004) series, following the Ural Mountains in the east and the Ural River in the south and the Caspian Sea along the Don Kuma-Manitsh depression to the Black Sea. Therefore, the Ciscaucasian slopes, the Asiatic part of Turkey, and Cyprus are excluded, as well as the Canaries, Madeira, and the Azores. To ensure comparable spatial entities for the analysis, the work was done in the coordinate reference system IGNF:ETRS89LAEA – ETRS89 Lambert Azimutal Equal Area (unit meter), which results in a distortion of angular degrees and distances, but keeps areas undistorted. The scanned distribution maps from the ebook version of Hausmann (2004) were georeferenced using the tool ‘georeferencer’ using 41 constant reference points (see Appendix table A2 and Figure A1).

A grid was created using the QGIS tool "Create grid" with a resolution of 50 x 50 kilometres (which led to a total of 4,659 grid cells covering European land mass). Then, all grid cells of the grid layer overlapping with the referenced distribution, or such that happen to include individual records according to the georeferenced GMoE distribution map, were selected and exported to a new shapefile. This was done for each species separately. Unverified records or areas where species are believed to be extinct were excluded. This led to the exclusion of two species: *Rhodostrophia terrestraria* and *Rhodostrophia sieversi*.

Rhodostrophia terrestraria shows a Turanian distribution with a single record from southern European Russia. However, this record is possibly mislabelled, and the species was therefore disregarded from the study. *Rhodostrophia sieversi* has only one doubtful record from south-western Croatia, which was never confirmed, leading to this species' exclusion from further analysis. The digitalization resulted in 205 separate shapefiles (one per species) containing distribution ranges, that were exported to a single geopackage and the GBIF records were spatially connected to the digitized data. The GBIF records were checked for plausibility before integration. Their plausibility was dependent on their distance to the distribution suggested in the literature resources and in ambiguous cases an expert was consulted (Konrad Fiedler, personal communication). Additionally, the national literature for the Iberian Peninsula, the United Kingdom, and Norway was consulted, by checking topographically whether any distribution areas or entries had to be added. In case of a new record the grid cells that showed overlap were selected, copied, and saved to the species feature in the shapefile. In most cases there were only few new records from GBIF or the national literature, that were usually close to the suggested distribution from the GMoE series. However, in Northern Europe, such as the United Kingdom and Norway there were minor areal extensions towards northern regions.

2.1.2. Genetic data

The partial sequences of the mitochondrial COI gene were downloaded from BOLD (https://boldsystems.org). 25 unpublished sequences were provided by Axel Hausmann. Thus, for 205 out of all 207 European Sterrhinae species COI sequences were available and included in the data analysis. In addition to this mitochondrial sequence, sequence data for seven nuclear genes (CAD, MDH, IDH, wingless, Ef1a, GDPH, Rs5ps) were downloaded from GenBank and subsequently used to build a phylogeny. While COI sequences were available for almost all species, nuclear genes were only available for few species (see Appendix table A1 for information on available sequence data for each species). The completeness for the studied genes were: COI = 99%, Ef1a = 14.8%, RpS5 = 12.9%, wingless = 12.4%, CAD = 10%, MDH = 10%, IDH = 9.6%, GADPH = 8.1%.

2.1.3. Ecological and environmental data

For each species, the available ecological information on voltinism, larval food plants, and elevational range were extracted from the GMoE series (Hausmann, 2004). Additionally, it was noted whether the species showed any distribution outside of Europe. Each species was assigned into a category for diet breadth: 1 – feeding only on one plant genera (monophagous); 2 – feeding on only one plant family (oligophagous); 3 – feeding on 2-4 plant families (moderately polyphagous); and 4 – feeding on more than 5 plant families (highly polyphagous). Species with unknown host plant or only records from rearing experiments were assigned to the category "unknown" and therefore excluded from the analysis. Several detrivorous species fell into the "unknown" category, since these were often described as unselective feeders. Voltinism mode was categorized in strictly univoltine species and species that are flexible in the number of generations emerging per

year. There were only very few species with strictly bi- or trivoltine life cycles. Here as well, a category "unknown" was introduced if information was lacking on a species' voltinism mode.

Climate data were downloaded in GeoTIFF format from CHELSA V2.x-V1.xx (https://chelsa-climate.org/downloads), including mean annual temperature, mean annual temperature range, mean diurnal temperature range, maximum temperature of the warmest month, minimum temperature of the coldest month and mean annual precipitation (Karger et al., 2017). Elevation data were assessed using the GMBA mountain inventory data (Körner et al., 2017) for Europe. Climate data were included into the grid with the QGIS tool 'zonal statistics', where the mean per grid cell was calculated. Latitude for each grid cell was exported via the field calculator of QGIS as latitudinal degrees of EPSG 4326.

Distribution area and latitudinal range of each species was calculated with the field calculator in QGIS and ecological traits data (extracted from the literature) of each species was linked to the species occurrence shapefile in QGIS. Then, using spreadsheet editors, the percentage of monophagous/polyphagous and univoltine/flexible-voltine species per grid cell was calculated.

For integrating mountain areas into the grid cells, an overlap analysis was performed for the mountain and the grid layer and from the resulting overlap-layer grid cells that showed more than 30% overlap with mountain areas were selected and saved as "mountain" cells to a new shapefile. They became an extra column in the dataset with the binary values 1 (mountainous cell) and 0 (lowland cell).

2.2. Methods

2.2.1. Phylogeny

COI sequences were transformed into fasta format using R with the packages "ape" (Paradis & Schliep 2019), "vegan" (Oksanen et al. 2022), and "seqinr" (Charif & Lobry 2007). The sequence data from GenBank were already downloaded as fasta format. Species without sequences were included into the fasta files with all-gap sequences as well, to be able to analyse all species. Sequences were edited in BioEdit and submitted to the online version of MAFFT version 7 (https://mafft.cbrc.jp/alignment/server/index.html) using default settings for each gene separately. Ends of the sequences were checked, and if required edited as well, to ensure that most sequences started and ended on the same nucleotides. They were sorted by name and saved to phylip format using R. Utilizing python and partitionfinder (version 1.1.1) the best-fitting partitioning scheme was calculated (see Appendix table A3). The fasta-files were loaded into BEAUTi and settings were adjusted according to the best scheme. Tree models were linked among all partitions and site models were set for each partition. Two optimized relaxed clock models were used, one for COI and one for all nuclear genes, both rates for both clocks were estimated. Because nuclear genes were not available for all species, priors were set for genera and tribes (according to Hausmann 2004), and for relationship between tribes (after Murillo-

Ramos et al. 2019; meanwhile supported by Õunap et al., 2024) to support already established phylogenetic relationships (see Appendix table A4). Genera were assumed to be monophyletic, trusting on morphological characters that are used to separate those taxa. The root was set to a log normal distribution centred around 70 million years (derived from Wahlberg et al. 2023). A xml file was generated with BEAUTi and used to calculate a phylogenetic tree in BEAST using the birth death model with 220 million generations, sampling every 20,000th tree. The resulting log files were observed with Tracer v1.7.2. and checked for effective sample size, which needed to be higher than 200. Using TreeAnnotator version 2.7.4. with a burn-in percentage of 10% (i.e., 11,000,000 trees), a maximum clade credibility tree was annotated. Since this annotated tree was only poorly supported at several basal branches, the entire tree sample of 10,000 trees was used for all further analysis, in order to incorporate phylogenetic uncertainty.

COI sequences were available for all but two species. To test whether exclusion of these two species made a difference, a second tree without those species was calculated, and an ANOVA and Tukey test was conducted with the two trees, which showed that there was no difference when excluding the two species with missing sequences.

2.2.4. Analyses

All subsequent spatial analyses were conducted using QGIS and R. First, grid cells that happened to have less than 30% overlap with land (i.e. the modified Europe map from the EEA) were excluded to avoid artificial inflation of land area, resulting in a total of 3988 grid cells. Due to this constraint, several grid cells containing only small islands were excluded from the main analysis (e.g., Malta, Ibiza, etc…). While most of the excluded islands represented only small parts of the distribution of inhabiting Sterrhinae species, there is one case, where a species -*Idaea ibizaria*- was present only on Ibiza, which fell below the 30% land coverage threshold. As *I. ibizaria* only occurred on Ibiza however, it is assumed that the exclusion of this species did not influence diversity metrics in surrounding areas. Another species, *Idaea textaria*, which has its main distribution in Asia close to the defined borders of Europe, was not present in European grid cells with more than 30% land mass, which led to the exclusion of this species. The exclusion of *Idaea ibizaria* and *Idaea textaria* resulted in 203 species present in Europe which were part of this study.

Using the tools 'Join attributes by location (summary)' the species count was calculated for each grid cell, and by operating an intersection with the original distribution layer the qualitative information on which species occurred in which grid cell(s) was added. Diversity metrics were calculated for each grid cell with all 10,000 trees and statistical parameters were taken, namely: mean, median, standard deviation and lower and upper 95% confidence interval using the packages "pez" version 1.2.4 (Pearse et al. 2015), DescTools version 0.99.48 (Signorell 2023), and "picante" version 1.8.2 (Kembel et al. 2010) for PD and PE, the package "PhyloMeasures" version 2.1 (Tsirogiannis & Sandel 2017) for NRI and NTI, and "matrixStats" version 1.0.0 (Bengtsson 2023) for formatting output-files. The standard deviation of diversity metrics calculated using different trees was very

low and there was no significant difference in the calculated metrics detected between extreme trees (which was tested with an ANOVA). Thus, the mean was considered to be an adequate statistical parameter for this purpose. For calculating NRI and NTI only grid cells with more than 8 species were included. This threshold was decided from plotting all NRI and NTI values (of all 10,000 trees) against number of species and then visually determine the point where variation was stabilized (which was around 8). Evolutionary distinctiveness was calculated for each species with all 10,000 trees, using the package "phyloregion" version 1.0.8 (Daru et al., 2020a, Daru et al., 2020b; Daru et al., 2017). Then it was linked with the species occurrence shapefile in QGIS and the mean evolutionary distinctiveness per grid cell was calculated. To see how the different metrics were correlated, a correlation matrix was calculated with the Pearson method using the cor() function of Base R.

The CANAPE approach was applied to distinguish between different types of endemism, using the package canaper version 1.0.1 (Nitta & Iwasaki 2021). Here, only one tree was used to calculate relative phylogenetic endemism (null model "curveball" with 100,000 iterations and 20 repetitions) and subsequently for classification of endemism types. The results were again compared to the results of "extreme" trees (minima and maxima of standard deviation) and tested with an ANOVA, which showed no difference.

Linear and quadratic models were calculated with the function 'lm' of the "stats" package version 4.3.1 (R Core Team 2023) to better understand and visualize relationships between variables. It has to be noted that in most cases the residuals were not strictly normally distributed according to Shapiro-Wilk tests ("stats" package, version 4.3.1, R Core Team 2023). Models were only retained, if all other criteria for linear regression were met and if they performed well in diagnostic plots. For large sample sizes it has been demonstrated that the assumption of normally distributed residuals does not in all cases need to be fulfilled to avoid unnecessary bias (e.g., Lumley et al., 2002; Schmidt & Finan, 2018). To correct for spatial autocorrelation each relationship was also tested in a generalized estimating equation (gee) using the R package "spind" version 2.2.1 (Carl et al., 2018), where the coordinates of the grid cells (i.e., their relative position to each other) were included in the analysis.

For editing tables, file-formats, graphs and figures, spreadsheet editors, Notepad++ v8.1.2 (64-bit) https://notepad-plus-plus.org/), the R packages "ggplot2" (version 3.4.3; Wickham, 2016), "ggpubr" (version 0.6.0, Kassambara, 2023), "ggcorrplot" (version 0.1.4.1, Kassambara, 2023) and Inkscape were used.

3. Results

3.1. Diversity metrics: Spatial patterns across Europe

3.1.1. Species richness

The maximum count of species in one grid cell was 91 in central Catalonia, while the lowest count was just 1 in northern-most Scandinavia and Russia. Sterrhinae species richness is highest in southern Spain, Catalonia, the Pyrenees, along the Mediterranean coast of France as well as in southern Bulgaria (see Figure 1). Additional areas with intermediate-high species richness were identified in the west of the study area in Italy and Eastern France. In Southern Central Europe, these areas are found from the East of France to the Pannonian Areas of Slovakia and Hungary, and with a particularly high level in the southern Central Alps. East Romania, Greece, Ukraine, and South-Eastern European Russia show intermediate-high taxon numbers as well, especially in Crimea, the Dnepr-valley, and around the Volga valley. In contrast, Northern Great Britain, Scandinavia, Northern European Russia and, the area north of the Caspian Sea are extremely species poor. Moreover, the low mountain ranges north of the Alps, the northern Balkans, the northern lowlands of Germany and the central and northern mountains of Spain showed very low species numbers.

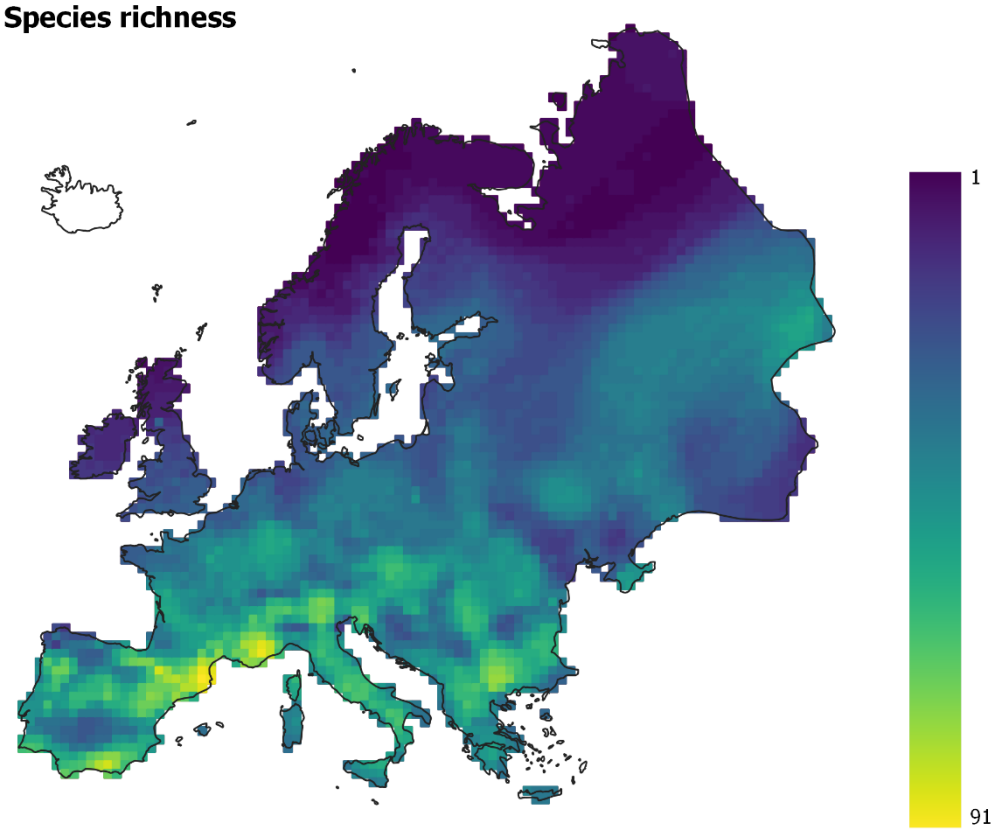

Figure 1: Species richness of Sterrhinae in Europe. Map (study area) colour-coded by number of species per grid cell (dark blue = one species to bright yellow = 91 species).

3.1.2. Phylogenetic diversity

Similar to species richness, mean PD is highest in southern and north-eastern Spain and southern France, being generally high along the entire Mediterranean coastal and adjacent areas of Southern Europe (see Figure 2). Intermediate to high values for PD are found in Central and eastern Europe. Overall, there is a latitudinal gradient present, with the highest PD values located in the South, which decrease towards higher latitudes. On the eastern border of the study area one can see a patch with increased PD, which is probably the result of overlapping distribution areas from species who's primarily spread is over eastern (Asian) Russia.

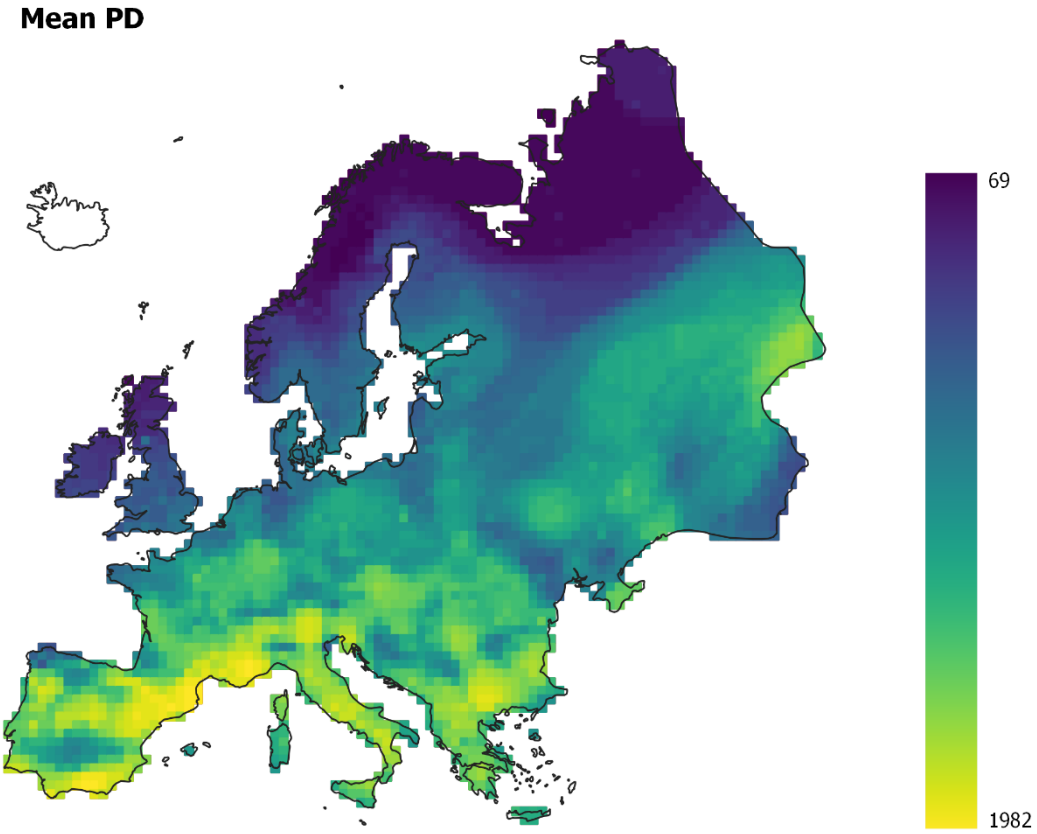

Figure 2: Phylogenetic diversity (Faith's PD) of Sterrhinae in Europe. Map (study area) colour-coded by mean PD per grid cell (dark blue = low PD to bright yellow = high PD).

3.1.3. Phylogenetic structure

Phylogenetic clustering was observed in different regions, when comparing mean NTI and mean NRI values (see Figure 3). Phylogenetic clustering indicated by NTI > 0 was detected only in northern Europe, with highest values in Great Britain and Southern Scandinavia. Here it is important to notice, that those are areas with low taxon number, which may affect calculations of NTI. The standard deviation and range of NTI values were highest in the southern regions, where more taxa occur. Phylogenetic clusters detected by NRI > 0 were observed in Southern Europe and Great Britain, with the highest values occurring in southern Spain. Phylogenetic overdispersion was detected for NRI in almost whole central to northern Europe, while for NTI it was highest in southern Europe. Standard

deviation and range of NRI were highest in northern Spain and France and were high in central Europe and southern Scandinavia. Significant p-values for NRI were observed in southern Spain (clustering) and central Europe to southern Scandinavia (overdispersion) (see Figure 4). NTI showed significant p-values in central Europe, England, Ireland and southern Scandinavia (clustering).

