Original Article

Climatic niche conservatism and ecological diversification in the Holarctic cold-dwelling butterfly genus *Erebia*

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ABSTRACT

The evolution and distribution of alpine species have been modulated by their climatic niches. However, the relative roles of climatic niche conservatism promoting geographical speciation and of climatic niche diversification are poorly understood in diverse temperate groups. Here, we describe the evolution of climatic niche in a species rich butterfly genus, *Erebia*, which occurs across cold regions of the Holarctic and its diversity centre lies in European mountains. We inferred a nearly complete molecular phylogeny and modelled the climatic niche evolution using 25 thousand geo-referenced occurrence records. First, we reconstructed the evolution of the climatic niche. Second, we tested how the species' climatic niche width changes across the occupied climate gradient and compared the two main *Erebia* clades, the European and the Asian clade. Third, we explored climatic niche overlaps among species. We revealed that the evolution of *Erebia* has been shaped by climatic niche conservatism, supported by a strong phylogenetic signal and niche overlap in sister species, promoting allopatric speciation and by ecological speciation driven by specialization of climatic niches. However, the two main clades evolved their climatic niches toward different local optima. In addition, niche width decreases in extreme conditions of low and high temperatures and species in the diverse European clade have narrower niches compared to the Asian clade. This may be related to the gradient of climate seasonality, with lower European seasonality favouring the evolution of narrower niches. Our findings, coupled with declining diversification rates through time, support a diversity-dependent radiation scenario.

Keywords: alpine grasslands, climatic variability, Eastern and Western Palearctic, insect, rapid divergence, temperate mountains

Running Title: Climatic niche evolution in *Erebia*

INTRODUCTION

Mountains are major global biodiversity reservoirs whose communities have been shaped by evolutionary and ecological processes linked with topographical complexity and elevational gradients (Wiens and Graham 2005, Schmitt et al. 2016, Condamine et al. 2018). However, temperate mountains host poorer species diversity compared to tropical mountains. In the tropics, narrower climatic niches (Janzen 1967) and rapid climatic niche evolution (lability) might have further accelerated diversification rates and driven a greater accumulation of taxa compared to temperate mountains (Kozak and Wiens 2010). In temperate mountains, climatic niche conservatism associated with broad temperature seasonality seems to predominate (Kozak and Wiens 2007). The climatic niche conservatism shapes regional species diversity by enhancing dispersal along elevational gradients during climatic changes (Cadena et al. 2012, Qian et al. 2021) and drives allopatric diversification within mountain ranges (Xing and Ree 2017, Ding et al. 2020). While niche conservatism and broad climatic niches seem to have determined the extant species richness in several temperate groups of vertebrates (Smith et al. 2005, Pyron and Burbrink 2009), macro-evolutionary mechanisms driving diversity gradients across temperate mountains have rarely been addressed in species-rich insect groups.

The extant species diversity of temperate mountains has been primarily shaped by dispersal mediated by climatic niche conservatism (Condamine et al. 2018, Liu et al. 2021), but also by specialisation to extreme climatic conditions (Su et al. 2020), and by diversity-dependent radiation across empty niches on isolated mountain ranges (Peña et al. 2015). Such ecological intra- and inter-specific interactions in diverse groups may promote diversification, phenomenon called diversity-dependent radiation (Calcagno et al. 2017). Next, ecological (sympatric) speciation can be driven by climatic-niche lability (Pitteloud et al. 2017) or niche divergence, which may be induced by climatic gradients across mountain slopes. At climatic margins of occurrence, a decrease of fitness may force species to diversify by niche specialisation as an adaptive response to the extreme climates (O'Brien et al. 2022). However, the role of niche specialisation across climatic gradients as s possible driver of species diversification is still understudied.

Here we ask whether the evolutionary history of a species-rich group of temperate cold-dwelling butterflies, the genus *Erebia*, has been influenced by climatic-niche conservatism or lability, and how climatic niche specialisation might have shaped the extant species diversity pattern. The genus contains 90-100 species (Warren 1936), and most of its diversity is concentrated in mountain ranges

across the Holarctic region, with several species occurring in the Arctic and a few species found in lowlands (Warren 1936). *Erebia* larvae are polyphagous, feeding on widespread grasses (Poaceae) (Warren 1936), thus, their geographical distribution has likely not been constrained by their host plants unlike in other insect herbivores (Su et al. 2020). An adaptive radiation scenario has been proposed for *Erebia* based on an apparent slowdown in diversification rates toward the present (Martin et al. 2000, Peña et al. 2015). Alternatively, a diversification scenario under climatic niche conservatism was invoked to explain dispersal during climatic fluctuations followed by vicariant differentiation (Schmitt et al. 2016). The adaptive scenario is supported by climatic niche differentiation and contrasting microhabitat use observed in sympatric butterflies (Kleckova et al. 2014). In contrast, the studies of *Erebia* secondary zones suggest preceding allopatric differentiation connected with coevolution with endosymbionts (Lucek et al. 2021). To shed more light on processes driving the diversification of *Erebia* , we ask three sets of questions in this study:

1. Have species' climatic niches evolved gradually following the niche conservatism hypothesis? Alternatively, have the climatic niches evolved toward local optima or rapidly during the early evolution of the genus in congruence with an adaptive radiation scenario?
2. Do sister species have more similar climatic niches compared to non-sister species pairs? In addition, do sympatric sister species have distinct climatic niches to avoid inter-specific competition?
3. Is the high species diversity found in European mountains explained by the accumulation of taxa with narrow climatic niches? Additionally, do species occurring in extreme climates on the periphery of their distributional ranges have broad climatic niches or are they climatic niche specialists?