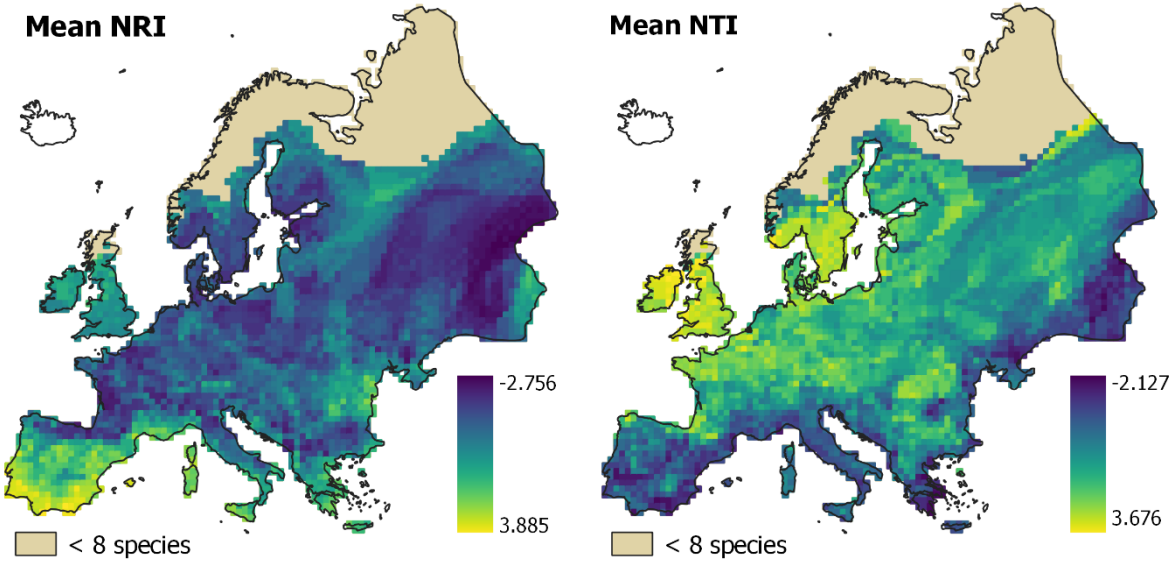

Figure 3: Phylogenetic structure (net relatedness index, NRI; and nearest taxon index, NTI) of Sterrhinae in Europe. Map (study area) colour-coded by mean NRI (left) and mean NTI (right) per grid cell (dark blue = low NRI/NTI to bright yellow = high NRI/NTI). Grid cells with less than 8 species were excluded for the calculation of NRI and NTI and are coloured in beige.

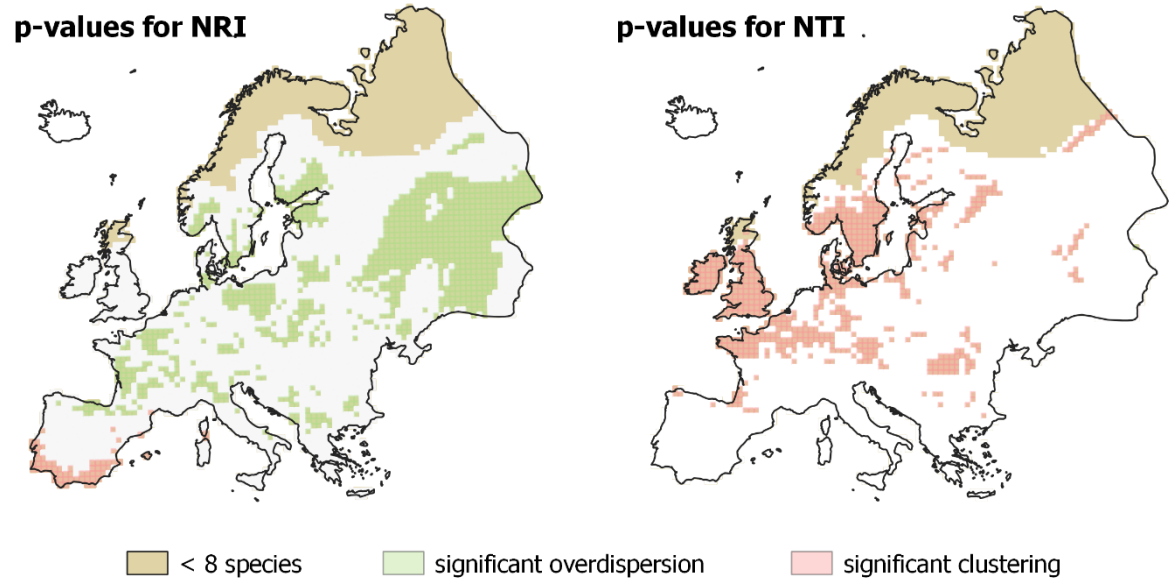

Figure 4: Significance of phylogenetic structure (net relatedness index, NRI; and nearest taxon index, NTI) of Sterrhinae in Europe. NRI (left) and NTI (right). Orange grid cells show significant clustering, while green grid cells show significant overdispersion. Grid cells with less than 8 species were excluded for the calculation of NRI and NTI and are coloured in beige.

3.1.4. Phylogenetic endemism and CANAPE

Phylogenetic endemism among Sterrhinae moths was highest on the Iberian Peninsula, the Mediterranean Islands, southern France, and Italy and Greece (see Figure 5). It was lowest in northern Russia and Scandinavia, but generally low throughout all other parts of Europe. Standard deviation and range of PE values were quite similar to the mean PE patterns, being highest in the south and lowest in Central and Northern Europe.

Centres for paleo- and neo-endemism were identified using the "CANAPE" approach. While for most parts of Europe no significant categorisation of endemism was possible, the southern-most and eastern-most regions showed significant patterns (see Figure 5). Southern Spain was found to include large areas of super-endemism. Super-endemism was also found in southern Italy and Greece, as well as on the Mediterranean islands Mallorca, northern Corsica, Crete, and Lesbos. Large areas of the Iberian Peninsula, as well as southern France and Italy, eastern Greece and south-eastern European Russia showed mixed endemism (= both paleo- and neo-endemism). Paleo-endemism was recorded in southern Greece and on the eastern borders of European Russia. No area of pure neo-endemism was identified.

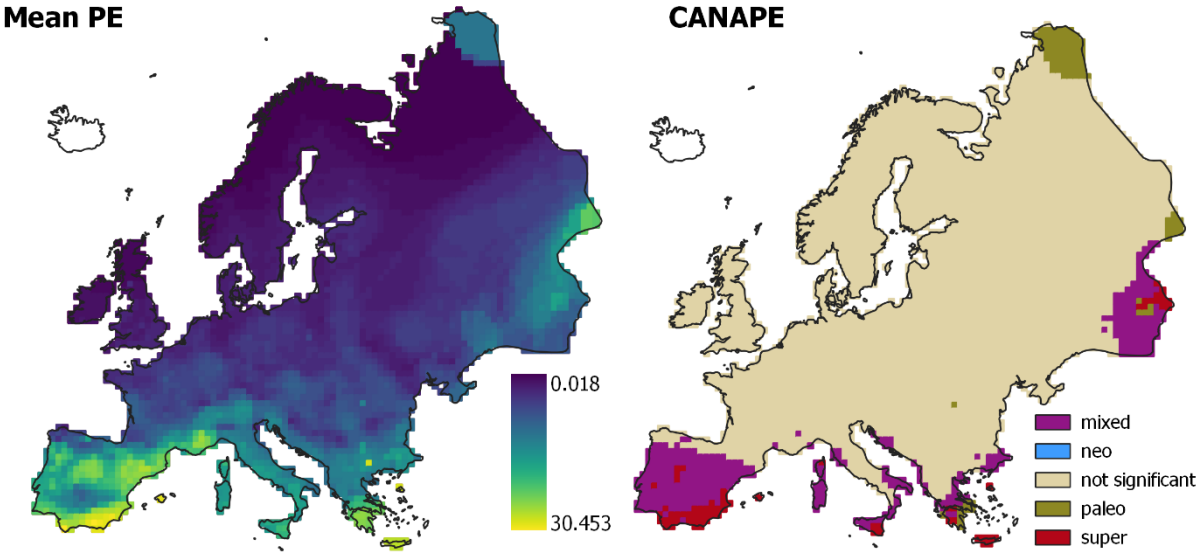

Figure 5: Left: Phylogenetic endemism (PE) of Sterrhinae in Europe. Map (study area) colour-coded by mean PE per grid cell (dark blue = low PE to bright yellow = high PE). Right: CANAPE analysis for European Sterrhinae in Europe, colour-coded for different types of endemism (blue = neo-endemism, olive-green = paleo-endemism, purple = mixed endemism, red = super-endemism, beige = not significant).

3.1.5. Evolutionary distinctiveness

Results for mean evolutionary distinctiveness were similar to the patterns of the CANAPE analysis, highlighting the eastern parts of Europe as places with high evolutionary distinctiveness (see Figure 6). However, for most parts of Europe mean evolutionary distinctiveness was even.

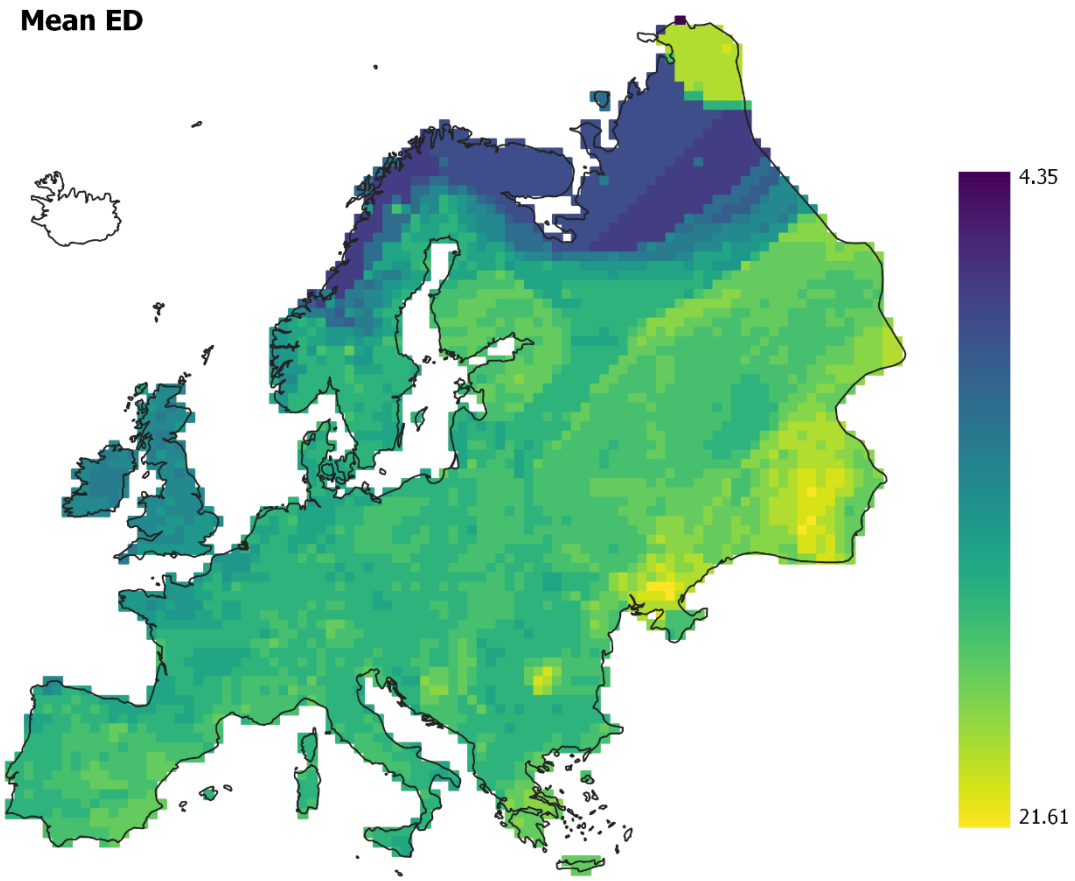

Figure 6: Evolutionary distinctiveness (ED) of Sterrhinae in Europe. Map (study area) colour-coded by mean ED per grid cell (dark blue = low ED to bright yellow = high ED).

3.1.6. Overall patterns

The distribution patterns of Sterrhinae in Europe follow roughly a latitudinal gradient with high species richness PD, PE, NRI clustering and NTI overdispersion in southern regions, followed by intermediate species richness, high PD, low PE, NRI overdispersion and NTI clustering in central Europe and low species richness, low PD and low PE in northern Europe.

3.1.7. Correlation between metrics

The calculation of each diversity metric using the 10,000 tree-sample yielded overall similar results, as shown by values for standard deviation and range per grid cell. For this reason, all regression and correlation analysis were calculated by using the mean of each metric per grid cell. Some of the diversity metrics were highly correlated (see Figure 7). Especially species richness and PD were closely related and also PE was positively correlated with PD and species richness.

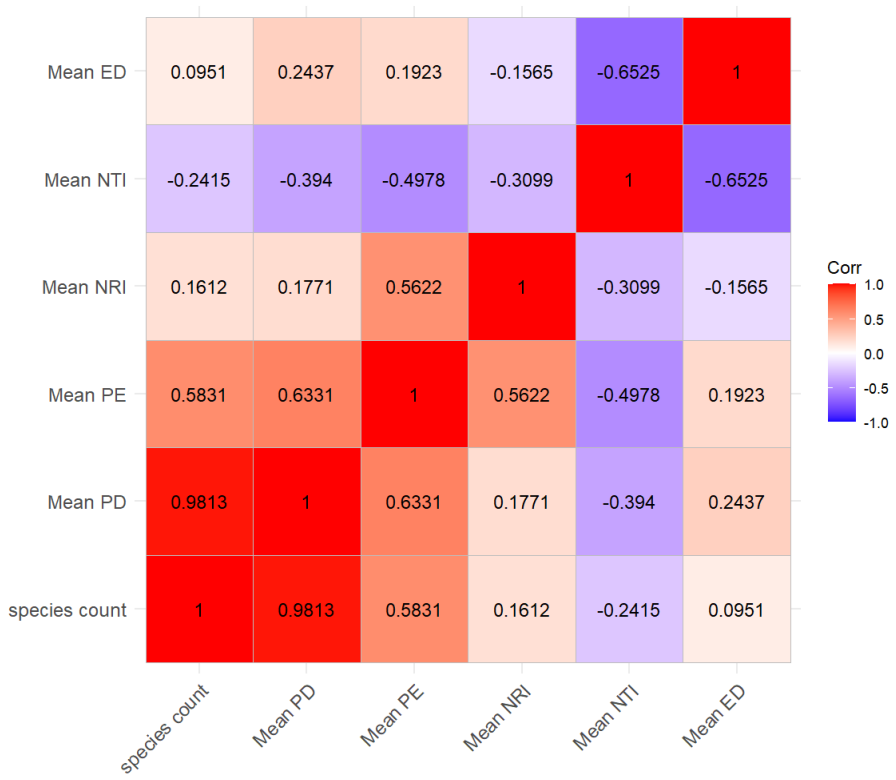

Figure 7: Correlation matrix of investigated diversity metrics, calculated with the pearson correlation coefficient, without spatial autocorrelation. Abbreviations: ED = Evolutionary Distinctiveness, NRI = Net relatedness index, NTI = Nearest Taxon Index, PD = Phylogenetic Diversity (Faith), PE = Phylogenetic Endemism

Especially PD and PE correlated strongly with species richness (see Figure 8). These positive correlations were significant (PD: adjusted $R^2 = 0.974$, $p<0.001$; PE: adjusted $R^2 = 0.332$, $p<0.001$), also after correcting for spatial autocorrelation ($p<0.001$). For NRI and NTI, the relationship with species richness was also significant ($p<0.001$), and both showed a higher adjusted R^2 when using a quadratic model (NRI: adjusted $R^2 = 0.133$, $p<0.001$; NTI: adjusted $R^2 = 0.066$, $p<0.001$). The quadratic models remained significant after correction for spatial autocorrelation (NRI: $p = 0.003$, NTI: $p = 0.004$) and were also favoured by the AIC compared to the linear model (NRI AIC linear: 8295.505, NRI AIC quadratic: 7913.930; NTI AIC linear: 8651.996, NTI AIC quadratic: 8626.287).

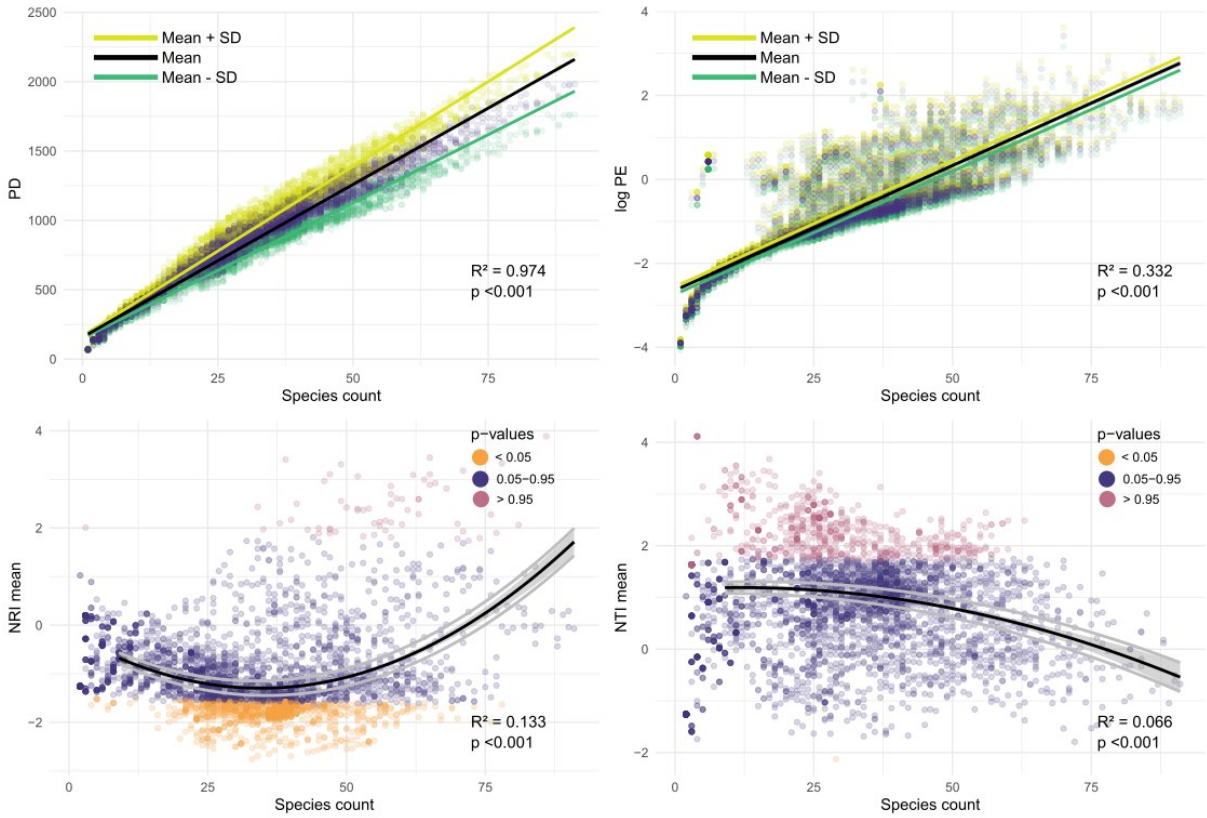

Figure 8: Relationship between diversity metrics (PD, PE, NRI, NTI) and species richness for each grid cell. For PD and PE mean and standard deviation are plotted in different colour. For NRI and NTI p-values are coloured: p-values < 0.05 indicate significant phylogenetic clustering, while p-values > 0.95 indicate significant phylogenetic over-dispersion. Grey lines show the standard deviation. Note: for NRI and NTI all observations are plotted, however regression curves are fitted with observations from grid cells with more than 8 species present. Abbreviations: NRI = Net relatedness index, NTI = Nearest Taxon Index, PD = Phylogenetic Diversity (Faith), PE = Phylogenetic Endemism

3.2. Phylogenetic diversity and environmental factors

3.2.1. Temperature

Phylogenetic diversity was higher in warmer climates (see Figure 9). Mean annual temperature was a significant predictor for PD (adjusted $R^2 = 0.535$, $p<0.001$), showing a roughly linear relationship especially in regions with a mean annual temperature above 0°C. However, when correcting for spatial autocorrelation, the relationship was not formally significant ($p = 0.069$). PE increased significantly with rising mean annual temperature (adjusted $R^2 = 0.236$, $p <0.001$). However, after correcting for spatial autocorrelation, the significance was no longer given ($p = 0.086$). The relationship between mean annual temperature and NRI as well as NTI was significant too (both $p<0.001$), in this case a quadratic expression may better explain the variance than a linear one (NRI: adjusted $R^2 = 0.439$, AIC linear: 7583.051, AIC quadratic: 6494.794; NTI: adjusted $R^2 = 0.177$; AIC linear: 8524.423, AIC quadratic: 8212.797). NRI was generally increasing with rising temperature, showing significant patterns of phylogenetic clustering in the warmer grid cells and phylogenetic overdispersion in grid cells with intermediate temperature. NTI was highest in grid cells with intermediate temperature and dropped in warmer grid

cells. The quadratic relationship between mean annual temperature and the phylogenetic metrics NRI and NTI remained significant, even after correcting for spatial autocorrelation (NRI: p = 0.037, NTI: p= 0.003).

When comparing different climate parameters (mean annual temperature, mean temperature warmest month, mean temperature coldest month, annual temperature range and annual precipitation), mean annual temperature was the strongest predictor for explaining variance of the diversity metrics, except for NTI, where mean temperature of the warmest month had a higher adjusted R^2 (see Appendix table A9).

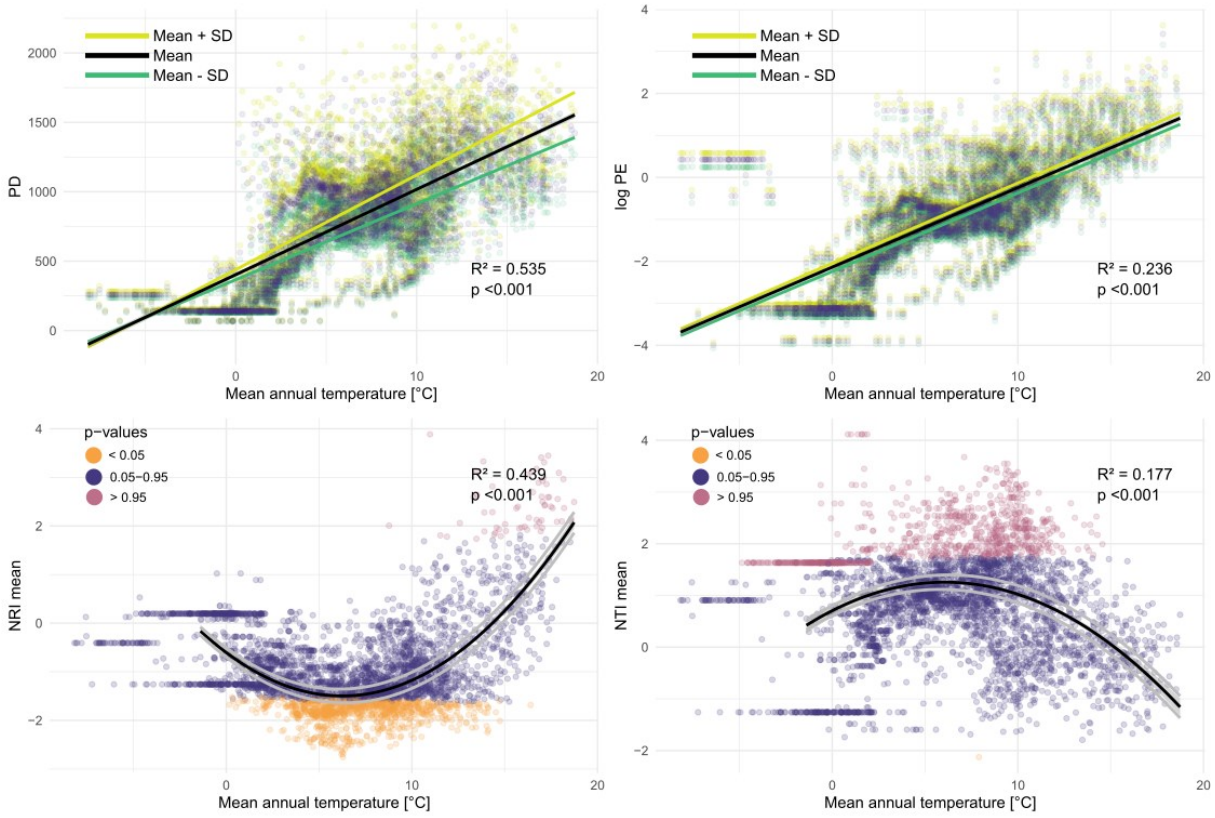

Figure 9: Relationship between diversity metrics (PD, PE, NRI, NTI) and mean annual temperature for each grid cell. For PD and PE mean and standard deviation are plotted in different colour. For NRI and NTI p-values are coloured: p-values < 0.05 indicate significant phylogenetic clustering, while p-values > 0.95 indicate significant phylogenetic over-dispersion. Grey lines show the standard deviation. Note: for NRI and NTI all observations are plotted, however regression curves are fitted with observations from grid cells with more than 8 species present. Abbreviations: MAT = Mean Annual Temperature, NRI = Net relatedness index, NTI = Nearest Taxon Index, PD = Phylogenetic Diversity (Faith), PE = Phylogenetic Endemism

3.2.2. Latitude

PD and PE declined with increasing latitude (see Figure 10). Latitude was a significant predictor for PD, showing a high adjusted R^2 of 0.724 ($p<0.001$). For PE latitude was a significant predictor too, however adjusted R^2 was much higher ($R^2 = 0.581$, $p <0.001$), when PE was square root transformed. NRI and NTI showed significant quadratic relationships with latitude (adjusted R^2 NRI = 0.463, adjusted R^2 NTI = 0.263, NRI and NTI $p <0.001$,), with NRI decreasing and NTI increasing with latitude. The quadratic relationship was a better fit, than the linear one (NRI AIC linear: 7694.410.423, NRI AIC

quadratic: 6518.132; NTI AIC linear: 8512.845, NTI AIC quadratic: 8142.449). All of these relationships remained highly significant after correcting for spatial autocorrelation (PD: $p < 0.001$, PE: $p < 0.001$, NRI: $p < 0.001$, NTI: $p = 0.005$). Evolutionary distinctiveness was linked to latitude as well, showing a quadratic relationship, that reached a maximum in latitudes between 45° and 55°, and decreased at higher latitudes. The quadratic model had an adjusted R^2 of 0.419 and was significant with and without correction for spatial autocorrelation ($p < 0.001$) (AIC linear: 19007.33, AIC quadratic: 18492.30).

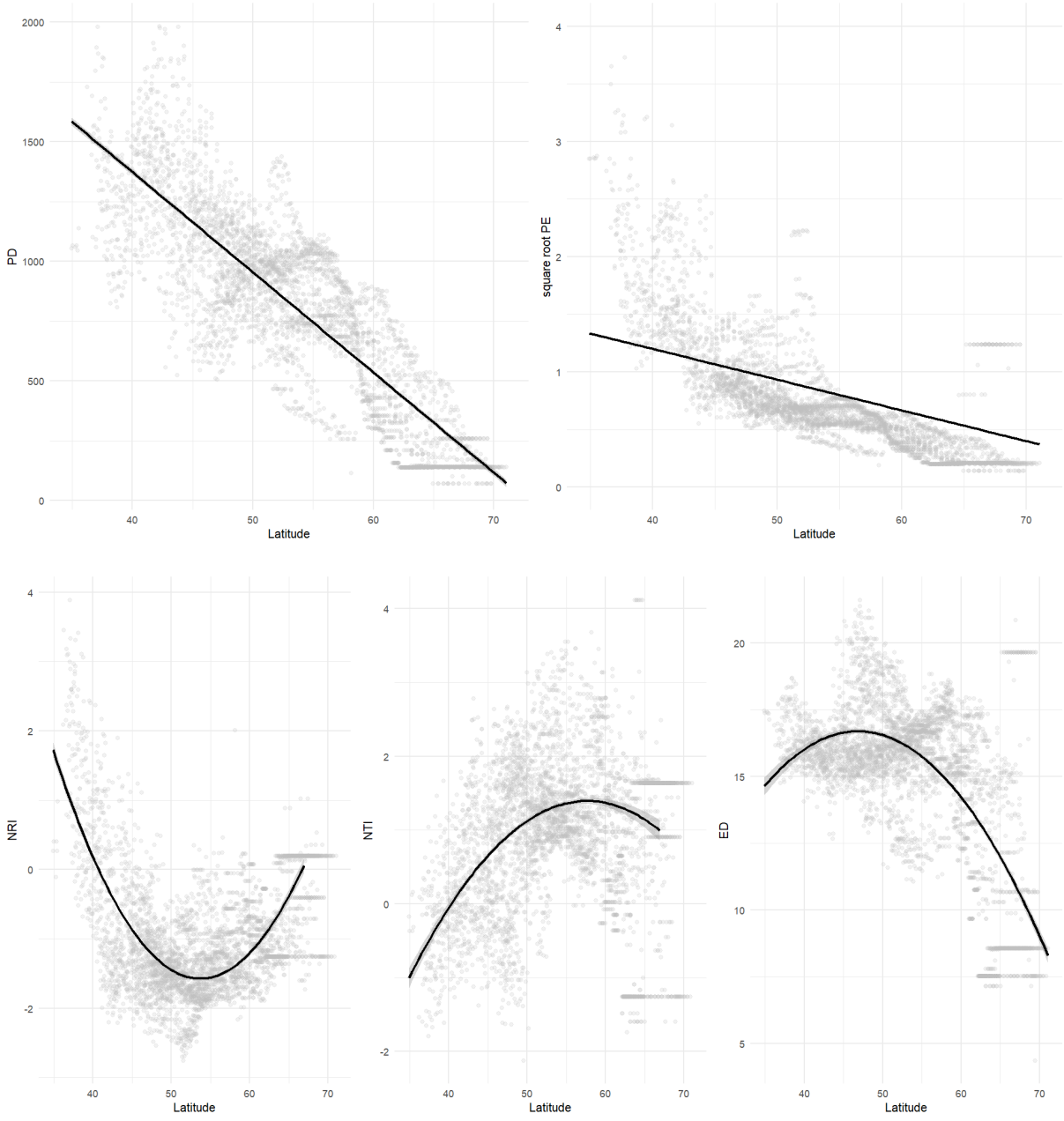

Figure 10: Relationship between diversity metrics (PD, PE, NRI, NTI, ED) and latitude. Abbreviations: ED = Evolutionary distinctiveness, NRI = Net relatedness index, NTI = Nearest Taxon Index, PD = Phylogenetic Diversity (Faith), PE = Phylogenetic Endemism

3.2.3. Mountains

Species richness, phylogenetic diversity, phylogenetic endemism, and NRI were slightly higher in mountainous grid cells compared to the lowland areas (see Figure 11). A Wilcoxon test was performed and showed that there was a significant difference in means of the diversity metrics (species richness, PD, PE, NRI, and NTI) of mountainous compared to lowland grid cells (in all cases $p<0.001$). However, the effect size (calculated with the formula: $r = \frac{z}{\sqrt{N}}$) was small for all metrics (species richness: $r = 0.218$, PD: $r = 0.215$, PE: $r = 0.207$, NRI: $r = 0.098$, NTI: $r = 0.139$).

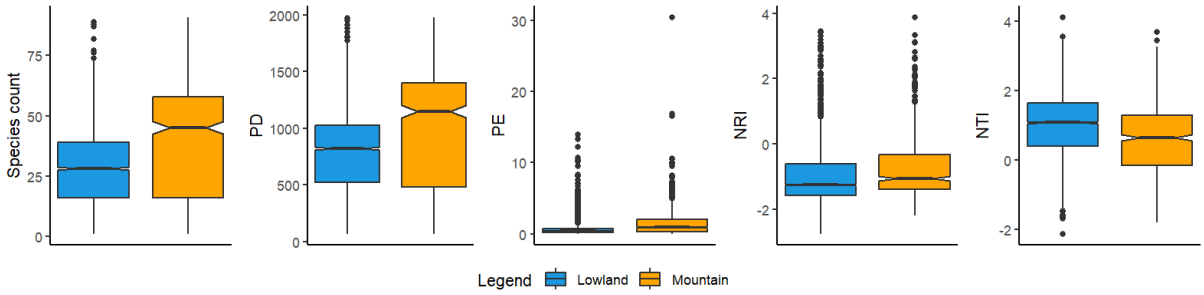

Figure 11: Comparison of diversity metrics (species richness, PD, PE, NRI, NTI) between lowland (blue) and mountains (orange). Note, that sample sizes vary between group (lowland vs mountain) and none of these differences were significant. Abbreviations: NRI = Net relatedness index, NTI = Nearest Taxon Index, PD = Phylogenetic Diversity (Faith), PE = Phylogenetic Endemism

3.3. Ecological traits

3.3.1. Food specialization / Mean diet breadth

Mean diet breadth increased towards northern Europe (see Figure 12). While most specialists were present in lower latitudes, especially on the Iberian Peninsula, and some southern grid cells along the Mediterranean coastline, the rest of Europe showed intermediate to wide mean dietary breadths. In Ukraine and eastern Russia there was also a high amount of specialist species, resulting in very small mean diet breadth scores for the grid cells there. When excluding this eastern cluster of specialist dominated grid cells (that might be an artefact due to low species numbers, with very few records for food specialisation as well as edge effects from species showing their main distribution in Asia in environments different to those in Europe) linear models found latitude and temperature as significant predictors for Mean diet breadth (latitude: $R^2 = 0.642$, $p<0.001$; temperature: $R^2 = 0.435$ $p<0.001$) (see Figure 13). After correcting for spatial autocorrelation, the relationship between diet breadth and latitude remained significant, however the significance of the relationship between diet breadth and temperature was no longer given.

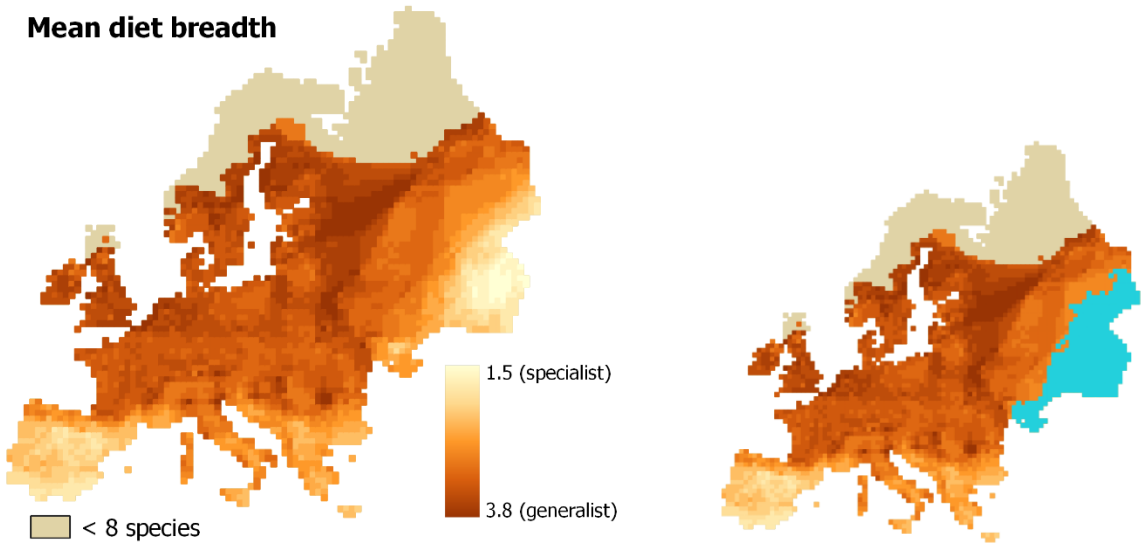

Figure 12: Mean diet breadth of Sterrhinae in Europe. Map (study area) colour-coded by mean diet breadth per grid cell (white = narrow mean diet breadth, dark orange = wide mean diet breadth). Mean diet breadth was evaluated by taking the average diet breadth score of the species present per grid cell, categorized as follows: 1 – feeding only on one plant genera (monophagous); 2 – feeding on only one plant family (oligophagous); 3 – feeding on 2-4 plant families (moderately polyphagous); and 4 – feeding on more than 5 plant families (highly polyphagous). Grid cells with less than 8 species were excluded and are coloured in beige. Map on the right shows in light blue the eastern outliers that were excluded for later analysis.

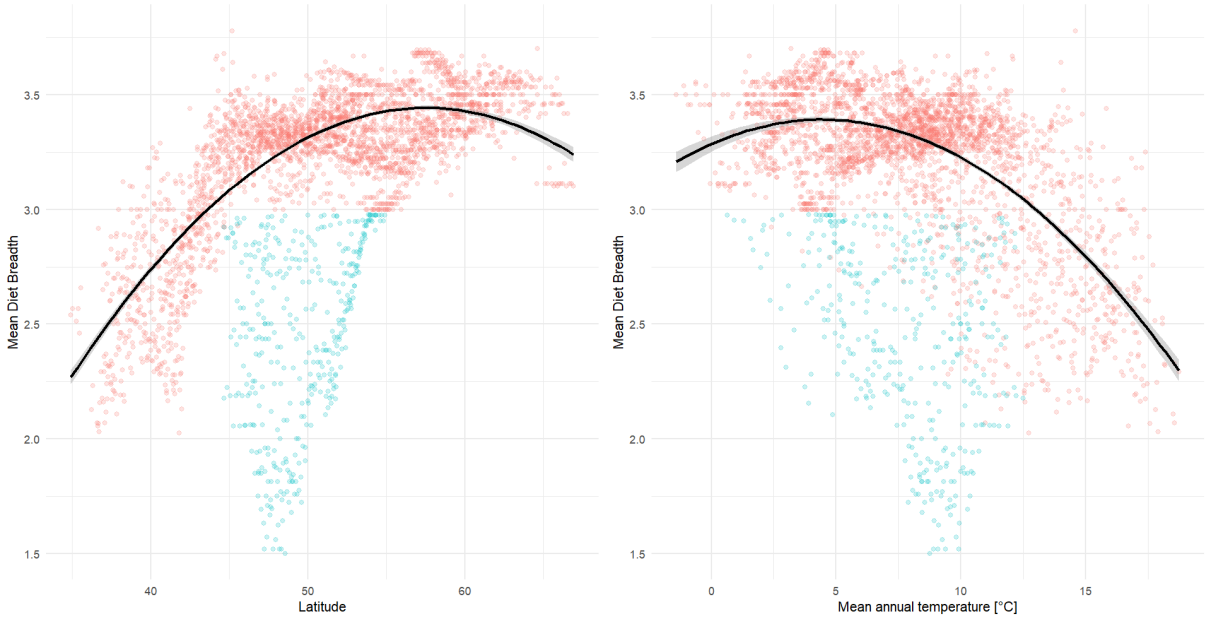

Figure 13: Relationship between mean diet breadth and latitude and mean annual temperature as predictors for grid cells with more than 8 species present. Note: all observations are plotted, however eastern outliers (light blue) are excluded for calculating the regression curves. Mean diet breadth was evaluated by taking the average diet breadth score of the species present per grid cell, categorized as follows: 1 – feeding only on one plant genera (monophagous); 2 – feeding on only one plant family (oligophagous); 3 – feeding on 2-4 plant families (moderately polyphagous); and 4 – feeding on more than 5 plant families (highly polyphagous).

3.3.2. Voltinism

Voltinism was correlated with mean annual temperature and latitude (see Figure 14). Univoltine species (one generation per year) were increasingly frequent in colder climates (quadratic relationship mean annual temperature and univoltine species with adjusted R^2 = 0.610, p <0.001, AIC linear: 35811.38, AIC quadratic: 33832.57). The opposite holds true for species that are known to be flexible in their numbers of generations per year, which were showing increasing presence in warmer regions. There was a steep rise in univoltine species towards higher latitudes, which was best described in a quadratic model with latitude as predictor (adjusted R^2 = 0.664, p <0.001, AIC linear: 36020.76, AIC quadratic: 33241.12). Not only did latitude as predictor explain more variance than temperature does (according to the adjusted R^2 values), but it also remained significant (p<0.001) after correction for spatial autocorrelation, which was not the case for mean annual temperature (p>0.3).

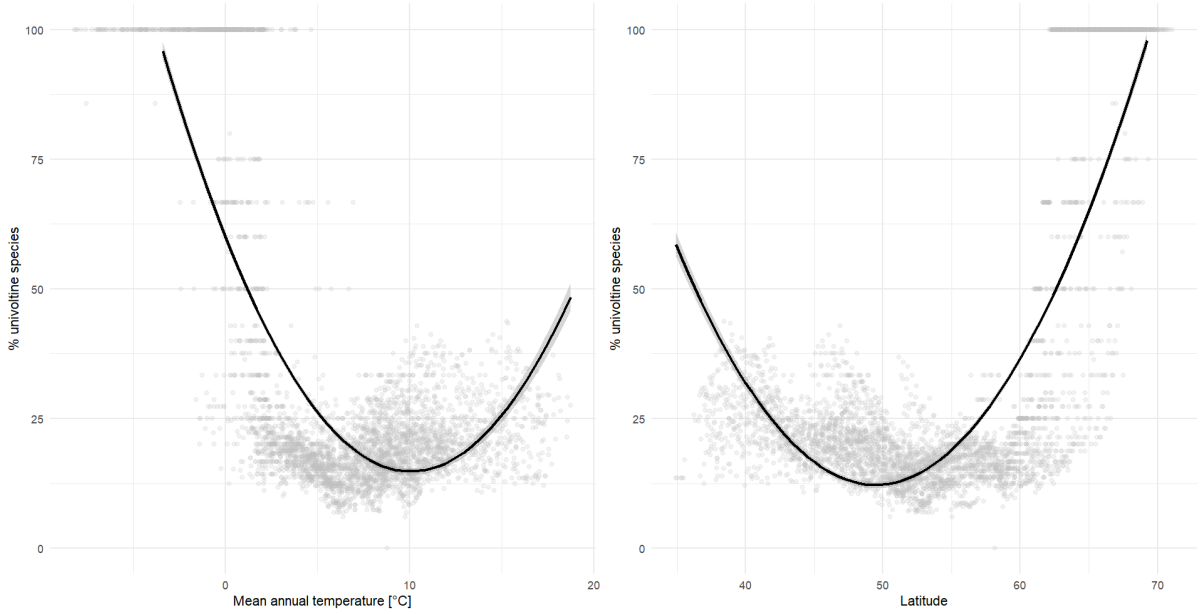

Figure 14: Relationship between univoltinism and mean annual temperature and latitude as predictors.