METHODS

Phylogeny and divergence times

To obtain a nearly complete phylogeny of the genus *Erebia*, we extended the dataset from (Peña et al., 2015) by sequencing 1 mitochondrial (COI) and 3 nuclear gene fragments (GAPDH, RpS5, wingless). Our dataset includes 8 outgroups and 83 representatives of the genus (Supplementary materials, Table S1), thus, covering 80-90% of the *Erebia* species diversity. Divergence times were estimated in the software BEAST v2.6.0 (Bouckaert et al. 2019). Alignment partitions and substitution models were specified by PartitionFinder 2 (Lanfear et al. 2012). However, due to low effective sample sizes (ESS) in preliminary analyses, we reduced the complexity of the substitution

models for the mitochondrial partitions (Supplementary materials, Table S2). We used a log-normal relaxed molecular clock and the birth-death incomplete sampling process. Other priors were left as default. As fossil records have not been identified for the genus *Erebia*, we used secondary calibrations from the comprehensive, fossil-based Nymphalidae chronogram (Chazot et al. 2021):

1. The root age of the tribe Satyrini Boisduval 1833 was defined by a uniform distribution between 37.45 to 45.55 Ma;
2. The crown node of the strongly supported clade within the tribe Satyrini, consisting of the subtribes Erebiina, Pronophilina, Satyrina, and Melanargiina was specified by a uniform distribution between 23.12 to 31.39 Ma;
3. The split between the genera *Maniola* and *Erebia* had a uniform distribution between 26.98 to 35.64 Ma.

The length of the Markov chain Monte Carlo (MCMC) chain was set to 100 million, storing the estimated parameters every 10,000 steps. We reconstructed the consensus tree from 1000 randomly sampled trees from the posterior distribution using the program TreeAnnotator implemented in Beast v1.10.4. software (Suchard et al. 2018) and calculated mean node heights to obtain divergence times. For downstream biogeographical and climatic niche evolution analyses, we pruned the outgroups in the estimated phylogeny by using the drop.tip command in the APE package (Paradis et al. 2004) using the software R v 4.1.2 (R Core Team 2021).

Biogeography

We specified 3 biogeographical regions: Western Palaearctic (A), Eastern Palaearctic (B), and North America (C) (Supplementary materials, Table S3). We estimated ancestral ranges along the phylogeny of *Erebia* using the R package BioGeoBEARS v1.1.2 (Matzke 2013). We compared six competing biogeographical models using the Akaike information criterion (AICc) (Akaike 1973). The analysed models were the dispersal–extinction–cladogenesis model (DEC) (Ree and Smith 2008), a model resembling the dispersal-vicariance model of (Ronquist 1997) ("DIVALIKE") and a model resembling the BayArea-like model (Landis et al. 2013) ("BAYAREALIKE"). We also tested a modified version of each of these three models to include the founder-event speciation J parameter (Matzke 2014). Although the usage of the J parameter has been criticized (Ree and Sanmartín 2018), it has been recently shown that model comparison of models including such a parameter is statistically valid (Matzke preprint).

Climatic niche

The climatic niche of the genus *Erebia* was analysed by the Principal Component Analysis (PCA) based on occurrence points. We collected 25,694 vetted occurrence points from the literature and biodiversity databases (Supplementary material, Table S4). For each species, we extracted bioclimatic variables from WorldClim v. 2.1. at the 30" resolution (about 1 km^2, ESRI grid) in the R package Raster v. 3.5 (Hijmans and van Etten 2012). To describe the climatic niche, we used four bioclimatic variables: annual mean temperature (bio1), temperature seasonality (bio4), annual precipitation (bio12), and precipitation seasonality (bio15). The larger values of seasonality indices represent larger variability of temperature or precipitation during the year (O'Donnel and Ignizio 2012). Further, we have extracted WorldClim variable Elevation for every occurrence point and used the mean elevation of species occurrence records as an additional proxy of climatic niche.

First, we delimited background climate to describe the full range of conditions over the entire range of the genus *Erebia*, as recommended by (Broennimann et al. 2012). The background climatic data were extracted from a rectangle delimited by the minimum and maximum longitude and latitude of the occurrence points. We extracted values of the four bioclimatic variables from >100,000 points in a regular grid covering the rectangle. Second, we added climatic data from our occurrence points to the background dataset. Then, we performed the PCA and calculated duality diagrams (dudi) implemented in R package ade4 v. 1.7.18 (Dray and Dufour 2007) for the 4 bioclimatic variables following (Broennimann et al. 2012).