3.3.3. Range size

Range size and latitudinal range were significantly correlated, showing a positive linear relationship (adjusted $R^2 = 0.8347$ and $p < 0.001$). Species that showed a wide distribution range were usually also present over a large latitudinal amplitude (see Figure 15).

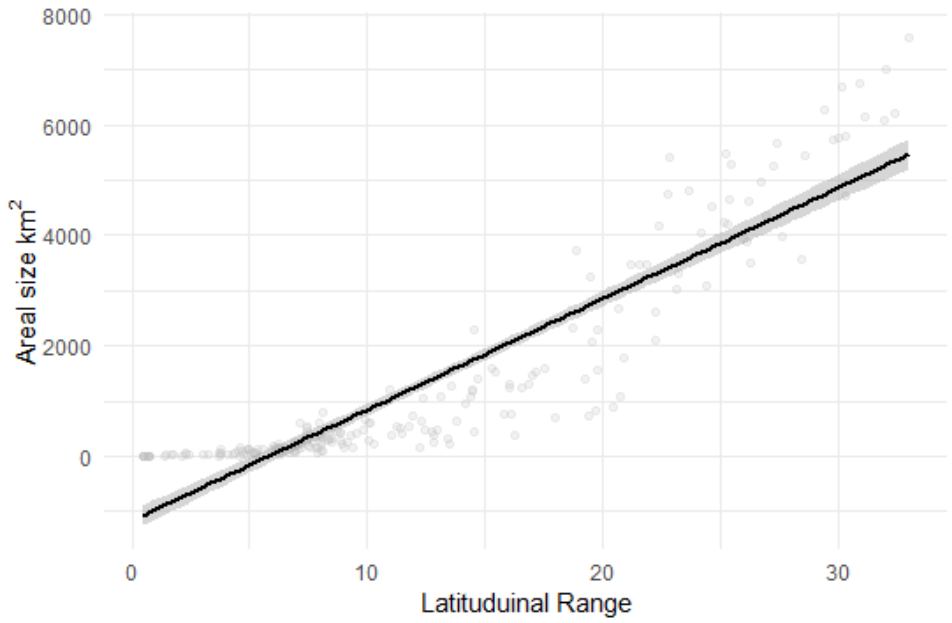

Figure 15: Relationship between range size and latitudinal range of European Sterrhinae species. Each dot represents a species. 95% confidence intervals in grey.

4. Discussion

The current study provides insights into the phylogeographic patterns of a whole subfamily of European geometrids. This is the first study analysing phylogenetic diversity, endemism and structure as well as ecological trait patterns of Sterrhinae in Europe. Spatial and genetic biodiversity approaches do not only help us understand global patterns of biodiversity and biogeographic history of taxa, but they also inform decision making in conservation. Combining (phylo)genetic- and spatial data has been successfully used in recent studies to investigate insect biodiversity patterns (Earl et al., 2021; French et al., 2023). The spatial resolution of these macroecological/macrogenetic studies varies, usually depending on the study area size. For example, a study on phylogenetic diversity on butterflies in North America used a grid with the resolution of 100 x 100 km (Earl et al., 2021) and a study on global insect genetic diversity one of 193 km × 193 km (French et al., 2023). The current study gives insights into the whole Sterrhinae subfamily for the European continent on a very fine spatial scale of 50 x 50 km.

While this study benefited from open source data such as GBIF for distribution data and BOLD for genetic data, I want to highlight that it would not have been possible to compile such a detailed and reliable database, complemented by life-history and biological information on a species level, without the extensive descriptions of the 'Geometrid Moths of Europe' series, by Hausmann and colleagues (2004, 2012, 2019). Such monographs on taxonomic groups are extremely valuable for any large scale macroecological analysis.

4.1. Phylogenetic diversity metrics and structure

4.1.1. Diversity patterns of European Sterrhinae

The observed species richness pattern reflected in a quantitative manner the preferences of Sterrhinae for warmer climates, established qualitatively by earlier authors (Hausmann, 2004), being generally higher in lower latitudes and showing the highest numbers of species in Mediterranean Spain, France, Italy, and Greece. In vast northern areas, in contrast, species richness was very low. Phylogenetic diversity (Faith' PD) showed very similar patterns as species richness, indicating that in areas with warm climates more phylogenetic lineages have accumulated. This latitudinal gradient of biodiversity in Europe has historically been explained with biotic impoverishment through Pleistocene glacial oscillations (Hewitt, 1996; Brown, 2014). The reoccurring periods of ice cover restricted species to lower latitudes and inhibited spreading, resulting in parapatric and allopatric divergence events that lead to high taxon numbers in lower latitudes (Hewitt 1996; Brown, 2014). Additionally, even if some species managed to spread northwards, only few of them were successful in persisting in the harsh environments of higher latitudes, as they are more difficult to adapt to (Hewitt, 1996; Brown, 2014).

An increase in genetic diversity towards lower latitudes has been recorded within species as well (Hewitt 1996; Fonseca et al., 2023; French et al., 2023). It has been suggested that

populations with low genetic variation are often derived from rapid expansions (i.e., small number of colonizing individuals that define the majority of genotypes of the new population) often in addition with or solely from bottleneck effects (Hewitt, 1996; Swaegers et al., 2013; Schär et al., 2017). For example, lycaenid butterflies show a decrease in genetic variation at higher latitudes, which is thought to be the result rapid range extensions between or after glaciation events and founder effects (Schmitt & Seitz, 2001; Kühne et al., 2017; Schär et al., 2017). There is evidence from many other European insects that genetic diversity is lower in northern populations, which is often assumed to be caused by glaciation cycle depending re-colonializations (Hewitt, 1996; Schmitt & Seitz, 2001; Kerdelhué et al., 2009). Another possible explanation is that founder populations in higher latitudes were locked in northern refugia during reoccurring cold periods which led to a decrease of genetic variance, as for example in the butterfly *Polyommatus icarus* in the British Isles (Keyser et al., 2012). These effects may also explain the low phylogenetic diversity of Sterrhinae in northern regions of Europe (see Figure 2) that were likely colonized from southern refugia by few closely related species or species that split up after the colonisation.

It is interesting to note that within the central European region species richness and particularly phylogenetic diversity was considerable low in northern alpine regions, and northern lowlands such as North Germany. Also, within the Iberian Peninsula, which represents the hotspot for Sterrhinae diversity, there are places of very low species richness and phylogenetic diversity, congruent with mountainous areas (which represent the colder regions within Spain). This can be explained again by the preference of Sterrhinae for warm and arid environments.

It has been demonstrated successfully for Orthopterans, that the current distribution and phylogeny of xerothermophilous species can be closely linked to migratory routes from Mediterranean refugia to other parts of Europe during interglacial periods (Hewitt, 1996; Keyneres et al., 2009). The adaptation to aridity happened probably during the Messinian crisis in the Pliocene, when the Mediterranean turned into an arid-semiarid environment. During glaciation, the Mediterranean hosted many species, which explains the high taxon richness of especially xerothermophilous species (Keyneres et al., 2009). Sterrhinae seem to be no exception as they showed highest phylogenetic diversity and endemism in Mediterranean regions. The high amount of endemism on Mediterranean islands can be explained by the subsequent isolation of islands from other islands as well as from the mainland due to sea level rise, and breakdown and fragmentation of an earlier continental plate (Keyneres et al., 2009). Also, dispersion events from Africa might have affected current biogeography patterns. A study on tenebrionid beetles showed that the Mediterranean *Blaps* species probably originated in the Arabian and north-east African region and dispersed to Europe via western North Africa (Condamine et al., 2013). There are also many Sterrhinae genera in Europe that are widely distributed in Africa (Hausmann, 2004), suggesting that migration between Africa and Europe is a possible scenario. For example many species of the genus *Idaea*, which are present in North Africa, are in Europe distributed only on the southern coasts or island of Italy and Spain (e.g., *I. attenuaria*, *I.completa*, *I. mutilata*, *I. raineri*). For other lepidopterans it could be shown that they possibly survived glaciations outside the 'classic' mediterranean refugia, such as

the Alpine and Carpathian regions, the Balkan Peninsula and the Caucasus (Schmitt et al., 2007; Haubrich & Schmitt, 2007; Paučulová et al., 2016; Andersen et al., 2017). Those 'extra-mediterranean' refugia however don't seem to have played a particular role for Sterrhinae species, as reflected by their ecological niche and also as displayed by current diversity and dispersal patterns as shown in this study.

Phylogenetic diversity of Sterrhinae was also high in regions with high endemism, which is congruent with the hypothesis that refugia are usually more diverse in their species and genetic assemblages (Hewitt, 1996; Keppel et al., 2012; Paučulová et al., 2016). The genetic structures of populations living in glacial refugia areas are thought to be heavily influenced by past expansions and contractions of the ranges of these species (Hewitt, 1996; Andersen et al., 2017; Andersen et al., 2019). For European Sterrhinae, the link between evolutionary distinctiveness and latitude shows that distinct lineages tend to accumulate in lower latitudes. This, again, leads to the conclusion, that Mediterranean communities contain more genetic diversity than northern ones.

However, though highly correlated, differences between species richness patterns and PD were observed in central Europe. While species richness showed a clear south-north pattern from high to low species richness with hotspots in Spain and southern France, phylogenetic diversity had its maxima in Portugal, southern and central Spain, almost along the entire coast from Italy to the Balkans, and on Mediterranean islands. Furthermore, there were patterns of increased PD distributed over several parts of central and eastern Europe, especially France, Germany and Pannonic areas. These places in central and eastern Europe probably provide patches of dry grassland habitats, that may be not high in species number, however rich in phylogenetic lineages. This might be the effect of phylogenetically distinct relict species, such as for example *Emmiltis pygmaearia*, which is primarily distributed in southern Europe (Italy, France) but also present in the southern Alps, or also phylogenetically distinct but wide-spread species of the genera *Lythria* and *Rhodostrophia*, which increase the phylogenetic diversity in the grid cells of their distribution area. Those areas also correlated with significant amounts of phylogenetic overdispersion (NRI), indicating accumulation of distantly related lineages in those places. These places in central Europe might inhabit a combination of species from different refugia, both the south (Mediterranean refugia) and the east (refugia in eastern Europe and relict species from steppe and grassland habitats).

4.1.2. Phylogenetic structure and species assemblages

Phylogenetic diversity and structure not only tell us about high or low amounts of distant evolutionary lineages, but it can also help to investigate whether those lineages diverged long ago or rather recently. The metrics NRI (net relatedness index) and NTI (nearest taxon index) are both indicators for phylogenetic clustering (positive values) and phylogenetic overdispersion (negative values) (Manish, 2021). NRI is more sensitive in detecting old phylogenetic splits, while NTI is more sensitive to recent ones. As NRI and NTI were negatively correlated across regional assemblages of European Sterrhinae moths, this shows that they detected different areas for clustering and overdispersion. The

high NRI values in species-rich regions with high phylogenetic diversity (i.e, southern Spain and southern France) were statistically significant, which indicates that the accumulated lineages in those areas go back to rather ancestral radiation/divergence events. Sterrhinae species assemblages in the Mediterranean regions of Europe are therefore built up from several clades that split up early but have not necessarily diverged much since then. A well-established explanation how this type of assemblages may form is "environmental- or ecological filtering" (Webb et al., 2002; Cavender-Bares et al., 2009). It describes that closely related species which share similar functional traits are more likely to withstand certain environmental conditions and therefore co-occur in environments where other species-groups will not persist (Webb et al., 2002; Kembel & Hubbel, 2006; Emerson & Gillespie, 2008). In the case of Sterrhinae, these would concern xerothermic habitats, where apparently several ancestral lineages of Sterrhinae were able to persist. A different concept explaining the opposite phenomenon (phylogenetic overdispersion) has been often interpreted as an indicator for competitive exclusion and other negative density-dependent interactions (Kembel & Hubbel, 2006; Cavender-Bares et al., 2009). This is often assumed, as closely related species are more likely to share similar traits, a reason why the phenomenon of increased competition among closely related species is also known as the phylogenetic limiting similarity hypothesis (Violle et al., 2011). However, there is no direct evidence for European Sterrhinae, that competition (especially at the scale of the current study) had a particular effect on phylogeographic patterns. The only region, where this hypothesis might apply, is Central Europe, because of its high phylogenetic overdispersion (referring to NRI), however a more likely explanation for this pattern is that the variety of habitats in Central Europe is appealing to both generalists and specialists, therefore not filtering for a specific phylogenetic clade.

Explanations like environmental filtering or competitive exclusion need to be considered carefully, as the scale of their influence on the species assemblages remains still unknown (Cadotte & Tucker, 2017). Furthermore, there are several additional factors that can influence the phylogenetic structure of species assemblages, such as mutualism, predation, isolation, or ongoing disturbances (Vamosi & Vamosi, 2007; Verdu & Pausas, 2007; Cavender-Bares et al., 2009). It is also important to note that the spatial scale of a study on community phylogenetic structure, has to be considered when interpreting the results (Webb et a., 2002). In this case the spatial scale of the analysis results in a lack of fine-scaled resolution (one grid cell having the area of 2500 km²). The differentiations between "true" species communities might therefore be difficult, as the spatial units of my study (i.e., grid cells) do not represent habitats but rather geographic entities. The present study works on a regional scale, allowing it to differentiate between assemblages of different environments (coastal, inland, etc). The phylogenetic structure therefore rather takes into account a larger regional species pool, more prone to environmental- than habitat-filtering. To conclude, on the scale of this study environmental filtering (for extremely phylogenetically conserved traits) provides an explanation to some degree, while competitive exclusion rather doesn't.

For the northernmost regions of Europe not enough species were present to interpret the phylogenetic structure. This is not surprising, since the subfamily of Sterrhinae is generally known to be mostly absent from boreal regions (Hausmann, 2004, Seifert et al.

2022a). In the temperate and central-northern regions of Europe mainly recent significant phylogenetic clustering events as indicated by high NTI values (significant) were found (Figure 3 and 4). As these regions are rather species poor, this could be the result of few generalist sister species which were the only ones able to inhabit these regions, such as *Timandra comae*, *Timandra griseata*, as well as several *Cyclophora* species.

Places of high biodiversity, so-called hot spots, are often categorized either as "cradles" (places where rapid radiation happens and many recent speciation events are observed) or "museums" (places where many old evolutionary lineages accumulate) (Rahbeck et al., 2019a; but see Vasconcelos et al., 2022). In this study, the biodiversity hotspots, which were identified in the Mediterranean region, are mostly congruent with high NRI values. High NRI values indicate phylogenetic clustering of old lineages, which can therefore be used to identify the European hotspots of Sterrhinae diversity as "museums".

4.1.3. Phylogenetic endemism

Phylogenetic endemism was only prominent in the southern and eastern regions of Europe, being highest on the Iberian Peninsula, and these were also the areas with significant patterns of super- paleo- and mixed endemism as indicated by the CANAPE approach. The CANAPE approach has been successfully applied to investigate endemism patterns of plants (Mishler et al., 2014; Mishler et al., 2020; Albassatneh et al., 2021; Kougioumoutzis et al., 2021), but has only been rarely included into studies on insects. Especially the paleo-endemism pattern in southern Spain is also highlighted by significant NRI results for phylogenetic clustering, indicating the presence of closely related (old) lineages that apparently did not disperse far away. These patterns of endemism appear to be a good fit the glacial refugia of Europe, namely southern Spain, Italy, and the Balkans (Hewitt, 1996). The apparent paleo-endemism (relict lineages, apparently spatially restricted) observed in eastern Europe is probably an artefact caused by species that are more widely distributed across Ukraine and Russia but have only small parts of their distribution located in Europe. The other ("true") European endemics were identified mainly as mixed- and super-endemics, indicating both old and young evolutionary lineages.

There have been attempts to distinguish between types of endemism centres and to understand their emergence. Currently, the two main explanations are: 1) environmentally stable areas that are largely inaccessible/remote and mostly inhabited by endemics that evolved in these areas (in-situ refugia after Keppel et al., 2012; evolutionary refugia after Davis et al., 2013; or evolutionary endemicity centres/EVOcs after Menchetti et al., 2021) and 2) areas to which several species with similar ecological preferences migrated (ex-situ refugia after Keppel et al., 2012; ecological refuges after Davis et al., 2013; or ecological endemicity centres/ECOcs after Menchetti et al., 2021). The former are generally expected to show higher (phylo)genetic diversity, while the latter show higher phylogenetic clustering (Keppel et al., 2012; Menchetti et al., 2021). This study found a significant and roughly linear positive relationship between phylogenetic endemism and phylogenetic diversity in European Sterrhinae. This leads to the assumption that

endemism emerged mainly due to old speciation events of Sterrhinae species which never left their habitats, rather than representing single relict clades that went extinct everywhere else. As there was also a significant positive relationship between mean evolutionary distinctiveness and mean phylogenetic endemism, it appears that within hotspots of phylogenetic endemism there is an accumulation of several older lineages, which again appears to be consistent with the concept of in-situ refugia (i.e., evolutionary refugia and EVOcs).

A note has to be made on the decision how this study deals with species which are not truly endemic to Europe, but rather achieve high endemism values due to their distributional range barely intersecting this study's geographical boundaries. For many regions, such as in Northern and Eastern Europe, such species were easy to identify as they produced peculiarly shaped areas of phylogenetic endemism in regions where species richness and phylogenetic diversity were generally low. Most such occurrences revealed when checked, that species with centres of distribution located in Ukraine or Russia had but small parts of their distributional ranges overlapping the study area. This phenomenon fortunately only applied on the northern and eastern boundaries of the study's borders as it was only there that they did not reflect true ecological boundaries (i.e., the sea). While excluding such species from endemism analyses would have been possible, I decided to retain them, as the resulting artefacts were easily identified, and special caution was applied when interpreting the results.

4.2. Ecological traits

4.2.1. Larval food specialization / Diet Breadth

Several recent studies on European geometrids have focused on how host plant choice is connected to other life history traits (Seifert et al., 2022a; Seifert et al., 2022b; Seifert et al., 2023). For non-Sterrhinae geometrids, it was successfully demonstrated that dietary specialization increases in lower latitudes and dietary niche breadth is concomitantly higher in higher latitudes (Seifert et al. 2022a). Sterrhinae are different in their feeding habits from other subfamilies within Geometridae, in their ability of feeding on dead and decaying plant material, or even being strictly detritivorous (Hausmann, 2004), which is also the reason, why previous studies on geometrid plant-host-interactions excluded this taxon (Seifert et al., 2022a; Seifert et al., 2022b; Seifert et al., 2023). Sterrhinae might be more generalistic *per se*, compared to other geometrid species, in terms of the taxonomic breadth of their larval food substrates and it has to be acknowledged that for many species host plants were unknown or only guessed, which led to 43.7% of all Sterrhinae species being assigned to the category "unknown" and therefore were not included in the analysis.

The results from this study showed that overall Sterrhinae have similar patterns like other geometrids, as there is a trend of increasing food specialization in southern Europe, particularly the Iberian Peninsula and some parts of the mediterranean coast and eastern Europe. Most Sterrhinae species from central to northern Europe show rather generalistic behaviour and mean diet breadth per grid cell increased with latitude and decreasing

temperature. This relationship however was very vague, due to a separated patch of grid cells in Ukraine and Russia, that showed high food specialization (narrow diet breadth) which was more similar to the patterns observed in southern Spain than to any of the neighbouring areas. It might be that low species numbers, with very few records for food specialisation have led to this effect, or it could also be an artefact resulting from the influence of species predominantly distributed over Asia in different environments compared to those in Europe). When excluding these grid cells, the relationship between mean diet breadth and latitude, as well as mean annual temperature were far more obvious.

4.2.2. Voltinism

The majority of European Sterrhinae are either univoltine or flexible in their number of generations per year. For this study, strictly bivoltine, trivoltine and plurivoltine species were excluded, as there were too few of them for comparisons. The remaining univoltine and flexible species showed unsurprisingly opposite patterns, which is the reason, why the results focus on univoltinism. Expectedly, there was a clear trend in strictly univoltine species being more frequent in colder climates at higher latitudes and flexible voltinism being more frequent in lower latitudes and warmer regions. That is not surprising, since temperature is one of the main factors restricting adult reproductive activity and development of larvae in insects (Gilbert & Raworth 1996; Bale et al. 2002; Seifert et al., 2022b). Variation in voltinism between populations regarding latitude and climate has been reported from other Geometridae taxa as well (Välimäki et al., 2013; Seifert et al., 2023). The available information on voltinism has to be handled carefully, however, especially for widely distributed species that may show multiple generations in the south, while in the north they might reproduce only once (which would here be considered as flexible), but probably have not been studied in their whole distributional range and species scorings are therefore prone to biases.

4.2.3. Range size and latitudinal range

Rapoport's rule states latitudinal range size to increase at higher latitude (Stevens, 1989). There is evidence for European geometrid moths (excluding Sterrhinae) showing smaller latitudinal ranges at lower latitudes (Seifert et al. 2022a). The correlation between latitudinal range and latitude was indeed very high for other Geometridae (Spearman's rank correlation coefficients $r_s = .99$, $p < .001$) (Seifert et al., 2022a). The current study uncovered a strong significant relationship between area size and latitudinal distribution, explaining more than 80% of variation of the area size. Sterrhinae show patterns comparable to non-Sterrhinae geometrid moths, however it has to be noted that different variables were tested here (Sterrhinae: areal size vs. other Geometridae: latitudinal range). Sterrhinae species inhabiting areas in higher latitudes are more likely to be distributed over large ranges (however including both latitudinal and longitudinal range). This can be explained that those species of Sterrhinae that show higher tolerance towards colder climate and in general harsher conditions, might be able to inhabit various habitats

in the North, while the highly specialized species from the Mediterranean area are quite restricted to places where they adapted to. It is generally assumed, that species inhabiting the northern parts of Europe were probably under strong selection to endure a variety of harsh environmental conditions, and to disperse over wide ranges of latitudes during glacial oscillations, which is also very likely the case for other Geometridae (Seifert et al. 2022a). In addition, extreme climatic changes during the Pleistocene are believed to have impacted the distribution of northern as well as southern animal species in Europe, with the former adapting for crossing long latitudinal distances in order to survive glaciation cycles while the latter remained restricted in their range size (Brown, 1995). The increased distributional range of species towards higher latitudes has been found to be a general phenomenon in other animal groups as well (Lawrence & Fraser, 2020) and it can be assumed that species with the ability to inhabit a larger latitudinal amplitude are more likely to spread in general. For European butterflies it could be shown, that niche breadth regarding climate, diet and habitat explained areal size better than for example actual body size (Hausharter et al., 2021).

4.2.4. Mountains

Many studies have shown that mountains inhabit sometimes immense amounts of taxa and tend to be hotspots of biodiversity, independent from latitude (Rahbek et al. 2019a; Rahbek et al., 2019b; Nielsen et al. 2022). Mountains are also known to act as refugia. For example, in butterflies is has been found, that the lower elevations of mountains and surrounding areas have been used as refugia by several species (Haubrich & Schmitt, 2007; Paučulová, et al., 2016; Kühne et al 2017).

European Sterrhinae did not show significant patterns of high diversity in the mountainous regions. However, on average, there was a small effect of increased diversity (species richness, phylogenetic diversity) and phylogenetic endemism in grid cells overlapping with mountains. This could probably be due to many low land areas in northern Europe inhabiting only very few species. Sterrhinae species are not particularly associated with montane habitats compared to other geometrid moths even though some species can be found at quite high elevations (Brehm & Fiedler, 2003; Hausmann, 2004; Axmacher et al., 2004). For example, a couple of *Idaea* species even have their main distribution in the Spanish mountains and Pyrenees (e.g., *Idaea luteolaria, Idaea korbi, Idaea calunetaria and Idaea joannisiata*). However, it is also highly likely that the spatial resolution was not fine enough to be able to detect relationships between mountains and Sterrhinae diversity and ecology.

4.3. Is Phylogenetic Diversity an important conceptual complement to Species Richness in capturing Biodiversity Patterns?

In this study I could demonstrate that phylogenetic diversity metrics contain additional information on biodiversity than just species richness, since different regions of Europe could be distinguished by phylogenetic structure and phylogenetic diversity of their Sterrhinae assemblages. While species richness was highest in Spain and southern France, centres of phylogenetic diversity were located in Portugal, central Spain, large parts of Italy, the Balkans, Mediterranean islands as well as some parts of central Europe. This demonstrates 1) that species richness captures different effects than PD and 2) that PD is able to locate biodiversity hotspots, where species richness alone fails to do so.

I found that besides the most obvious areas in Europe that represent their preferred habitat type (warm, semi-arid), also several areas in Central Europe, like the Pannonic basin, central Germany and France comprise regions of intermediate-high diversity. Those places in Central and eastern Europe are probably small-scale steppe habitats, inhabiting relict species that outlasted the late cold phases there, and not comparable to the large semi-arid areas on e.g., the Iberian Peninsula – however this study shows that they host a significant amount of phylogenetic diversity. It is therefore important for Central European biodiversity conservation to protect habitat diversity, especially small patches of warm and dry habitats for xerothermophilous species, such as Sterrhinae. Those areas need to be protected, especially as we can see species loss there already. For example, five *Idaea* species, five *Scopula* species and two *Cyclophora* species have been reported to be already extinct in parts of Germany (Hausmann, 2004).

Widespread Eurasiatic species that are originally distributed in northern and central Europe seem to be of least concern, as especially with the warming effects of climate change their distribution range will probably broaden. For other lepidopterans, it has been shown already that with increasing temperature immigrations towards the North are increasing (Sparks et al., 2005; Chapman et al., 2012; Forsman et al., 2016; Betzholtz et al., 2023). A prominent example are noctuid moths, which are able to travel long distances at comparable speeds like passerine birds and are increasingly settling in northern areas (Alerstam et al., 2011; Betzholtz et al., 2023). Sterrhinae are probably not comparable to Noctuidae in their capabilities of immigrating towards higher latitudes, however there are already indications from England and Sweden, that many currently present species are migrants from more southern parts of Europe (Randle et al. 2019; Betzholtz et al., 2023).

There are several reasons, why phylogenetic diversity is a valuable concept in conservation research: phylogenetic diversity can be used as an indicator not only for richness, but for rarity, historical distinctiveness, functional potential as well as evolutionary potential (Winter et al. 2013). Especially the aspect of functional and evolutionary potential of a species assemblage becomes more and more crucial, as climate change and other anthropogenically induced environmental disturbances challenge organisms to become more adaptive, which is easier for assemblages comprising a broad range of genetic

potential (Winter et al. 2013; Rahbek et al., 2019a). Furthermore, PD has been found to positively influence ecosystem productivity (Cadotte, 2013; Coelho de Souza et al., 2019).

PD can also aid in decisions on prioritization of conservation areas (Vane-Wright et al., 1991; Pollock et al., 2017). While species richness mainly detects areas where high rates of speciation take place, phylogenetic diversity metrics can help in discovering places of more ancestral phylogenetic lineages as well. It is therefore important to distinguish between places of high biodiversity due to rapid radiation, and places hosting mainly evolutionary distinctive lineages and to conserve both of these diversity pools. On a side note it is worth mentioning, that even if this distinction may help to identify hotspots of different types of diversity, both phenomena can occur in the same place and the strictly dichotomic concept of "cradles" and "museums" is not well applicable for many situations (e.g., tropical biodiversity) and some authors even rejected it entirely (Rangel et al., 2018; Sonne et al., 2022; Vasconcelos et al., 2022)

Even if phylogenetic diversity is still underrepresented in conservations studies (Winter et al., 2013; Llorente-Culebras et al., 2023), the increasing availability of genetic data and improvement of guidelines for the use of different phylogenetic metrics will hopefully make that approach more appealing for future studies.

5. Conclusion

This study investigated the diversity and phylogenetic structure of European Sterrhinae moths, a species-rich subfamily of Geometridae, highlighting the southern parts of Europe, including the Iberian Peninsula, Mediterranean islands and the Balkans as hotspots of phylogenetic diversity. Central Europe revealed some areas of intermediate phylogenetic diversity, while phylogenetic diversity decreased constantly with increasing latitude. This analysis indicates that the rich regions (in terms of species number and phylogenetic diversity) constitute clusters of rather "old" lineages, which diverged with time, while phylogenetic overdispersion was mainly present in places of intermediate phylogenetic diversity in central Europe. Phylogenetic endemism was highest in southern and eastern Europe, showing super-, paleo- and mixed endemism, which is in congruence with glacial refugia, but also possible due to immigration from northern Africa and western Asia. European Sterrhinae show more univoltinism and higher generalistic behaviour in northern regions, probably due to harsher conditions in these colder climates. This fits well with results obtained from other geometrid moths in Europe.

Contrary to a pure assessment of species richness, phylogenetic diversity was able to highlight additional areas with fewer species but reflecting richer evolutionary history. Especially the temperate regions of central Europe showed some patches of intermediate-high PD, which might be explained by the small-scale habitat diversity in this region which may inherit relict steppe-species from eastern refugia. Spain, France, Italy and in general the southern Alps and Balkans are promising targets for conservation of Sterrhinae phylogenetic diversity. The investigation of phylogenetic structure gives insights into biodiversity patterns and species assemblages, which are valuable for ecological research. According to NTI values, recent radiations in northern Europe (UK, Scandinavia) must have happened after the dispersion of few species from the Mediterranean towards higher latitudes, while high NRI values indicating phylogenetic clustering in the Mediterranean region support the assumption that those regions acted as refugia during cold periods. The coastal regions around the Mediterranean area harbour high numbers of phylogenetically diverse Sterrhinae species, making those xerothermic areas important places for protection and conservation.

References

Literature

Aarvik, L., Hansen, L. O. & Kononenko, V. (2009). Norges sommerfugler, Handbok over Norges dagsommerfugler og nattsvermere. Norsk entomologisk forening, Naturhistorisk Museum, Oslo

Albassatneh, M. C., Escudero, M., Monnet, A. C., Arroyo, J., Bacchetta, G., Bagnoli, F., Dimopoulos, P., Hampe, A., Leriche, A., Médail, F., Nikolic, T., Ponger, L., Vendramin, G. G. & Fady, B. (2021). Spatial patterns of genus-level phylogenetic endemism in the tree flora of Mediterranean Europe. Diversity and Distributions, 27(5), 913-928. https://doi.org/10.1111/ddi.13241

Alerstam, T., Chapman, J. W., Bäckman, J., Smith, A. D., Karlsson, H., Nilsson, C., Reynolds, D. R., Klaassen, R. H. G. & Hill, J. K. (2011). Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds. Proceedings of the Royal Society B: Biological Sciences, 278(1721), 3074-3080. https://doi.org/10.1098/rspb.2011.0058

Andersen, J. C., Havill, N. P., Caccone, A., & Elkinton, J. S. (2017). Postglacial recolonization shaped the genetic diversity of the winter moth (*Operophtera brumata*) in Europe. Ecology and Evolution, 7(10), 3312-3323. https://doi.org/10.1002/ece3.2860

Andersen, J. C., Havill, N. P., Mannai, Y., Ezzine, O., Dhahri, S., Ben Jamâa, M. L., Caccone, A. & Elkinton, J. S. (2019). Identification of winter moth (*Operophtera brumata*) refugia in North Africa and the Italian Peninsula during the last glacial maximum. Ecology and Evolution, 9(24), 13931-13941. https://doi.org/10.1002/ece3.5830

Axmacher, J. C., Holtmann, G., Scheuermann, L., Brehm, G., Müller-Hohenstein, K. & Fiedler, K. (2004). Diversity of geometrid moths (Lepidoptera: Geometridae) along an Afrotropical elevational rainforest transect. Diversity and Distributions, 10(4), 293-302. https://doi.org/10.1111/j.1366-9516.2004.00101.x

Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., Butterfield, J., Buse, A., Coulson, J. C., Farrar, J., Good, J. E. G., Harrington, R., Hartley, S., Jones, T. H., Lindroth, R-. L., Press, M. C., Symrnioudis, I., Watt, A. D. & Whittaker, J. B. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology, 8(1), 1-16. https://doi.org/10.1046/j.1365-2486.2002.00451.x

Bänziger, H. & Fletcher, D. S. (1985). Three new zoophilous moths of the genus Scopula (Lepidoptera: Geometridae) from South-east Asia. Journal of Natural History, 19(5), 851–860. https://doi.org/10.1080/00222938500770531

Bermudez, G. M. & Lindemann-Matthies, P. (2020). "What matters is species richness"—high school students' understanding of the components of biodiversity. Research in Science Education, 50(6), 2159–2187. https://doi.org/10.1007/s11165-018-9767-y

Betzholtz, P. E., Forsman, A. & Franzén, M. (2023). Associations of 16-year population dynamics in range-expanding moths with temperature and years since establishment. Insects, 14(1), 55. https://doi.org/10.3390/insects14010055

Brehm, G. & Fiedler, K. (2003). Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest. Journal of Biogeography, 30(3), 431–440. https://doi.org/10.1046/j.1365-2699.2003.00832.x

Brown, J. H. (1995). Macroecology. University of Chicago Press.

Brown, J. H. (2014). Why are there so many species in the tropics? Journal of Biogeography, 41(1), 8-22. https://doi.org/10.1111/jbi.12228

Cadotte, M. W., Davies, J. T., Regetz, J., Kembel, S. W., Cleland, E. & Oakley, T. H. (2010). Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. Ecology Letters, 13(1), 96–105. https://doi.org/10.1111/j.1461-0248.2009.01405.x

Cadotte, M. W., Carscadden, K. & Mirotchnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology, 48(5), 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Cadotte, M. W. (2013). Experimental evidence that evolutionarily diverse assemblages result in higher productivity. Proceedings of the National Academy of Sciences - PNAS, 110(22), 8996–9000. https://doi.org/10.1073/pnas.1301685110

Cadotte, M. W. (2017). Functional traits explain ecosystem function through opposing mechanisms. Ecology Letters, 20(8), 989–996. https://doi.org/10.1111/ele.12796

Cadotte, M.W., Davies, T. J. & Peres-Neto, P.R. (2017), Why phylogenies do not always predict ecological differences. Ecological Monographs, 87: 535–551. https://doi.org/10.1002/ecm.1267

Cadotte, M. W. & Tucker, C. M. (2017). Should environmental filtering be abandoned? Trends in Ecology and Evolution, 32:429–437. https://doi.org/10.1016/j.tree.2017.03.004

Cavender-Bares, J., Keen, A. & Miles, B. (2006). Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology, 87(sp7), S109-S122. https://doi.org/10.1890/0012-9658(2006)87[109:PSOFPC]2.0.CO;2

Cavender-Bares, J., Kozak, K. H., Fine, P. V. & Kembel, S. W. (2009). merging of community ecology and phylogenetic biology. Ecology Letters, 12(7), 693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

Chapman, J. W., Bell, J. R., Burgin, L. E., Reynolds, D. R., Pettersson, L. B., Hill, J. K., Bonsall, M. B. & Thomas, J. A. (2012). Seasonal migration to high latitudes results in major reproductive benefits in an insect. Proceedings of the National Academy of Sciences, 109(37), 14924-14929. https://doi.org/10.1073/pnas.1207255109

Coelho de Souza, F., Dexter, K. G., Phillips, O. L., Pennington, R. T., Neves, D., Sullivan, M. J. P., Alvarez-Davila, E., Alves, Átila, Amaral, I., Andrade, A., Aragao, L. E. O. C., Araujo-Murakami, A., Arets, E. J. M. M., Arroyo, L., Aymard C, G. A., Bánki, O., Baraloto, C., Barroso, J. G., Boot, R. G. A., … & Castro, W. (2019). Evolutionary diversity is associated with wood productivity in Amazonian forests. Nature Ecology & Evolution, *3*(12), 1754–1761. https://doi.org/10.1038/s41559-019-1007-y

Condamine, F. L., Soldati, L., Clamens, A. L., Rasplus, J. Y. & Kergoat, G. J. (2013). Diversification patterns and processes of wingless endemic insects in the Mediterranean Basin: historical biogeography of the genus *Blaps* (Coleoptera: Tenebrionidae). Journal of Biogeography, 40(10), 1899-1913. https://doi.org/10.1111/jbi.12144

Craven, D., Eisenhauer, N., Pearse, W. D., Hautier, Y., Isbell, F., Roscher, C., Bahn, M., Beierkuhnlein, C., Bönisch, G., Buchmann, N., Byun, C., Catford, J. A., Cerabolini, B. E., Cornelissen, J. H., Craine, J. M., De Luca, E., Ebeling, A., Griffin, J. N., Hector, A., …& Manning, P. (2018). Multiple facets of biodiversity drive the diversity–stability relationship. Nature Ecology & Evolution, 2(10), 1579–1587. https://doi.org/10.1038/s41559-018-0647-7

Davis, J., Pavlova, A., Thompson, R., & Sunnucks, P. (2013). Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. Global Change Biology, 19(7), 1970-1984. https://doi.org/10.1111/gcb.12203

Earl, C., Belitz, M. W., Laffan, S. W., Barve, V., Barve, N., Soltis, D. E., Allen, J. M., Soltis, P. S., Mishler, B. D., Kawahara, A. Y. & Guralnick, R. (2021). Spatial phylogenetics of butterflies in relation to environmental drivers and angiosperm diversity across North America. iScience, 24(4), 102239–102239. https://doi.org/10.1016/j.isci.2021.102239

Emerson, B. C., Gillespie, R. G. (2008). Phylogenetic analysis of community assembly and structure over space and time. Trends in Ecology and Evolution, 23, 619–630. https://doi.org/10.1016/j.tree.2008.07.005

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. Biological Conservation, 61(1), 1–10. https://doi.org/10.1016/0006-3207(92)91201-3

Fonseca, E. M., Pelletier, T. A., Decker, S. K., Parsons, D. J., & Carstens, B. C. (2023). Pleistocene glaciations caused the latitudinal gradient of within-species genetic diversity. Evolution Letters, 7(5), 331-338. https://doi.org/10.1093/evlett/qrad030

Forsman, A., Betzholtz, P. E. & Franzén, M. (2016). Faster poleward range shifts in moths with more variable colour patterns. Scientific Reports, 6(1), 36265. https://doi.org/10.1038/srep36265

French, C. M., Bertola, L. D., Carnaval, A. C., Economo, E. P., Kass, J. M., Lohman, D. J., Marske, K. A., Meier, R., Overcast, I., Rominger, A. J., Staniczenko, P. P. A. & Hickerson, M. J. (2023). Global determinants of insect mitochondrial genetic diversity. Nature Communications, 14(1), 5276. https://doi.org/10.1038/s41467-023-40936-0

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E. M., Steffan-Dewenter, I., Emmerson, M., Potts, S. G., Tscharntke, T., Weisser, W. & Bommarco, R. (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proceedings of the Royal Society. B, Biological Sciences, 282(1801), 20142620–20142620. https://doi.org/10.1098/rspb.2014.2620

Gaston, K., J. & Lawton, J. H. (1988). Patterns in the distribution and abundance of insect populations. Nature (London), 331(6158), 709–712. https://doi.org/10.1038/331709a0

Gilbert, N., & Raworth, D. A. (1996). Insects and temperature—a general theory. The Canadian Entomologist, 128(1), 1-13. https://doi.org/10.4039/Ent1281-1

Guariento, E., Strutzenberger, P., Truxa, C. & Fiedler, K. (2020). The trinity of ecological contrasts: a case study on rich insect assemblages by means of species, functional and phylogenetic diversity measures. BMC Ecology, 20(1), 29–29. https://doi.org/10.1186/s12898-020-00298-3

Gumbs, R., Gray, C. L., Böhm, M., Hoffmann, M., Grenyer, R., Jetz, W., ... & Rosindell, J. (2020). Global priorities for conservation of reptilian phylogenetic diversity in the face of human impacts. Nature Communications, 11(1), 2616. https://doi.org/10.1038/s41467-020-16410-6

Haila, Y. & Kouki, J. (1994). The phenomenon of biodiversity in conservation biology. Annales Zoologici Fennici, 31:1, 5–18. https://www.jstor.org/stable/23735495

Hamilton, T. H. & Rubinoff, I. (1967). On Predicting Insular Variation in Endemism and Sympatry for the Darwin Finches in the Galapagos Archipelago. American Naturalist, 101(918), 161-171.

Haubrich, K., & Schmitt, T. (2007). Cryptic differentiation in alpine-endemic, high-altitude butterflies reveals down-slope glacial refugia. Molecular Ecology, 16(17), 3643-3658. https://doi.org/10.1111/j.1365-294X.2007.03424.x

Hausharter, J., Rashid, S., Wessely, J., Strutzenberger, P., Moser, D., Gattringer, A., Fiedler, K., Hülber, K. & Dullinger, S. (2023). Niche breadth explains the range size of European-centred butterflies, but dispersal ability does not. Global Ecology and Biogeography, 32(9), 1535-1548. https://doi.org/10.1111/geb.13717

Hausmann, A. (2004). The geometrid moths of Europe. Vol. 2, Sterrhinae. Apollo Books

Hausmann, A., Godfray, H. C., Huemer, J., Mutane, M., Rougerie, R., Nieukerken, E. J. van, Ratnasingham, S. & Hebert, P. D. (2013). Genetic patterns in European geometrid moths revealed by the Barcode Index Number (BIN) System. PloS One, 8(12), e84518–e84518. https://doi.org/10.1371/journal.pone.0084518

Hausmann, A. & Viidalepp, J. (2012). The geometrid moths of Europe (Vol. 3). Apollo Books.