Models of trait evolution

We compared the fit of three models to describe the evolution of the climatic traits and elevation: the Brownian Motion (BM), the Ornstein-Uhlenbeck (OU) (Butler and King 2004) and the Early Burst (EB) models (Simpson 1953). We used the R package Geiger (Pennell et al. 2014) and its fitContinuous function and used AICc to compare model fit. Under Brownian motion, trait evolution is expected to change randomly, without limits, along branches in a phylogenetic tree. It includes the Brownian rate parameter (σ^2), which describes how fast the traits randomly change through time. Under the OU model, a trait is expected to evolve toward a local optimum. The OU model includes the parameter θ describing the optimal value of the trait (long term mean value of the trait), σ^2 as in the BM, and the attraction strength α (Cooper et al. 2016). If $\alpha = 0$, the OU model is identical with BM, and higher values of α suggest strong deviation from a simple random walk and a faster evolution

toward the optimum trait value. Under the Early burst model, it is expected that the rate of trait evolution decreases trough time, described by the parameter *a*, having the highest rate close to the root of the phylogeny.

Evolution of the climatic niche

To quantitatively measure the degree to which evolutionary history predicts ecological similarity among species, we tested for any phylogenetic signal in the mean values of the bioclimatic variables and elevation. The recovery of strong phylogenetic signal is an indicator of niche conservatism because closely related species would share more similar trait states than random taxa from the phylogeny. We used the phylosig function of the R package Phytools v. 0.7.90 (Revell 2012) to calculate two indices of phylogenetic signal, Pagel's λ (Pagel 1999) and Blomberg's K statistics (Blomberg et al. 2003). We cross-validated those two indices because their estimation might be affected by branch lengths uncertainties in time-calibrated phylogenies (Molina-Venegas and Rodríguez 2017). To account for tree topology uncertainties, we calculated both indices using 1,000 trees from the posterior distribution and we calculated their mean values and 95% confidence limits. Both λ and K values close to 0 denote independent evolution of species' traits. Pagel's λ ranges from 0 to 1, with increasing values indicating stronger phylogenetic signal. K ranges from 0 (no phylogenetic signal) to infinity, with K=1 suggesting that the trait has evolved according to the Brownian motion model of evolution and K values >1 suggesting that closely related species are more similar than expected under the Brownian motion model (Blomberg et al. 2003).

Climatic niche evolution in *Erebia* was visualised by ancestral reconstructions of mean values of the four bioclimatic variables, along the species-level time-calibrated tree using the fastAnc function in the R package Phytools. We used the OU models for reconstructions of all climatic traits, as these models had the best fit to our data. Elevation can be used as another proxy of species climatic and habitat requirements (Yu et al. 2016), thus, we also carried out niche evolution analyses using the mean elevation of species occurrences as another trait.

Analysis of climatic niche width

The range of climatic conditions inhabited by individual species is described as the niche width. First, we calculated the total climatic niche width based on the PCA of the 4 bioclimatic variables. Species with ≤ 5 distinct geo-referenced occurrence records and associated climate data were excluded; we

kept 68 species in our climatic niche width analyses. We calculated the relative area of the polygon described by the species-specific occurrence points in the two-dimensional representation of its niche estimated by PCA (Broennimann et al. 2012). We also calculated niche width separately for each bioclimatic variable and for elevation. The niche width for individual variables was approximated using the 0.05 and 0.95 quantiles of the variable to limit the influence of outliers on our niche width estimates. Annual precipitation (bio12) was $\log_{10}$-transformed prior to niche width calculation.

We used generalised linear models (GLM) with Gaussian error distribution to compare the climatic niche width between species from the European and Asian clades. To account for the potential confounding effect of the number of records on species' niche width estimates, we also included the number of occurrence points (log-transformed) and membership in the Asian or European clade for each species as additional explanatory variables in the GLMs. Next, we tested whether species' niche width depends on the position of their niche along the gradients of individual climate variables and along the altitudinal gradient, i.e., whether species occurring in more extreme conditions are more specialised. To test this hypothesis, we fitted a generalised linear model (GAM, R package mgcv v. 1.8-38, Wood 2017) with Gaussian error distribution and a smooth function (cubic spline) describing the changes of species' niche width along the gradient of individual climate variables or elevation. We fitted a separate model for each variable.

Climatic niche overlap among sister and non-sister species pairs

Divergence of the climatic niche between sister species, particularly when they are sympatric, could represent a possible signature of climate-driven ecological speciation. We calculated the mean overlap of climatic niches for all sister vs. non-sister species pairs and for sympatric vs. allopatric sister species pairs. For each species pair, we calculated the overlap of the total climatic niche based on the PCA with four climate variables (bio1, bio4, bio12, and bio15) and, separately, the niche overlaps for each of the four climate variables and the species' altitudinal ranges. We followed the approach of (Broennimann et al. 2012) using the R package ecospat v. 3.2 (di Cola et al. 2017). We extracted PCA scores of occurrence locations for individual species and calculated the occurrence densities grid using a resolution of 100×100 pixels (Broennimann et al., 2012; di Cola et al., 2017). We kept the 68 species with > 5 occurrence points in our dataset for analysis. Then, we calculated the total climatic niche overlap of all species pairs using the Schoener's D index following (Bandeira et al. 2021). The resulting pairwise matrix contained climatic niche overlap values for all species pairs (Supplementary material, Table S5). We separately calculated the overlap of each of the four bioclimatic variables

(Supplementary material, Table S6-S9) and the overlaps of the elevational ranges (Supplementary material, Table S10) of individual species pairs. We calculated the overlap of each variable for all species pairs again using the Schoener's D index.

To compare the niche overlap values (i.e., the estimated Schoener's D) between sister species pairs and non-sister species pairs, we carried out two-tailed Mantel tests with 9,999 permutations using the ecodist v. 2.0.7 package for R (Goslee and Urban 2007, Goslee 2010). We compared the pairwise climatic niche overlap matrix (Supplementary materials, Table S5-S10) against a matrix containing the value of 1 for sister species pairs and the value of 0 for all non-sister species pairs (Supplementary material, Table S11). Furthermore, we compared the values of the niche overlaps between sympatric and allopatric sister species pairs (Supplementary material, Table S12) using generalised linear models (GLM) with Gaussian error distribution. This analysis included 16 sister species pairs after the exclusion of species with an insufficient number of observations (≤ 5 distinct locations).

RESULTS

Phylogenetic tree and biogeography

The age of origin of extant *Erebia* lineages was estimated at 22.4 ± 4.60 Ma. The two main clades, the European clade and the Asian clade, diverged around the middle Miocene, 16 ± 4 Ma (Figure 1; Supplementary material, Figure S1). The European clade, including the *tyndarus* group, had a crown age of 15 ± 4 Ma. Most extant lineages diversified during the Miocene and the Pliocene (5 – 10 Ma).

The best-fit biogeographical model was the BayArea-like+J (J = 0.05) followed by DEC+J (J = 0.03) (ΔAICc = 6.4) and DEC models (ΔAICc= 12.7) (Supplementary material, Table S13). The estimated ancestral areas were consistent across all tested models, except of the ancestral area of the genus at the root of the phylogeny. The best-fit model (BayArea-like+J) estimated that the ancestral area was the Eastern Palaearctic (Supplementary material, Figure S2), whereas the DEC+J and the DEC models (Supplementary material, Figures S3 and S4) estimated a widespread distribution in the Eastern and Western Palaearctic for the crown *Erebia*. Members of the European clade expanded their distributions toward North America at least 5 times independently since 7 Ma (Figure S2). The representatives of the Asian clade further diversified within the region and they expanded toward North America twice, at about 3 Ma.

Evolution of the climatic niche

The evolution of the mean climatic niche of the genus *Erebia* held strong phylogenetic signal for the λ and the K indices, when analysed for the consensus tree (Table 1). The narrow range of confidence limits of λ and K suggested a consistent phylogenetic signal across estimated tree topologies. When analysed across posterior distribution of phylogenetic hypotheses, the mean annual temperature (Bio1), temperature seasonality (Bio4), and elevation held strong phylogenetic signal in both λ and K, whereas annual precipitation (Bio12) and precipitation seasonality (Bio 15) held phylogenetic signal only recovered by the λ index.

The climatic PCA analysis (Figure 1) suggested that members of the European clade inhabit warmer and wetter climates with lower seasonality, whereas members of the Asian clade inhabit places with colder, dryer, and more seasonal conditions (Table 2). The Ornstein-Uhlenbeck (OU) and Brownian motion (BM) models fit the evolution of climatic traits better than the Early Burst model. The annual mean temperature (bio1), annual precipitation (bio12) and precipitation seasonality (bio15) likely evolved toward local optima, given the better fit of the OU model (Table 3), though the deviation from Brownian motion, described by the parameter α, was low (< 0.2). The evolution of both temperature seasonality (Bio4) and elevation were described comparably well by both the OU, with little deviation from Brownian motion, and the Brownian motion models (Δ AICc < 2).

The reconstruction of the ancestral niches (Figure 2, panels C – G) is consistent with an adaptive radiation scenario with evolution of traits toward local optima in both clades. The members of the Asian clade evolved climatic niches characterised by colder (Figure 2C), dryer (Figure 2F), and more seasonal climate (Figure 2D, G), while the European clade shifted toward warmer, wetter, and less seasonal climate. The ancestral reconstruction of the elevational niche showed that related species occur in similar elevations (Figure 2E), with low elevations colonised in the cold Arctic areas and in warm (Figure 2C) areas of the temperate zone.

Climatic niche width

Comparison of niche width among the Asian clade and the European clade showed that the species of the European clade had narrower thermal niches based on annual mean temperature and temperature seasonality (Table 4). The width of the precipitation niche, the total niche inferred from the climatic PCA, and the elevation range were not significantly different between the two clades

(Table 4). In addition, the GAM models testing for changes of species niche width across climatic gradients (Figure 3) indicated that the climatic niche was narrower, thus, species were more specialised, under extreme environmental conditions, particularly strongly in the case of mean temperature.

Niche overlap among sister and non-sister species

The mean overlap of climatic niches between sister species was significantly higher than in non-sister species pairs for all climatic variables (Mantel test, $P < 0.05$ in all cases, Table 5). However, we have not detected any significant differences in the niche overlap between sympatric and allopatric sister species pairs, although we note that the number of observations was rather low in this analysis (GLM, $P > 0.05$ in all cases, Supplementary material, Table S14).