Hewitt, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of the Linnean Society, 58(3), 247-276. https://doi.org/10.1111/j.1095-8312.1996.tb01434.x

Hillebrand, H. & Matthiessen, B. (2009). Biodiversity in a complex world: consolidation and progress in functional biodiversity research. Ecology Letters, 12(12), 1405–1419. https://doi.org/10.1111/j.1461-0248.2009.01388.x

Iknayan, K. J., Tingley, M. W., Furnas, B. J. & Beissinger, S. R. (2014). Detecting diversity: emerging methods to estimate species diversity. Trends in Ecology & Evolution, 29(2), 97–106. https://doi.org/10.1016/j.tree.2013.10.012

Isaac, N. J. B., Turvey, S. T., Collen, B., Waterman, C. & Baillie, J. E. M. (2007). Mammals on the EDGE: Conservation priorities based on threat and phylogeny. PloS One, 2(3), e296–e296. https://doi.org/10.1371/journal.pone.0000296

IUCN. Phylogenetic Diversity Task Force. https://www.pdtf.org/, accessed in March 2023

Jetz, W., Thomas, G., Joy, J., Hartmann, K. & Mooers, A. O. (2012). The global diversity of birds in space and time. Nature 491, 444–448. https://doi.org/10.1038/nature11631

Jetz, W., Thomas, G. H., Joy, J. B., Redding, D. W., Hartmann, K. & Mooers, A. O. (2014). Global distribution and conservation of evolutionary distinctness in birds. Current Biology, 24(9), 919–930. https://doi.org/10.1016/j.cub.2014.03.011

Kamilar, J. M., Beaudrot, L. & Reed, K. E. (2015). Climate and species richness predict the phylogenetic structure of African mammal communities. PLoS ONE 10(4): e0121808. https://doi.org/10.1371/journal.pone.0121808

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, P. & Kessler, M. (2017): Climatologies at high resolution for the Earth land surface areas. Scientific Data. 4 170122. https://doi.org/10.1038/sdata.2017.122

Kelly, S., Grenyer, R. & Scotland, R. W. (2014). Phylogenetic trees do not reliably predict feature diversity. Diversity and Distributions, 20(5), 600-612. https://doi.org/10.1111/ddi.12188

Kembel, S. W. & Hubbell, S. P. (2006). The phylogenetic structure of a neotropical forest tree community. Ecology, 87(sp7), S86-S99. https://doi.org/10.1890/0012-9658(2006)87[86:TPSOAN]2.0.CO;2

Kenyeres, Z., Racz, I. A. & Varga, Z. (2009). Endemism hot spots, core areas and disjunctions in European Orthoptera. Acta Zoologica Cracoviensia. Ser. B, Invertebrata, 52(1), 189–211. https://doi.org/10.3409/azc.52b_1-2.189-211

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., Schut, A. G. T., Hopper, S. D. & Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. Global Ecology and Biogeography, 21(4), 393–404. https://doi.org/10.1111/j.1466-8238.2011.00686.x

Kerdelhué, C., Zane, L., Simonato, M., Salvato, P., Rousselet, J., Roques, A., & Battisti, A. (2009). Quaternary history and contemporary patterns in a currently expanding species. BMC Evolutionary Biology, 9(220), 1-14. https://doi.org/10.1186/1471-2148-9-220

Keyser, R. D., Shreeve, T. G., Breuker, C. J., Hails, R. S., & Schmitt, T. (2012). Polyommatus icarus butterflies in the British Isles: evidence for a bottleneck. Biological Journal of the Linnean Society, 107(1), 123-136. https://doi.org/10.1111/j.1095-8312.2012.01925.x

Körner, C., Jetz, W., Paulsen, J., Payne, D., Rudmann-Maurer, K. & Spehn, E. (2017). A global inventory of mountains for bio-geographical applications. Alpine Botany 127(1): 1-15 https://doi.org/10.1007/s00035-016-0182-6 and the dataset DOI: 10.7892/boris.106896.

Kougioumoutzis, K., Kokkoris, I. P., Panitsa, M., Kallimanis, A., Strid, A. & Dimopoulos, P. (2021). Plant endemism centres and biodiversity hotspots in Greece. Biology, 10(2), 72. https://doi.org/10.3390/biology10020072

Kroschel, J., Sporleder, M., Tonnang, H. E. Z., Juarez, H., Carhuapoma, P., Gonzales, J. C. & Simon, R. (2013). Predicting climate-change caused changes in global temperature on potato tuber moth *Phthorimaea operculella* (Zeller) distribution and abundance using phenology modeling and GIS mapping. Agricultural and Forest Meteorology, 170, 228–241. https://doi.org/10.1016/j.agrformet.2012.06.017

Kühne, G., Kosuch, J., Hochkirch, A., & Schmitt, T. (2017). Extra-Mediterranean glacial refugia in a Mediterranean faunal element: the phylogeography of the chalk-hill blue *Polyommatus coridon* (Lepidoptera, Lycaenidae). Scientific Reports, 7(1), 43533. https://doi.org/10.1038/srep43533

Llorente-Culebras, S., Ladle, R. J. & Santos, A. M. (2023). Publication trends in global biodiversity research on protected areas. Biological Conservation, 281, 109988. https://doi.org/10.1016/j.biocon.2023.109988

Liu, X., Zhang, L. & Hong, S. (2011). Global biodiversity research during 1900-2009: a bibliometric analysis. Biodiversity and Conservation, 20(4), 807–826. https://doi.org/10.1007/s10531-010-9981-z

Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters, 11(10), 995-1003. https://doi.org/10.1111/j.1461-0248.2008.01229.x

Lumley, T., Diehr, P., Emerson, S., & Chen, L. (2002). The importance of the normality assumption in large public health data sets. Annual review of public health, 23(1), 151-169. https://doi.org/10.1146/annurev.publhealth.23.100901.140546

MacArthur, R. H. & Wilson, E. O. (1967). The theory of island biogeography. Princeton University Press. Princeton, UK

Margules, C. R. & Pressey, R. L. (2000). Systematic conservation planning. Nature (London), 405(6783), 243–253. https://doi.org/10.1038/35012251

Mazel, F., Pennell, M. W., Cadotte, M. W., Diaz, S., Dalla Riva, G. V., Grenyer, R., Leprieur, F., Mooers, A. O., Mouillot, D., Tucker, C. M. & Pearse, W. D. (2018). Prioritizing phylogenetic diversity captures functional diversity unreliably. Nature Communications, 9(1), 2888–2889. https://doi.org/10.1038/s41467-018-05126-3

Manish, K. & Pandit, M. K. (2018). Phylogenetic diversity, structure and diversification patterns of endemic plants along the elevational gradient in the Eastern Himalaya. Plant Ecology & Diversity, 11(4), 501–513. https://doi.org/10.1080/17550874.2018.1534147

Manish, K. (2021). Species richness, phylogenetic diversity and phylogenetic structure patterns of exotic and native plants along an elevational gradient in the Himalaya. Ecological Processes 10, 64. https://doi.org/10.1186/s13717-021-00335-z

Menchetti, M., Talavera, G., Cini, A., Salvati, V., Dincă, V., Platania, L., Bonelli, S., Balletto, E., Vila, R. & Dapporto, L. (2021). Two ways to be endemic. Alps and Apennines are different functional refugia during climatic cycles. Molecular Ecology, 30(5), 1297–1310. https://doi.org/10.1111/mec.15795

Mishler, B., Knerr, N., González-Orozco, C. E., Thornhill, A. H., Laffan, S. W. & Miller, J. T. (2014). Phylogenetic measures of biodiversity and neo-and paleo-endemism in Australian acacia. Nature Communications, 5(1), 4473–4473. https://doi.org/10.1038/ncomms5473

Mouquet, N., Devictor, V., Meynard, C. N., Munoz, F., Bersier, L.-F., Chave, J., Couteron, P., Dalecky, A., Fontaine, C., Gravel, D., Hardy, O. J., Jabot, F., Lavergne, S., Leibold, M., Mouillot, D., Münkemüller, T., Pavoine, S., Prinzing, A., Rodrigues, A. S. L., Rohr, R. P., Thebault, E. & Thuiller, W. (2012). Ecophylogenetics: advances and perspectives. Biological Reviews of the Cambridge Philosophical Society, 87(4), 769–785. https://doi.org/10.1111/j.1469-185X.2012.00224.x

Müller, B., Erlacher, S., Hausmann, A., Rajaei, H., Sihvonen, P., & Skou, P. (31 May. 2019). Ennominae II. Leiden, Niederlande: Brill. doi: https://doi.org/10.1163/9789004387485

Murillo-Ramos, L., Brehm, G., Sihvonen, P., Hausmann, A., Holm, S., Ghanavi, H. R., Õunap, E., Truuverk, A., Staude, H., Friedrich, E., Tammaru, T., & Wahlberg, N. (2019). A comprehensive molecular phylogeny of Geometridae (Lepidoptera) with a focus on enigmatic small subfamilies. PeerJ (San Francisco, CA), 2019(8), e7386–e7386. https://doi.org/10.7717/peerj.7386

Murillo-Ramos, L., Twort, V., Wahlberg, N., & Sihvonen, P. (2023). A phylogenomic perspective on the relationships of subfamilies in the family Geometridae (Lepidoptera). Systematic Entomology, 48(4), 618-632. https://doi.org/10.1111/syen.12594

Nielsen, S. N., Müller, F., & Marques, J. C. (2022). Humboldt's enigma viewed through the lens of ecosystem theory. Explanation by simple principles. Environmental and Sustainability Indicators, 13, 100165. https://doi.org/10.1016/j.indic.2021.100165

Nitta, J. H., Laffan, S. W., Mishler, B. D., & Iwasaki, W. (2023). canaper: Categorical Analysis of Neo-and Paleo-endemism in R. Ecography, 2023 (9), e06638. https://doi.org/10.1111/ecog.06638

Õunap, E., Nedumpally, V., Yapar, E., Lemmon, A. R., & Tammaru, T. (2024). Molecular phylogeny of north European Geometridae (Lepidoptera: Geometroidea). Systematic Entomology. https://doi.org/10.1111/syen.12638

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K. & Virtanen, R. (2010). Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. Conservation Biology, 24(1), 101–112. https://doi.org/10.1111/j.1523-1739.2009.01399.x

Paučulová, L., Šemeláková, M., Mutanen, M., Pristaš, P. & Panigaj, L. (2017). Searching for the glacial refugia of *Erebia euryale* (Lepidoptera, Nymphalidae)–insights from mt DNA-and nDNA-based phylogeography in the Western Carpathians. Journal of Zoological Systematics and Evolutionary Research, 55(2), 118-128. https://doi.org/10.1111/jzs.12156

Pellens, R. & Grandcolas, P. (2016). Phylogenetics and Conservation Biology: Drawing a Path into the Diversity of Life. In: Grandcolas, P. & Pellens, R. (2016). Biodiversity Conservation and Phylogenetic Systematics: Preserving Our Evolutionary Heritage in An Extinction Crisis (Volume 14.0) (Vol. 14). Springer Open. https://doi.org/10.1007/978-3-319-22461-9

Peña, C., Witthauer, H., Klečková, I., Fric, Z. & Wahlberg, N. (2015). Adaptive radiations in butterflies: evolutionary history of the genus Erebia (Nymphalidae: Satyrinae). Biological Journal of the Linnean Society, 116, 449–467. https://doi.org/10.1111/bij.12597

Pollock, L. J., Thuiller, W., & Jetz, W. (2017). Large conservation gains possible for global biodiversity facets. Nature, 546(7656), 141-144. https://doi.org/10.1038/nature22368

Rahbek, C., Borregaard, M. K., Antonelli, A., Colwell, R. K., Holt, B. G., Nogues-Bravo, D., Rasmussen, C. M. Ø., Richardson, K., Rosing, M. T., Whittaker, R. J. & Fjeldså, J. (2019).a Building mountain biodiversity: Geological and evolutionary processes. Science, 365(6458), 1114-1119. https://doi.org/10.1126/science.aax0151

Rahbek, C., Borregaard, M. K., Colwell, R. K., Dalsgaard, B. O., Holt, B. G., Morueta-Holme, N., David Nogues-Bravo, D., Whittaker, R. J. & Fjeldså, J. (2019).b Humboldt's enigma: What causes global patterns of mountain biodiversity? Science, 365(6458), 1108-1113. https://doi.org/10.1126/science.aax0149

Randle, Z., Evans-Hill, L. J., Parson, M. S., Tyner, A., Bourn, N. A. D., Davis, A. M., Dennis, E. B., O'Donnell, M., Prescott, T., Tordoff, G. M. & Fox, R. (2019). Atlas of Britain & Ireland's larger moths. Pisces Publications. Newbury

Rangel, T. F., Edwards, N. R., Holden, P. B., Diniz-Filho, J. A. F., Gosling, W. D., Coelho, M. T. P., Cassemiro, F. A. S., Rahbek, C. & Colwell, R. K. (2018). Modeling the ecology and evolution of biodiversity: Biogeographical cradles, museums, and graves. Science, 361(6399), eaar5452. https://doi.org/10.1126/science.aar5452

Rao, M. S., Rao, C. R., Vennila, S., Manimanjari, D., Maheswari, M. & Venkateswarlu, B. (2014). Estimation of number of generations of *Spodoptera litura* Fab. On peanut in India during near and distant future climate change scenarios. Scientific Research and Essays, 9(7), 195–203. https://doi.org/10.5897/SRE2013.5783

Redondo, V. M., Gaston, J. & Gimeno, R. (2009). Geometridae Ibericae. Apollo Books. Stenstrup, Denmark

Ricklefs, R. E. (2006). Evolutionary diversification and the origin of the diversity–environment relationship. Ecology, 87(sp7), S3-S13. https://doi.org/10.1890/0012-9658(2006)87[3:EDATOO]2.0.CO;2

Rosauer, D. F., Laffan, S. W., Crisp, M. D., Donnellan, S. C. & Cook, L. G. (2009). Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. Molecular Ecology, 18(19), 4061–4072. https://doi.org/10.1111/j.1365-294X.2009.04311.x

Rosauer, D. F., Pollock, L. J., Linke, S. & Jetz, W. (2017). Phylogenetically informed spatial planning is required to conserve the mammalian tree of life. Proceedings of the Royal Society London, Series B 284, 20170627. http://dx.doi.org/10.1098/rspb.2017.0627

Sarkar, S. & Margules, C. (2002). Operationalizing biodiversity for conservation planning. Journal of Biosciences, 27(4), 299–308. https://doi.org/10.1007/BF02704961

Schär, S., Vila, R., Petrović, A., Tomanović, Ž., Pierce, N. E., & Nash, D. R. (2017). Molecular substitution rate increases with latitude in butterflies: evidence for a trans-glacial latitudinal layering of populations? Ecography, 40(8), 930-935. https://doi.org/10.1111/ecog.02487

Schmidt, A. F., & Finan, C. (2018). Linear regression and the normality assumption. Journal of Clinical Epidemiology, 98, 146–151. https://doi.org/10.1016/j.jclinepi.2017.12.006

Schmitt, T., & Seitz, A. (2001). Allozyme variation in *Polyommatus coridon* (Lepidoptera: Lycaenidae): identification of ice-age refugia and reconstruction of post-glacial expansion. Journal of Biogeography, 28(9), 1129-1136. https://doi.org/10.1046/j.1365-2699.2001.00621.x

Schmitt, T. Molecular biogeography of Europe. (2007). Pleistocene cycles and postglacial trends. Frontiers in Zoololgy, 4(11). https://doi.org/10.1186/1742-9994-4-11

Seifert, C., Strutzenberger, P., Hausmann, A., Fiedler, K. & Baselga, A. (2022)a. Dietary specialization mirrors Rapoport's rule in European geometrid moths. Global Ecology and Biogeography, 31(6), 1161–1171. https://doi.org/10.1111/geb.13493

Seifert, C.L., Strutzenberger, P. & Fiedler, K. (2022)b, Ecological specialisation and range size determine intraspecific body size variation in a speciose clade of insect herbivores. Oikos, 2022: e09338. https://doi.org/10.1111/oik.09338

Seifert, C. L., Strutzenberger, P. & Fiedler, K. (2023). How do host plant use and seasonal life cycle relate to insect body size: A case study on European geometrid moths (Lepidoptera: Geometridae). Journal of Evolutionary Biology, 36(5), 743–752. https://doi.org/10.1111/jeb.14169

Sihvonen, P. (2005). Phylogeny and classification of the Scopulini moths (Lepidoptera: Geometridae, Sterrhinae). Zoological Journal of the Linnean Society, 143(4), 473–530. https://doi.org/10.1111/j.1096-3642.2005.00153.x

Sihvonen, P. & Kaila, L. (2004). Phylogeny and tribal classification of Sterrhinae with emphasis on delimiting Scopulini (Lepidoptera: Geometridae). Systematic Entomology, 29(3), 324–358. https://doi.org/10.1111/j.0307-6970.2004.00248.x

Sihvonen, P. Murillo-Ramos, L., Brehm, G., Staude, H. & Wahlberg, N. (2020). Molecular phylogeny of Sterrhinae moths (Lepidoptera: Geometridae): towards a global classification. Systematic Entomology, 45(3), 606–634. https://doi.org/10.1111/syen.12418

Sonne, J., Dalsgaard, B., Borregaard, M. K., Kennedy, J., Fjeldså, J., & Rahbek, C. (2022). Biodiversity cradles and museums segregating within hotspots of endemism. Proceedings of the Royal Society B, 289(1981), 20221102. https://doi.org/10.1098/rspb.2022.1102

Sparks, T. H., Roy, D. B., & Dennis, R. L. H. (2005). The influence of temperature on migration of Lepidoptera into Britain. Global Change Biology, 11(3), 507-514. https://doi.org/10.1111/j.1365-2486.2005.00910.x

Stebbins, G. L. & Major, J. (1965). Endemism and speciation in the California flora. Ecological Monographs, 35(1), 2-35. https://doi.org/10.2307/1942216

Swaegers, J., Mergeay, J., Therry, L., Larmuseau, M. H. D., Bonte, D. & Stoks, R. (2013). Rapid range expansion increases genetic differentiation while causing limited reduction in genetic diversity in a damselfly. Heredity, 111(5), 422-429. https://doi.org/10.1038/hdy.2013.64

Stevens, G. C. (1989). The latitudinal gradient in geographical range: how so many species coexist in the tropics. The American Naturalist, 133(2), 240-256. https://doi.org/10.1086/284913

Theissinger, Fernandes, C., Formenti, G., Bista, I., Berg, P. R., Bleidorn, C., Bombarely, A., Crottini, A., Gallo, G. R., Godoy, J. A., Jentoft, S., Malukiewicz, J., Mouton, A., Oomen, R. A., Paez, S., Palsbøll, P. J., Pampoulie, C., Ruiz-López, M. J., Secomandi, S., …& Höglund, J. (2023). How genomics can help biodiversity conservation. Trends in Genetics. https://doi.org/10.1016/j.tig.2023.01.005

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. Science, 277(5330), 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Tribsch, A. & Schoenswetter, P. (2003). Patterns of endemism and comparative phylogeography confirm palaeo-environmental evidence for Pleistocene refugia in the Eastern Alps. Taxon, 52(3), 477–497. https://doi.org/10.2307/3647447

Tucker, C. M., & Cadotte, M. W. (2013). Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent. Diversity and Distributions, 19(7), 845-854. https://doi.org/10.1111/ddi.12087

Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., Grenyer, R., Helmus, M. R., Jin, L. S., Mooers, A. O., Pavoine, S., Purschke, O., Redding, D. W., Rosauer, D. F., Winter, M. & Mazel, F. (2017). A guide to phylogenetic metrics for conservation, community ecology and macroecology. Biological Reviews of the Cambridge Philosophical Society, 92(2), 698–715. https://doi.org/10.1111/brv.12252

Välimäki, P., Kivelä, S. M., Mäenpää, M. I. & Tammaru, T. (2013). Latitudinal clines in alternative life histories in a geometrid moth. Journal of evolutionary biology, 26(1), 118–129. https://doi.org/10.1111/jeb.12033

Vane-Wright, R. I., Humphries, C. J. & P. H. Williams (1991). What to protect? – Systematics and the agony of choice. Biological Conservation, 55, 235-254. https://doi.org/10.1016/0006-3207(91)90030-D

Vamosi, J. C. & Vamosi, S. M. (2007). Body size, rarity, and phylogenetic community structure: insights from diving beetle assemblages of Alberta. Diversity and Distributions, 13(1), 1–10. https://doi.org/10.1111/j.1472-4642.2006.00299.x

Vasconcelos, T., O'Meara, B. C. & Beaulieu, J. M. (2022). Retiring "cradles" and "museums" of biodiversity. The American Naturalist, 199(2), 194-205. https://doi.org/10.1086/717412

Verdu, M. & Pausas, J. G. (2007). Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. Journal of Ecology, 95, 1316–1323. https://doi.org/10.1111/j.1365-2745.2007.01300.x

Violle, C., Nemergut, D. R., Pu, Z. & Jiang, L. (2011). Phylogenetic limiting similarity and competitive exclusion. Ecology Letters, 14(8), 782-787. https://doi.org/10.1111/j.1461-0248.2011.01644.x

Wahlberg, N., Wheat, C.W., Pena, C. (2013). Timing and patterns in the taxonomic diversification of Lepidoptera (butterflies and moths). PLoS ONE 8(11): e80875. https://doi.org/10.1371/journal.pone.0080875

Webb, C. O., Ackerly, D. D., McPeek, M. A. & Donoghue, M. J. (2002). Phylogenies and community ecology. Annual Review of Ecology and Systematics, 33(1), 475-505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Webb, C. O., Losos, J. B., & Agrawal, A. A. (2006). Integrating phylogenies into community ecology 1. Ecology, 87(sp7), S1-S2. https://doi.org/10.1890/0012-9658(2006)87[166:E]2.0.CO;2

Werno, A. (2020). Rote Liste und Gesamtartenliste der Nachtfalter (Lepidoptera p. p.) des Saarlandes. 4./2. Fassung. Ministerium für Umwelt und Verbraucherschutz und DELATTINIA 2020. Saarbrücken und Landsweiler-Reden

Wilson, E. O. (1988). Biodiversity. National Academy Press, Washington, D.C.