DISCUSSION

The extant species diversity of mountain butterflies in the genus *Erebia* was likely shaped by adaptation to local climates in both Europe and Asia (Table 2) and by their strong climatic niche conservatism within these local optima (Figure 2, Table 1). The conservatism within the two main *Erebia* clades might have resulted in repeated cycles of range expansion and isolation linked to past climatic fluctuations (Schmitt et al. 2016). Climatic niche specialisation might have further contributed to the occupancy of regions with climatic extremes at the margins of species' distribution across the Holarctic (Figure 3), in terms of annual mean temperature, seasonality of temperature and precipitation, and elevation. The European clade is characterized by narrower niches in temperature and its seasonality compared to members of the Asian clade (Table 4). Also, the precipitation niche was narrower in the high-precipitation (mainly European) and broader in low-precipitation (mainly Asia) parts of the precipitation gradient (Figure 3, panel C). We argue that spatial sorting (Comerford and Egan 2022) might have preceded climatic niche specialization in the European clade. Then, the niche specialization might lead to speciation (Vamosi et al. 2014) or, vice versa, high species richness and competition for resources in zones of secondary contact might drive niche specialization to decrease the level of competition (Vázquez and Stevens 2004).

Climatic niche conservatism as primary driver of speciation

The major and rapid radiation of *Erebia* in the mid-Miocene (Figure 1) was concurrent with the uplift

of the main mountain massifs in the Palearctic, such as the Qinghai-Tibetan Plateau (Valdiya 2016), European Alps (Ager 1975, Botsyun et al. 2020), and the Caucasus (Hrivniak et al. 2020). The newly arising mountain areas have likely promoted a burst in speciation in *Erebia* (Peña et al. 2015), similarly to other Palearctic mountains butterflies (Su et al. 2020), mayflies (Hrivniak et al. 2020), and plants (Hörandl and Emadzade 2012, Folk et al. 2019). Although the climate was warmer during the Miocene and the Pliocene than during the Pleistocene (Botsyun et al. 2020), the isolated mountain ridges could have represented islands of grassland habitats necessary for *Erebia*. Indeed, grassland habitats spread in Europe since the mid-Miocene, about 8.5 Ma (Feurdean and Vasiliev 2019).

As soon as newly available areas became occupied early in the evolutionary history of *Erebia*, diversification rates have slowed down toward the present (Peña et al. 2015). The climatic niche evolution seems to be directed toward local optima in Europe and Asia as suggested by OU models of trait diversification (Table 3), but the deviation from Brownian motion model of trait evolution was low. The niche conservatism (Table 1) in both the European (wet and less seasonal climatic niche) and the Asian clade (dryer and more seasonal climatic niche), might have driven allopatric speciation thanks to dispersal and isolation of populations during past climatic fluctuations. Similarly, climatic niche conservatism has been linked to allopatric speciation in temperate groups (Wiens and Graham 2005), such as insular bees (Dorey et al. 2020), mountain rodents (Wan et al. 2018), and micropterigid moths in the Japanese Archipelago (Imada et al. 2011). In line with this, the climatic niche similarity found between sister species (Table 5) reinforces the hypothesis that *Erebia* species likely diversified in allopatry (or parapatry) (Schmitt et al. 2016) rather than by rapid climatic niche evolution (lability) (Pitteloud et al. 2017) which might have resulted in substantial speciation rates in sympatry. The similarity in climatic niches between sister species is also in agreement with observations of closely related species often occurring, and not fully overlapping, in spatially nearby areas with similar climates (Sonderegger 2005).

Niche specialisation contributed to species diversification

Specialisation to climatic extremes in *Erebia* is evidenced by the hump-shaped dependence of niche width on climatic gradients (Figure 3). We detected higher niche specialisation under extreme values of the annual mean temperature, the temperature and precipitation seasonality, and the elevation. The interpretation of this finding is that taxa occupying areas with extreme climatic conditions tend to have narrow niches. This pattern has been found in amphibians (Bonetti and Wiens 2014), but rarely documented in temperate insects. It indicates that the occupancy of both climatic margins, warm

lowlands and cold mountain summits, demands specialisation of physiology, which prevents the colonization of such areas by taxa having broad climatic niches. Indeed, we previously observed distinct thermoregulatory adaptations in European *Erebia* species in alpine and lowland habitats (Kleckova et al. 2014, Kleckova & Klecka 2016). Niche specialisation has been considered an evolutionary dead-end (Colles et al. 2009, Devictor et al. 2010) due to the tendency of specialists to inhabit smaller geographical ranges, which might have enhanced extinction rates. Adaptations to extreme conditions found in Palearctic mountain summits have also been detected in *Parnassius* butterflies (Su et al. 2020), whose species diversification in mountains was likely regulated by ecological limits (Condamine 2018). On the other hand, the linear decrease of precipitation niche with increasing precipitation (Figure 3, panel C) can reflect *Erebia* dependence on dry grasslands or steppe like-habitats. Such a pattern in climatic niche linked to precipitation has been also found in salamanders across a wide range of latitudes (Bonetti and Wiens 2014).

The sources of European diversity

The higher species diversity of the genus *Erebia* in Europe than in Asia is an exceptional pattern of biodiversity distribution in the Holarctic (Sanmartin et al. 2001). In the species rich European clade, we have detected generally narrower thermal niches than in the Asian clade (Figure 3, panel A). We argue that such pattern may relate to the west-east seasonality gradient, with lower seasonality in Europe than in Asia (Table 2). The higher variability of climatic conditions connected with climatic seasonality is assumed to cause general widening of climatic niches, such that temperate taxa are expected to have broader climatic niches than tropical ones (MacArthur 1972). In line with this expectation, the temperature seasonality niche width positively correlates with the temperature seasonality, with a few species occurring in the most seasonal conditions having narrow niches (Figure 3, panel B).

The disparate patterns in temperature niche width found in the European and Asian clades can be explained by several ecological and evolutionary mechanisms. For example, the narrower temperature niches of European lineages might have resulted from an adaptive radiation event (Peña et al. 2015), suggesting that competition for resources or other ecological processes have driven niche specialisation. Alternatively, the narrower niches can be seen as a “by-product” of allopatric speciation across and within mountain ranges, without any signs of adaptive or ecological processes. Under this scenario, species diversification might be explained by differentiation in molecular traits (Lucek, 2018), reproductive traits (Schat et al. 2022), and random evolution of the climatic niche.

Secondary contact zones among species diverged in allopatry might have resulted in competition for resources and niche partitioning in *Erebia* (Lorkovic 1958), leading to the narrow realized climatic niches. In the case of the polyphagous butterflies such as the genus *Erebia*, potential competition for resources is not limited to larval host plants but can be also related to the availability of nectar, microhabitat use (Kleckova et al., 2014), and competition for mates.

Study limitations

The macroevolutionary and macroecological patterns that we detected are robust. However, to further understand the processes leading to speciation in *Erebia*, we still need more detailed information about species ecology, physiology, morphology, and genome evolution. First, the climatic data was interpreted at a macroscale which might have limited the detection of ecological divergence in locally sympatric species. We estimated climatic niches on a relatively rough scale of 1 km^2, which does not capture fine-scale microclimatic differentiation (Kirchheimer et al. 2016). It is thus expected that regionally sympatric species might also display finer niche partitioning and differentiation of their realized climatic and microhabitat niches (Lorkovic 1958, Kleckova et al. 2014), which might have not been detected by our study (Supplementary material, Table S8). In addition, different *Erebia* species seem to have diversified in their adult phenologies, which might have further created niche partitioning (van Dam et al. 2019). Further, conditions undetected by our study, such as winter temperature minima or low snow cover (Konvicka et al. 2021), may affect more vulnerable stages of developmental cycle such as overwintering larvae (Vrba et al. 2017).