Winter, M., Devictor, V. & Schweiger, O. (2013). Phylogenetic diversity and nature conservation: where are we? Trends in Ecology & Evolution, 28(4), 199–204. https://doi.org/10.1016/j.tree.2012.10.015

Wong, M. K., Guénard, B. & Lewis, O. T. (2019). Trait-based ecology of terrestrial arthropods. Biological Reviews, 94(3), 999–1022. https://doi.org/10.1111/brv.12488

Software/Webpages

Bengtsson, H. (2023). matrixStats: Functions that Apply to Rows and Columns of Matrices (and to Vectors). R package version 1.0.0, https://CRAN.R-project.org/package=matrixStats

BioEdit Sequence Alignment Editor Copyright ®, 1997-2005 Tom Hall, version 7.0.5.3. http://www.mbio.ncsu.edu/BioEdit/bioedit.html (accessed April 2019)

BOLDSYSTEMs. http://v4.boldsystems.org (accessed April 2023)

Bouckaert, R., Vaughan, T. G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F. K., Müller, N. F., Ogilvie, H. A., du Plessis, L., Popinga, A., Rambaut, A., Rasmussen, D., Siveroni, I., Suchard, M. A., Wu, C-H, Xie, D., Zhang, C., Stadler, T., Drummond, A. J. (2019). BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. PLoS computational biology 15, no. 4 (2019): e1006650. BEAST Developers ©2022. All rights reserved. Site last generated: Mar 13, 2022. https://doi.org/10.1371/journal.pcbi.1006650. Beauti Version 2.7.4. Java Version 17.0.3. BEAST Version 2.7.4, 2002-2023. MCMC Trace Analysis Tool Version v1.7.2, 2003-2021. Partitionfinder (version 1.1.1)

Carl, G., Levin, S. C., Kuehn, I. (2018). spind: an R Package to Account for Spatial Autocorrelation in the Analysis of Lattice Data. Biodiversity Data Journal 10.3897/BDJ.6.e20760. Package Version 2.2.1

Chamberlain, S. & Boettiger, C. (2017). "R Python, and Ruby clients for GBIF species occurrence data." _PeerJ PrePrints_. https://doi.org/10.7287/peerj.preprints.3304v1

Chamberlain, S., Barve, V., Mcglinn, D., Oldoni, D., Desmet, P., Geffert, L. & Ram, K. (2023). _rgbif: Interface to the Global Biodiversity Information Facility API_. R package version 3.7.7, https://CRAN.R-project.org/package=rgbif

Charif, D. & Lobry, J. R. (2007) Seqin{R} 1.0-2: a contributed package to the {R} project for statistical computing devoted to biological sequences retrieval and analysis. In: Structural approaches to sequence evolution: Molecules, networks, populations. Package Version 4.2.30

Daru, B. H., Karunarathne P., & Schliep K. (2020)a, phyloregion: R package for biogeographic regionalization and macroecology. Methods in Ecology and Evolution, 11: 1483-1491. https://doi.org/10.1111/2041-210X.13478. Package Version 1.0.8

Daru, B. H., Elliott, T. L., Park, D. S. & Davies, T. J. (2017), Understanding the Processes Underpinning Patterns of Phylogenetic Regionalization. Trends in Ecology and Evolution, 32: 845--860. https://doi.org/10.1016/j.tree.2017.08.013. Package Version 1.0.8

Daru, B. H., Farooq, H., Antonelli, A. & Faurby, S. (2020)b, Endemism patterns are scale dependent. Nature Communications, 11: 2115. https://doi.org/10.1038/s41467-020-15921-6. Package Version 1.0.8

Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41:95-98.

Kassambara, A. (2023). _ggpubr: 'ggplot2' Based Publication Ready Plots_. R package, https://CRAN.R-project.org/package=ggpubr. Package Version 0.6.0

Kassambara, A. (2023). ggcorrplot: Visualization of a Correlation Matrix using 'ggplot2'. R package version 0.1.4.1, https://CRAN.R-project.org/package=ggcorrplot

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463-1464. https://doi.org/10.1093/bioinformatics/btq166

Lanfear, R., Calcott, B., Ho, S. Y W. & Guindon, S. (2012). PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29 (6): 1695-1701. http://dx.doi.org/10.1093/molbev/mss020

MAFFT Version 7 (Multiple alignment program for amino acid or nucleotide sequences, https://mafft.cbrc.jp/alignment/server/ (accessed June-July 2023)

Nitta, J. H. & Iwasaki, W. (2021). canaper: Categorical analysis of neo- and paleo-endemism in R. https://doi.org/10.1111/ecog.06638. Package Version 1.0.1

Notepad++ v8.1.2 (64-bit) https://notepad-plus-plus.org/

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M.,

Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C. & Weedon, J. (2022). _vegan: Community Ecology Package_. R package version 2.6.4, https://CRAN.R-project.org/package=vegan

Paradis, E. & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. _Bioinformatics_, *35*, 526-528. https://doi.org/10.1093/bioinformatics/bty633. Package Version: 5.7.1

Pearse, W.D., Cadotte, M.W., Cavender-Bares, J., Ives, A.R., Tucker, C. M., Walker, S.C. & Helmus, M.R. 2015. pez: Phylogenetics for the Environmental Sciences. Bioinformatics 31 (17): 2888-2890. https://doi.org/10.1093/bioinformatics/btv277. Version 1.2.4

QGIS 3.22.4. Białowieża. 2021. QGIS Geographic Information System. Open Source Geospatial Foundation Project. https://qgis.org/de/site/

Rambaut, A. 2006-2018. FigTree 1.4.4. 2018. http://tree.bio.ed.ac.uk/software/figtree/

RStudio Team (2022). RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/. Version 2022.7.2.576

R Core Team (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. R version 4.2.1 (2022-06-23 ucrt)

Signorell A (2023). _DescTools: Tools for Descriptive Statistics_. R package version 0.99.48, https://CRAN.R-project.org/package=DescTools

TreeAnnotator v2.7.4. 2002-2023

Tsirogiannis, C. & Sandel, B. (2017). PhyloMeasures: Fast and Exact Algorithms for Computing Phylogenetic Biodiversity Measures. R package version 2.1, https://CRAN.R-project.org/package=PhyloMeasures

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. Package Version 3.4.3

Appendix

Material

Table A1: all species included for the analysis with ID for genetic sequence data obtained from BOLD and GenBank (if available)

	Barcode Process ID	GenBank code CAD	GenBank code GADPH	GenBank code IDH	GenBank code MDH	GenBank code RpS5	GenBank code wingless	GenBank code Ef1a
Anthometra plumularia	GWOUH075-21							
Brachyglossina exilaria	GWORU509-10							
Brachyglossina hispanaria	GWOST158-11							
Brachyglossina manicaria	GWORA569-08							
Casilda anthophilaria	GWORP791-09							
Casilda consecraria	GWORA2306-09							
Cinglis andalusiaria	GWOSO561-11							
Cinglis humifusaria	GWOR3578-08							
Cleta filacearia	GWOTI839-12							
Cleta perpusillaria	GWOSU212-11							
Cleta ramosaria	GWOTZ238-18							
Cyclophora albiocellaria	GWOSI084-10							
Cyclophora albipunctata	LENOA797-11	MH522934.1	MG768379.1	MG768158.1	MH522905.1	MG767564.1		EU443297.1
Cyclophora annularia	EII388-15					MH522877.1		MH522957.1
Cyclophora ariadne	GWORU542-10							
Cyclophora hyponoea	GBLAF068-14							
Cyclophora lennigiaria	GWOTG328-12							
Cyclophora linearia	GBLAA2055-15							
Cyclophora pendularia	LEFIA354-10							
Cyclophora porata	GBLAA2315-15							
Cyclophora punctaria	GWOSH465-10	KX788584.1		GU829971.1	KX788791.1	KX788769.1	GU829482.1	EU443298.1
Cyclophora puppillaria	GWOSP881-11							
Cyclophora quercimontaria	GBLAF338-14							
Cyclophora ruficiliaria	GWORB1613-08							
Cyclophora serveti	GWOTZ256-18							
Cyclophora suppunctaria	GWORB1611-08							
Emmiltis pygmearia	GWORU476-10							
Glossotrophia alba	GBLAA2939-16							
Glossotrophia asellaria	GWORD2025-08							
Glossotrophia confinaria	GWORA2074-09							
Glossotrophia mentzeri	GWOR971-07							
Glossotrophia rufomixtaria	GWOSO564-11							
Glossotrophia sacraria	GWOR461-07							
Holarctias rufinaria	GBMNF22105-22							
Idaea acutipennis	GWOTZ247-18							
Idaea admiranda	GWOSE950-10							
Idaea albarracina	GWORA2078-09							
Idaea albitorquata	GWOSO522-11							
Idaea alicantaria	GWORE501-08							
Idaea alyssumata	GWOAL569-10							
Idaea attenuaria	GWOST180-11							
Idaea aureolaria	LEATH475-14							
Idaea aversata	GBLAC102-13	KX343822.1	KX343410.1	KX343351.1	KX343749.1	KX343277.1	EU443315.1	EU443294.1
Idaea barbuti								
Idaea belemiata	GWORB3619-08							
Idaea bigladiata	GWORU477-10							
Idaea biselata	GWOTI806-12	KX788596.1	KX788744.1		KX788804.1		KX788760.1	KX788721.1
Idaea blaesii	GWORA2152-09							
Idaea calunetaria	LEASW114-19							
Idaea camparia	GWORB1637-08							
Idaea carvalhoi	GWORU510-10							
Idaea cervantaria	GWOTF716-12							
Idaea circuitaria	GWOSO539-11							
Idaea completa	GWOTY1210-14							
Idaea consanguiberica	GWOAL585-10							
Idaea consanguinaria	GWORK632-09							
Idaea consolidata	GWOR197-07							
Idaea contiguaria	ABOLA395-14							
Idaea degeneraria	GWOTI820-12							
Idaea deitanaria	GWORU512-10							
Idaea descitaria	GWOTZ246-18							
Idaea determinata	GWOSO495-11							
Idaea deversaria	GWOSI076-10							
Idaea dilutaria	FBLMV299-09							
Idaea dimidiata	GBLAF382-14	MH522935.1	MH522854.1	MH540095.1	MH522906.1	MH522878.1	MH522834.1	MH522958.1
Idaea distinctaria	GWORL905-09							

Idaea dromikos	GWOUH083-21							
Idaea efflorata	GWORC1171-08							
Idaea elongaria	LEATD615-13							
Idaea emarginata	GBLAB792-13	MG768545.1	MG767566.1	MG768381.1	MG768002.1	MG767393.1	MG767316.1	MG768160.1
Idaea eugeniata	MPSC021-11							
Idaea figuraria	GWORU479-10							
Idaea filicata	LEASW182-19							
Idaea flaveolaria	ABOLA480-14							
Idaea fractilineata	GWORM283-09							
Idaea fuscovenosa	LENOA814-11							
Idaea gelbrechti	GWORZ703-10							
Idaea humiliata	GWOSO535-11							
Idaea ibizaria	GWORR691-10							
Idaea incalcarata	GWORP760-09							
Idaea incisaria	GWORM186-09							
Idaea infirmaria	GWOSO538-11							
Idaea inquinata	GWOSN706-11							
Idaea intermedia	GWOSO502-11							
Idaea joannisiata	GWOSC932-10							
Idaea josephinae	IBLAO1680-20							
Idaea korbi	GWOSO560-11							
Idaea laevigata	PHLAW098-13							
Idaea leipnitzi	GWOTI775-12							
Idaea libycata	GWORB2321-08							
Idaea litigiosaria	GWORO249-09							
Idaea lobaria	GWORL780-09							
Idaea longaria	GWOSP899-11							
Idaea lusohispanica	GWOTY423-13							
Idaea luteolaria	GWOTZ329-19							
Idaea lutulentaria	GWOTZ244-18							
Idaea macilentaria	GBLAB826-13							
Idaea mancipiata	GBLAD318-14							
Idaea mediaria	GWORI455-09							
Idaea metohiensis	GWOSO520-11							
Idaea minuscularia	GWOTI475-12							
Idaea moniliata	PHLAC567-10							
Idaea muricata	GWOSP724-11							
Idaea mustelata	GWOST097-11							
Idaea mutilata	GWOSP910-11							
Idaea nevadata	GWOTZ241-18							
Idaea nexata	GWOTZ330-19							
Idaea nigrolineata	GWORA592-08							
Idaea nitidata	ABOLD705-20							
Idaea obliquaria	GWOAL582-10							
Idaea obsoletaria	GWORL931-09							
Idaea ochrata	GWORC1157-08							
Idaea ossiculata	GWOSO496-11							
Idaea ostrinaria	GWOTI774-12							
Idaea palaestinensis	GWOR180-07							
Idaea pallidata	LEFIA280-10	MH522936.1	MH522855.1	MH540096.1	MH522907.1	MH522879.1	MH522835.1	MH522959.1
Idaea politaria	GWOSN330-11							
Idaea predotaria	GWOTF711-12							
Idaea rainerii	GWORU566-10							
Idaea rhodogrammaria	GWORD628-08							
Idaea robiginata	GWOTZ243-18							
Idaea rubraria	GWORB1717-08							
Idaea rufaria	GWOSO494-11							
Idaea rupicolaria	GWOTZ248-18							
Idaea rusticata	GWORB1773-08							
Idaea saleri	GWOTZ249-18							
Idaea sardoniata	GWORI460-09							
Idaea seriata	GBLAA669-14							
Idaea sericeata	LEATB667-13							
Idaea serpentata	ABOLA476-14	MH522937.1	MH522856.1	MH540097.1		MH522880.1	MH522836.1	MH522960.1
Idaea simplicior	GWORZ724-10							
Idaea spissilimbaria								
Idaea squalidaria	GWOTZ298-18							
Idaea straminata	GWORG006-08			JF785541.1		GU580657.1	AY948534.1	AY948507.1
Idaea subsaturata	GWOSN333-11							
Idaea subsericeata	GWORB1740-08							
Idaea sylvestraria	LEFIC719-10							
Idaea textaria	GWORC996-08							
Idaea tineata	GWOSR435-11							
Idaea trigeminata	GWOSO532-11							
Idaea troglodytaria	GWORL736-09							
Idaea typicata	LEATD613-13							
Idaea urcitana	GWOR3004-08							
Idaea vesubiata	GWORU511-10							
Limeria macraria	LEPAL440-14							

Lythria cruentaria	GWOSI823-10	JF785255.1		JF785529.1	JF784896.1	JF785005.1	EU443322.1	EU443302.1
Lythria plumularia	LEASV1194-19						GQ857127.1	GQ857125.1
Lythria purpuraria	GWOTD298-12						EU443324.1	EU443304.1
Lythria sanguinaria	GWOTD1007-12						EU443323.1	EU443303.1
Oar reaumuraria	GWORE485-08							
Ochodontia adustaria	GWOTH249-12							
Problepsis ocellata	LEASW1224-20					MZ798176.1	MZ798178.1	MZ798172.1
Rhodometra sacraria	GWORB1782-08	JF785181.1	JF785426.1	JF785488.1	JF784842.1	JF784953.1	JQ787020.1	EU443305.1
Rhodostrophia badiaria	GWORC621-07							
Rhodostrophia calabra	GWOSH381-10					KX788770.1	EU443314.1	EU443293.1
Rhodostrophia cretacaria	GWORU515-10							
Rhodostrophia discopunctata	GWORE1487-08							
Rhodostrophia jacularia	GBMNE3322-21							
Rhodostrophia pudorata	GWOSP935-11							
Rhodostrophia sieversi	GWORB3316-08							
Rhodostrophia tabidaria	GWORE1487-08							
Rhodostrophia terrestraria	GWORE1153-08							
Rhodostrophia vibicaria	GBLAB234-13	KX788585.1		KX788630.1	KX788792.1	KX788771.1	JF785107.1	EU443292.1
Scopula albiceraria	GBMNE3324-21							
Scopula arenosaria	GWOSF917-10							
Scopula beckeraria	GWORB3307-08							
Scopula cajanderi	GBMNE3325-21							
Scopula caricaria	LEFIF023-10	MH522940.1	MH522859.1		MH522910.1	MH522883.1		MH522961.1
Scopula concinnaria	GWOTZ253-18							
Scopula corrivalaria	GWOSV121-11							
Scopula decolor	GWOR274-07							
Scopula decorata	GWOSO505-11	MH522941.1	MH522860.1	MH540100.1	MH522911.1	MH522884.1	EU443317.1	EU443296.1
Scopula divisaria	GBMNE63266-22							
Scopula donovani	GWORL791-09							
Scopula drenowskii	GWORC1030-08							
Scopula emutaria	GWOSV110-11							
Scopula flaccidaria	GWORL788-09							
Scopula floslactata	LEFIA294-10	MG768691.1	MG768380.1	MG768159.1	MH522912.1	MG767565.1	KX788766.1	KX788730.1
Scopula frigidaria	LEFIF020-10				MK741144.1	MK741947.1		
Scopula honestata	GWOTZ157-16							
Scopula imitaria	GWORD672-08							
Scopula immistaria	GWORE1132-08							
Scopula immorata	LEATC103-13	JF785209.1		GU830032.1	GU830351.1	GU830646.1	GU829536.1	KX788707.1
Scopula immutata	GWORM040-09						KX788767.1	KX788731.1
Scopula incanata	GWORA1677-08	MH522942.1	MH522861.1	MH540101.1	MH522913.1	MH522885.1	MH522837.1	MH522962.1
Scopula luridata	GWOR270-07							
Scopula marginepunctata	GWORM038-09		MH522862.1			MH522886.1	MH522838.1	MH522963.1
Scopula minorata	GWORD668-08							
Scopula nemoraria	LEEUA516-11	MH522943.1		MH540102.1	MH522914.1	MH522887.1		MH522964.1
Scopula nigropunctata	GBLAF225-14	MH522944.1	MH522863.1	MH540103.1		MH522888.1	MH522839.1	MH522965.1
Scopula ochraceata	GWOSO488-11							
Scopula orientalis	MOTHS013-17							
Scopula ornata	GWORB1554-08			MH540104.1	MH522915.1	MH522889.1	EU443316.1	EU443295.1
Scopula rubellata	GWOTZ254-18							
Scopula rubiginata	LENOA832-11							
Scopula scalercii	GWORE1444-08							
Scopula submutata	GWOSO487-11							
Scopula subpunctaria	GWORD1112-08							
Scopula subtilata	GWOSQ813-11							
Scopula ternata	LEATD490-13	KX788600.1	MK740574.1		MK741142.1	MK741945.1		KX788728.1
Scopula tessellaria	GWOTI912-12							
Scopula turbidaria	GWORA2098-09							
Scopula turbulentaria	GWOSO559-11							
Scopula umbelaria	PHLAV026-12							
Scopula vigilata	GWOTI937-12							
Scopula virgulata	GBLAB1741-14							
Timandra comae	ABOLA491-14	MG768690.1	KX788734.1	KX788632.1	MH522916.1	KX788773.1	EU443320.1	EU443300.1
Timandra griseata	LEFIB848-10	JF785252.1	KX788733.1	KX788631.1	JF784893.1	KX788772.1	JF785118.1	EU443299.1

Methods:

Table A2: List of reference points (total = 41) for Georeferencing

1	Southwestern tip of Portuguese “Cabo de São Vicente,” Portugal	22	St. Petersburg, Russia
2	Gibraltar, UK	23	Pernau, Estonia
3	"Cabo de la Nao", Spain	24	Lidöfjärden, Sweden
4	Begur (Costa Brava), Spain	25	Malmö, Sweden
5	Northernmost border between France and Spain	26	Oslo, Norway
6	"Cabo Touriñán", Spain	27	Öndverðarnesviti, Iceland
7	Western Sicilia "Trapani", Italy	28	Látrar, Iceland
8	“Boot” of Italy (close by Policoro), Italy	29	Fontur, Iceland
9	Southernmost point of Istria "Pula", Croatia	30	Northernmost point of Lewis "Butt of Lewis", Scotland
10	Lezhë, Albania	31	Northernmost point in Scotland “Cape Wrath”
11	Southernmost point of Peleponnes "Cape Drepano", Greece	32	Peterhead, Scotland
12	Westernmost part of Crete, Greece	33	Fort William, Scotland
13	Easternmost part of Crete, Greece	34	Rossan, Ireland
14	Westernmost part of Cyprus	35	Drummore, UK
15	Easternmost part of Cyprus	36	Uwchmynydd, Wales
16	Easternmost part of Aserbaidschan "Absheron National Park", Aserbaudschan	37	"Butterwick Low", UK
17	Estuary of Don River into the Sea of Azov	38	St. Birdes Bay, UK
18	Sewastopol, Crimea	39	Deal, UK
19	Olenivka, Crimea	40	"Land's End", UK
20	Mys Kanin Nos, Russia	41	Brest, France
21	Southernmost border between Sweden and Finland		