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Figures

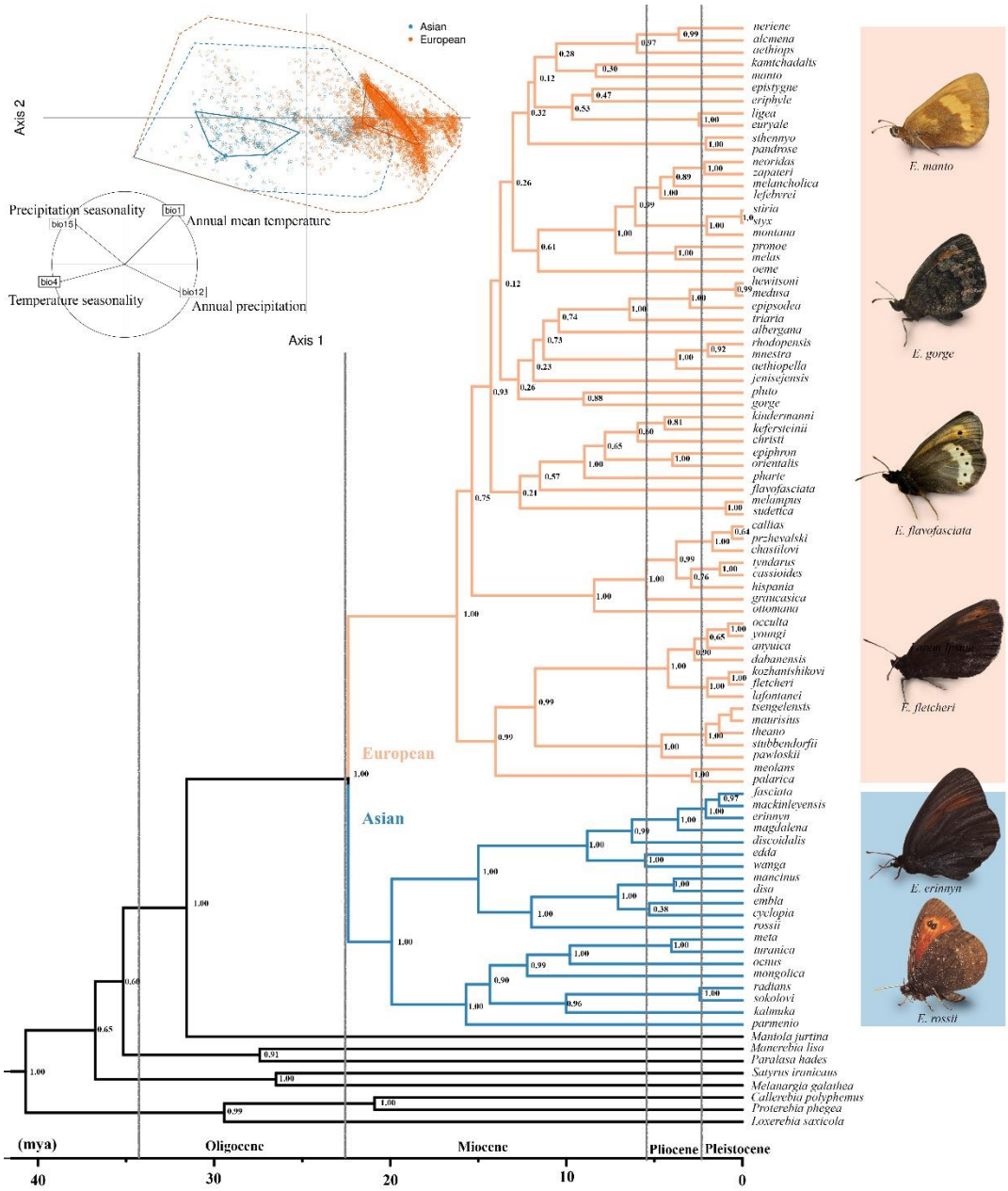

Figure 1. Phylogenetic relationships and divergence time estimates for the butterfly genus *Erebia*. The European clade diversified mainly in Europe (orange), the Asian clade in Asia (blue), although the geographic distribution of several species is not restricted to a single region (see Supplementary material, Figure S2). The full biogeographic reconstruction is shown in the Supplementary material, Figures S2-S4. Climatic PCA displays the climate occupied by the European and the Asian clades. The polygons show the full extent of the conditions occupied by each clade (dotted lines) and the core 50% of the climatic niche (solid lines). The inset shows the correlation of individual bioclimatic variables with the first and second PCA axes. The bioclimatic variables (bio1, bio4, bio12 and bio15) displayed significant phylogenetic signal (Table 2). The European clade inhabits warmer, more humid, and less seasonal climate compared to the Asian clade.

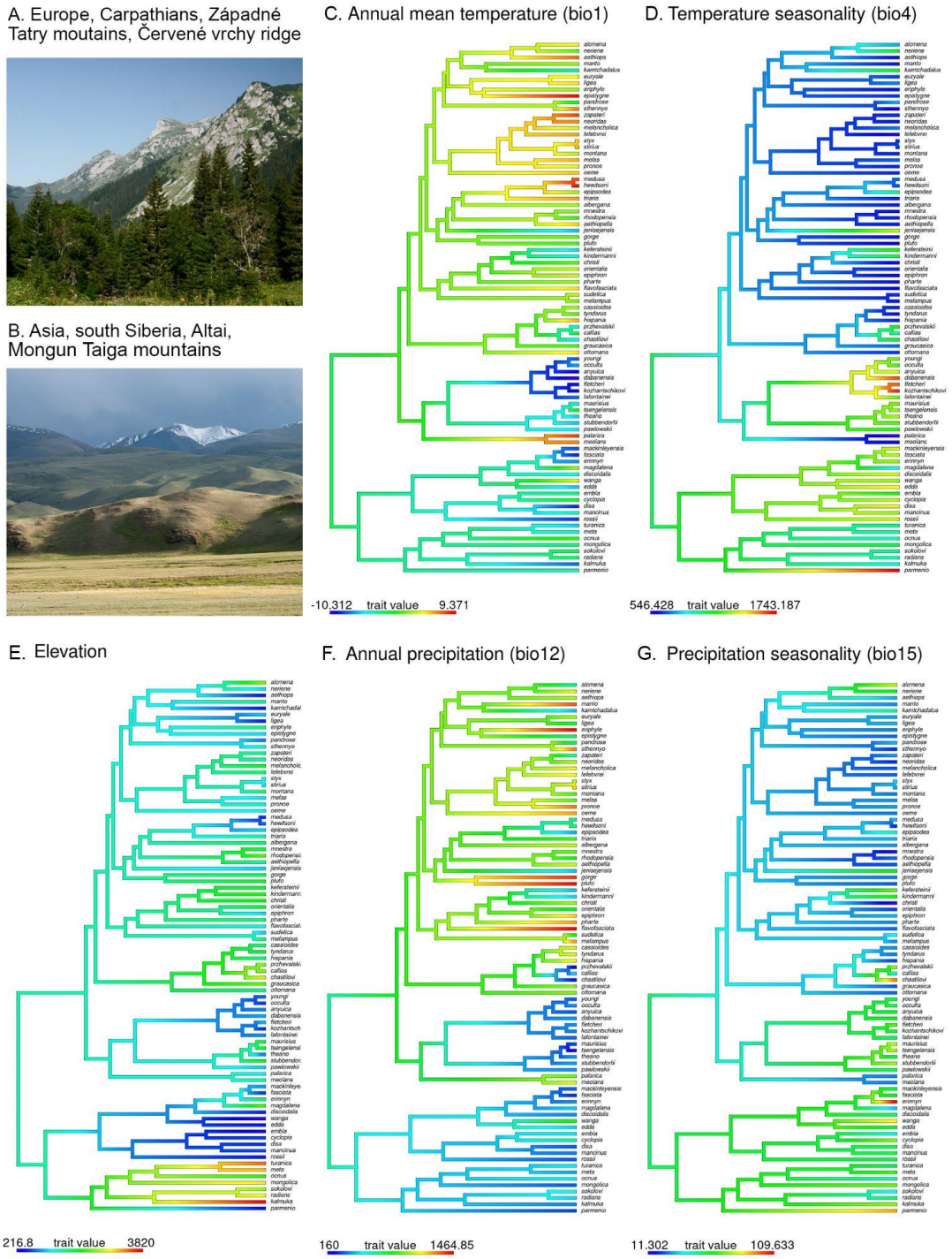

Figure 2. The ancestral niche reconstruction based on OU model of climates and elevations occupied by the butterfly genus *Erebia* based on the distribution of extant species (the bioclimatic variables bio1, bio4, bio12, bio15, and elevation).