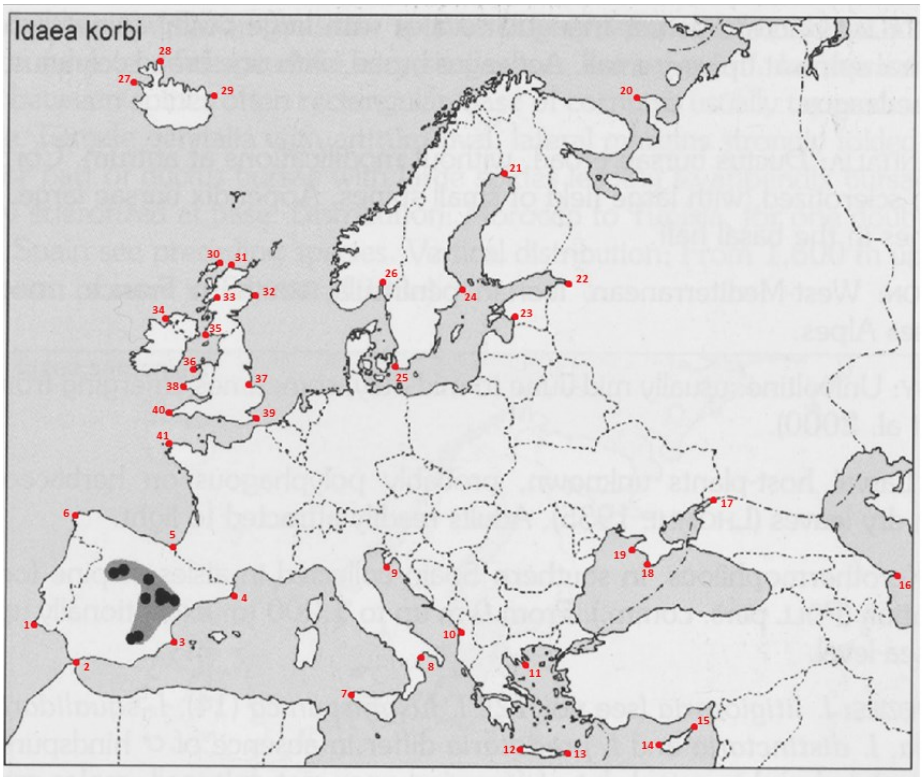

Figure A1: The scanned distribution map of *Idaea korbi* with reference points (red) used for Georeferencing

Table A3: Results of Partitionfinder analysis for subsets (used for BEAUTi and BEAST)

Subset partition	Subset sites	Best model
CO1_pos1	1-658\3	GTR+G
CO1_pos2	2-658\3	GTR+I+G
CO1_pos3	3-658\3	GTR+I+G
CAD_pos1	1-850\3	GTR+I+G
CAD_pos2	2-850\3	GTR+G
CAD_pos3	3-850\3	HKY+I+G
Ef1a_pos1	851-1733\3	GTR+I+G
Ef1a_pos2	852-1733\3	TrN+I+G
Ef1a_pos3	853-1733\3	HKY+I+G
GAPDH_pos1	1734-2424\3	GTR+I+G
GAPDH_pos2	1735-2424\3	TrN+I+G
GAPDH_pos3	1736-2424\3	HKY+I+G
IDH_pos1	2425-3098\3	HKY+I+G
IDH_pos2	2426-3098\3	GTR+I+G
IDH_pos3	2427-3098\3	TrN+I+G
MDH_pos1	3099-3834\3	GTR+I+G
MDH_pos2	3100-3834\3	GTR+G
MDH_pos3	3101-3834\3	HKY+I+G
RPS5_pos1	3835-4451\3	GTR+I+G
RPS5_pos2	3836-4451\3	TrN+I+G
RPS5_pos3	3837-4451\3	HKY+I+G
wingless_pos1	4452-4844\3	GTR+G
wingless_pos2	4453-4844\3	GTR+G
wingless_pos3	4454-4844\3	TrN+I+G

Table A4: Priors settings in BEAUTi and BEAST

Hierarchy	Name	Taxa included	Reference
Genus	*Casilda*	*Casilda*	Hausmann 2004
Genus	*Cinglis*	*Cinglis*	Hausmann 2004
Genus	*Cleta*	*Cleta*	Hausmann 2004
Genus	*Cyclophora*	*Cyclophora*	Hausmann 2004
Genus	*Glossotrophia*	*Glossotrophia*	Hausmann 2004
Genus	*Holarctias*	*Holarctias*	Hausmann 2004
Genus	*Idaea*	*Idaea, Brachyglossina*	Hausmann 2004
Genus	*Lythria*	*Lythria*	Hausmann 2004
Genus	*Rhodostrophia*	*Rhodostrophia*	Hausmann 2004
Genus	*Scopula*	*Scopula*	Hausmann 2004
Genus	*Timandra*	*Timandra*	Hausmann 2004
Tribe	Rhodometrini	*Rhodometra, Casilda, Ochodontia*	Hausmann 2004
Tribe	Scopulini	*Oar, Cinglis, Holarctias, Glossotrophia, Scopula, Problepsis*	Hausmann 2004
Tribe	Sterrhini	*Anthometra, Emmiltis, Cleta, Idaea, Brachyglossina, Limeria*	Hausmann 2004
Super-tribes	Lythriini+Rhodometrini+Cosymbini	*Lythria, Rhodometra, Casilda, Ochodontia, Cyclophora*	Murillo-Ramos et al. 2019
Super-tribes	Timandrini+Rhodometrini+Lythriini	*Lythria, Rhodometra, Casilda, Ochodontia, Cyclophora, Timandra*	Murillo-Ramos et al. 2019
Super-tribes	Rhodostrophini+Sterrhini+Scopulini	*Rhodostrophia, Anthometra, Emmiltis, Cleta, Idaea, Brachyglossina, Limeria, Oar, Cinglis, Holarctias, Glossotrophia, Scopula, Problepsis*	Murillo-Ramos et al. 2019
root	root	All species	Wahlberg et al. 2023

Statistic results

Table A5: Relationship between diversity metrics (PD, PE, NRI, NTI) and species richness. Abbreviations: NRI = Net relatedness index, NTI = Nearest Taxon Index, PD = Phylogenetic Diversity (Faith), PE = Phylogenetic Endemism

	PD		**PE**		**NRI**		**NTI**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
(Intercept)	158.80 *** (154.90 – 162.69)	**<0.001**	-0.45 *** (-0.52 – -0.39)	**<0.001**	-1.43 *** (-1.51 – -1.35)	**<0.001**	1.52 *** (1.44 – 1.60)	**<0.001**
Species Count	22.00 *** (21.89 – 22.12)	**<0.001**	0.04 *** (0.04 – 0.05)	**<0.001**	0.01 *** (0.01 – 0.01)	**<0.001**	-0.02 *** (-0.02 – -	**<0.001**
Observations	3988		3988		3264		3264	
R^2 / R^2 adjusted	0.973 / 0.973		0.332 / 0.332		0.026 / 0.026		0.058 / 0.058	
Species Count (Polynom 2nd deg.)					16.39 *** (14.79 – 17.98)	**<0.001**	-4.78 *** (-6.56 – -	**<0.001**
Observations					3264		3264	
R^2 / R^2 adjusted					0.133 / 0.133		0.066 / 0.066	
** p<0.05 ** p<0.01 *** p<0.001*								
Observations: NRI and NTI only for species count > 8								

Table A6: Relationship between diversity metrics (PD, PE, NRI, NTI, ED) and latitude. Abbreviations: ED = Evolutionary distinctiveness, NRI = Net relatedness index, NTI = Nearest Taxon Index, PD = Phylogenetic Diversity (Faith), PE = Phylogenetic Endemism

	PD		**square root PE**		**NRI**		**NTI**		**ED**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
(Intercept) latitude	3047.26 *** (3003.90 – 3090.62)	**<0.001**	3.34 *** (3.27 – 3.41)	**<0.001**	-1.09 *** (-1.11 – -1.07)	**<0.001**	0.98 *** (0.95 – 1.01)	**<0.001**	15.12 *** (15.04 – 15.20)	**<0.001**
Latitude	-41.87 *** (-42.67 – -41.06)	**<0.001**	-0.05 *** (-0.05 – -0.05)	**<0.001**						
Latitude (Polynom 2nd deg.)					27.09 *** (25.83 – 28.34)	**<0.001**	-13.47 *** (-15.05 – -11.89)	**<0.001**	-64.85 *** (-69.26 – -60.44)	**<0.001**
Observations	3988		3988		3264		3264		3988	
R^2 / R^2 adjusted	0.724 / 0.724		0.581 / 0.581		0.463 / 0.463		0.263 / 0.262		0.419 / 0.419	
** p<0.05 ** p<0.01 *** p<0.001*										
Observations: NRI and NTI only for species count > 8										

Table A7: Relationship between diversity metrics (PD, PE, NRI, NTI) and Mean Annual Temperature, Mean Temperature Warmest Month, Mean Temperature Coldest Month, Mean Temperature Range, Annual Precipitation. Abbreviations: AP = Annual Precipitation, MAT = Mean Annual Temperature, MTCM = Mean Temperature Coldest Month, MTWM = Mean Temperature Warmest Month, NRI = Net relatedness index, NTI = Nearest Taxon Index, PD = Phylogenetic Diversity (Faith), PE = Phylogenetic Endemism, TAR = Temperature Annual Range

	PD		**PE**		**NRI**		**NRI_poly**		**NTI**		**NTI_poly**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
(Intercept) MAT	402.96 *** (388.41 – 417.51)	<0.001	-0.07 * (-0.14 – -0.01)	0.031	-1.96 *** (-2.03 – -1.90)	<0.001	-1.09 *** (-1.11 – -1.07)	<0.001	1.60 *** (1.52 – 1.67)	<0.001	0.98 *** (0.95 – 1.01)	<0.001
Mean Annual Temperature	61.42 *** (59.64 – 63.20)	<0.001	0.14 *** (0.13 – 0.15)	<0.001	0.11 *** (0.10 – 0.11)	<0.001	23.52 *** (22.23 – 24.80)	<0.001	-0.08 *** (-0.08 – -0.07)	<0.001	-15.43 *** (-17.10 – -13.76)	<0.001
Observations	3988		3988		3264		3264		3264		3264	
R^2 / R^2 adjusted	0.535 / 0.535		0.236 / 0.236		0.217 / 0.217		0.439 / 0.439		0.094 / 0.094		0.177 / 0.177	
(Intercept) MTWM	-684.89 *** (-736.97 – -632.82)	<0.001	-2.69 *** (-2.91 – -2.47)	<0.001	-2.31 *** (-2.51 – -2.11)	<0.001	-1.09 *** (-1.12 – -1.06)	<0.001	5.10 *** (4.93 – 5.26)	<0.001	0.98 *** (0.95 – 1.00)	<0.001
Mean Temperature Warmest Month	64.68 *** (62.46 – 66.89)	<0.001	0.15 *** (0.14 – 0.16)	<0.001	0.05 *** (0.04 – 0.06)	<0.001	13.54 *** (11.93 – 15.15)	<0.001	-0.17 *** (-0.18 – -0.16)	<0.001	-7.03 *** (-8.40 – -5.65)	<0.001
Observations	3988		3988		3264		3264		3264		3264	
R^2 / R^2 adjusted	0.451 / 0.451		0.211 / 0.210		0.043 / 0.043		0.117 / 0.116		0.426 / 0.426		0.443 / 0.443	
(Intercept) MTCM	1057.10 *** (1041.94 – 1072.26)	<0.001	1.47 *** (1.42 – 1.53)	<0.001	-0.69 *** (-0.73 – -0.66)	<0.001	-1.09 *** (-1.12 – -1.07)	<0.001	0.96 *** (0.91 – 1.00)	<0.001	0.98 *** (0.95 – 1.01)	<0.001
Mean Temperature Coldest Month	31.87 *** (30.43 – 33.31)	<0.001	0.08 *** (0.07 – 0.08)	<0.001	0.07 *** (0.06 – 0.07)	<0.001	16.11 *** (14.71 – 17.51)	<0.001	0 (-0.01 – 0.00)	0.216	-8.56 *** (-10.37 – -6.74)	<0.001
Observations	3988		3988		3264		3264		3264		3264	
R^2 / R^2 adjusted	0.321 / 0.321		0.157 / 0.157		0.224 / 0.224		0.329 / 0.328		0.000 / 0.000		0.026 / 0.025	
** p<0.05 ** p<0.01 *** p<0.001*												
Observations: NRI and NTI only for species count > 8												
Table A7 continued												

	PD		PE		NRI		NRI poly		NTI		NTI poly	
(Intercept) TAR	1140.87 ***	<0.001	1.72 ***	<0.001	0.23 ***	0.001	-1.09 ***	<0.001	2.42 ***	<0.001	0.98 ***	<0.001
	(1084.17 – 1197 .57)		(1.52 – 1.92)		(0.10 – 0.37)		(-1.12 – -1.06)		(2.28 – 2.56)		(0.95 – 1.0 1)	
Temperature Annual Range	-10.70 ***	<0.001	-0.03 ***	<0.001	-0.04 ***	<0.001	-1.47	0.074	-0.05 ***	<0.001	2.72 **	0.002
	(-12.50 – -8.91)		(-0.03 – - 0.02)		(-0.05 – - 0.04)		(-3.09 – 0.14)		(-0.05 – - 0.04)		(0.99 – 4.4 5)	
Observations	3988		3988		3264		3264		3264		3264	
R^2 / R^2 adjusted	0.033 / 0.033		0.018 / 0.018		0.110 / 0.110		0.111 / 0.110		0.113 / 0.112		0.115 / 0.115	
(Intercept) AP	735.50 ***	<0.001	1.03 ***	<0.001	-1.22 ***	<0.001	-1.09 ***	<0.001	0.19 ***	<0.001	0.98 ***	<0.001
	(701.14 – 769.8 7)		(0.91 – 1.15)		(-1.31 – - 1.13)		(-1.12 – -1.06)		(0.10 – 0.28)		(0.95 – 1.0 1)	
Annual Precipitation	0.11 ***	<0.001	-0.00 **	0.008	0.00 **	0.002	-0.52	0.549	0.00 ***	<0.001	-14.62 ***	<0.001
	(0.06 – 0.16)		(-0.00 – - 0.00)		(0.00 – 0.00)		(-2.23 – 1.19)		(0.00 – 0.00)		(-16.29 – - 12.94)	
Observations	3988		3988		3264		3264		3264		3264	
R^2 / R^2 adjusted	0.005 / 0.005		0.002 / 0.002		0.003 / 0.003		0.003 / 0.002		0.094 / 0.094		0.169 / 0.168	
** p<0.05 ** p<0.01 *** p<0.001*												
Observations: NRI and NTI only for species count > 8												

Table A8: between mean dietary breadth score per grid cell and latitude and temperature.

	Mean Diet Breadth	
Predictors	*Estimates*	*p*
(Intercept) latitude	3.24 ***	**<0.001**
	(3.23 – 3.24)	
Latitude (Polynom 2nd deg.)	-6.43 ***	**<0.001**
	(-6.80 – -6.07)	
Observations	2877	
R^2 / R^2 adjusted	0.642 / 0.642	
(Intercept) mean annual temperature	3.24 ***	**<0.001**
	(3.23 – 3.24)	
Mean annual temperature (Polynom 2nd deg.)	-5.35 ***	**<0.001**
	(-5.80 – -4.89)	
Observations	2877	
R^2 / R^2 adjusted	0.435 / 0.435	
** p<0.05 ** p<0.01 *** p<0.001*		
Observations: only for species count > 8 and exluding outliers from Ukraine and Russia		

Table A9: Relationship between voltinism and Latitude and Mean Annual Temperature as predictors.

	univoltine		flexible voltinism	
Predictors	*Estimates*	*p*	*Estimates*	*p*
(Intercept) latitude	30.30 ***	**<0.001**	63.17 ***	**<0.001**
	(29.82 – 30.79)		(62.67 – 63.66)	
Latitude (Polynom 2nd deg.)	989.87 ***	**<0.001**	-895.95 ***	**<0.001**
	(959.26 – 1020.48)		(-926.99 – -864.91)	
Observations	3988		3988	
R^2 / R^2 adjusted	0.664 / 0.664		0.611 / 0.610	
(Intercept) mean annual temperature	30.30 ***	**<0.001**	63.17 ***	**<0.001**
	(29.78 – 30.83)		(62.65 – 63.69)	
Mean annual temperature (Polynom 2nd deg.)	851.32 ***	**<0.001**	-751.51 ***	**<0.001**
	(818.35 – 884.29)		(-784.39 – -718.63)	
Observations	3988		3988	
R^2 / R^2 adjusted	0.610 / 0.610		0.563 / 0.563	
** p<0.05 ** p<0.01 *** p<0.001*				

Deutschsprachiges Abstract

Biodiversität ist auf vielen Ebenen messbar und reicht weit über Artenvielfalt hinaus. Beispiele dafür sind funktionelle und genetische Diversität, welche Daten über ökologische und genetische Eigenschaften von Organismen miteinbeziehen. Phylogenetische Diversität (PD) gibt Auskunft über die Vielfalt an evolutionären Linien und phylogenetischen Beziehungen zwischen Arten innerhalb einer Artengruppe. Es gibt mehrere Möglichkeiten diese zu berechnen, eine der bekanntesten Formen davon ist die phylogenetische Diversität nach Faith, welche sich aus der Summer der phylogenetischen Astlängen aller Arten in einer Artengruppe zusammensetzt. Die vorliegende Studie präsentiert eine erstmalige Analyse der phylogenetischen Diversität, Struktur und Endemismus der Sterrhinae Europas (Geometridae, Lepidoptera). Die europäischen Sterrhinae sind überwiegend xerothermophil und fressen als Larven unter anderem an totem und verwittertem Pflanzenmaterial, was sie von anderen Geometridaen unterscheidet. Die Studie basiert auf der Digitalisierung von Verbreitungskarten aus taxonomischen Monographien, lokaler Literatur und GBIF-Einträgen in einen 50 x 50 km Rasters, der über Europa gelegt wurde. Ein phylogenetischer Baum für die europäischen Sterrhinae wurden anhand von mitochondrialen COI-Sequenzen und nukleären Markern berechnet. Die Ergebnisse der Analyse zeigen, dass die PD von europäischen Sterrhinaen am höchsten in den südwestlichen Gebieten Europas, entlang der gesamten mediterrane Küste und Teilen des Balkan ist. Dies sind ähnliche Muster wie die von Artenreichtum. PD war dementsprechend auch signifikant korreliert mit Artenreichtum und zusätzliche mit Latitude, während die Beziehung zur Jahresdurchschnittstemperatur nicht signifikant blieb nach der Durchführung einer spatialen Autokorrelation. Weitere Diversitätsmetriken (wie net relatedness index und nearest taxon index) gaben Einblicke in die phylogenetische Struktur der europäischen Sterrhinae und zeigten auf, dass die diversen südlichen Gebiete Europas hauptsächlich Cluster an evolutionär älteren Linien beherbergen, während rezentere Cluster, vor allem in Nordeuropa vorhanden waren. Phylogenetischer Endemismus war stark präsent in der iberischen Halbinsel und vielen mediterranen Inseln, weiters auch in Süd-Frankreich, -Italien und -Griechenland. Mit der CANAPE-Methode konnten die Endemismus-Zentren als eine Mischung aus Neo- und Paläoendemismus und teils Superendemismus identifiziert werden. Ökologische Merkmale, wie Futterpflanzenspezialisierung (Nieschenbreite), Voltinismus und Arealgrößen der Sterrhinae Arten folgten einem latitudinalen Gradienten: größere Areale, Nieschenbreite an Futterpflanzen und Univoltinismus waren häufiger in hohen Breitengraden, was möglicherweise mit den harschen Umweltbedingungen in nördlichen Gebieten zusammenhängt. Beim Vergleichen verschiedener Metriken fällt auf, dass im Gegensatz zu reinem Artenreichtum die räumlichen Muster von PD etwas feinstrukturierter waren und hohe Diversität auch abseits von artenreichen Regionen aufzeigen konnten, wie zum Beispiel in den temperaten Gebieten Zentraleuropas. Eine Aufnahme von mehreren Diversitätsmetriken kann demnach wichtige Zusatzinformationen für Biodiversitätsstudien liefern.