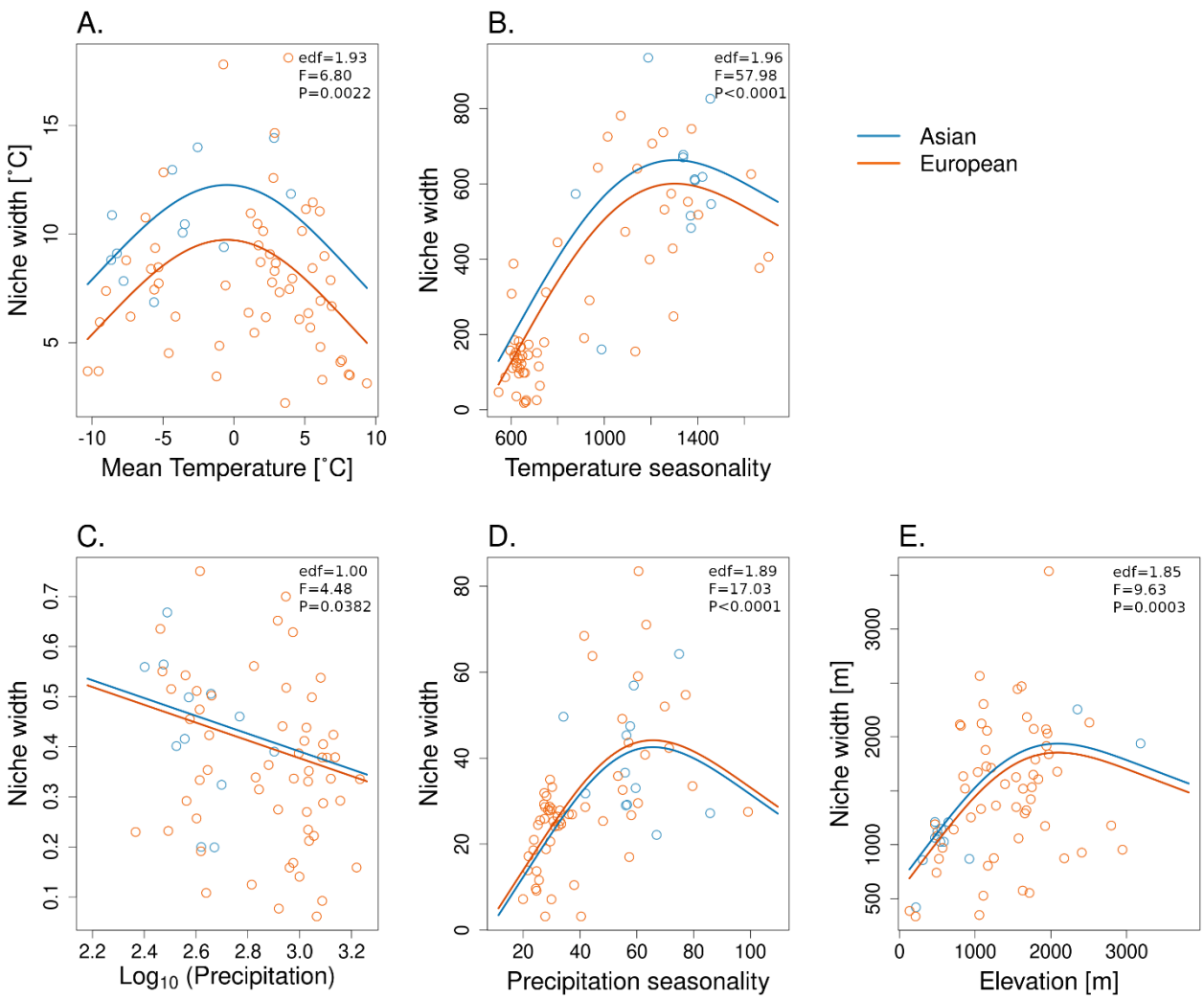

Figure 3. The relationships between climatic and elevational niche width, and niche position of the butterfly genus *Erebia*. The points correspond to the niche width (y-xis) and mean value of a climate variable or elevation for individual species (x-axis). The best fit of generalised additive models (GAM) is shown, in most cases a hump-shaped relationship was statistically significant. edf denotes the estimated degrees of freedom, which indicates the complexity of the non-linear relationship (edf = 1 corresponds to a linear relationship).

Tables

Table 1. Tests of phylogenetic signal in climatic variables and elevation in the butterfly genus *Erebia* for the consensus tree and for 1,000 trees randomly drawn from the posterior distribution (mean value and 95% confidence interval). LogL = log likelihood of the model with the estimated value of the Pagel's λ, LogL0 = log likelihood of a model with Pagel's λ=0. The presence of a significant phylogenetic signal is highlighted in bold.

		Pagel's λ				Bloomberg's K	
Variable	**Code**	**λ**	**LogL**	**LogL0**	**P**	**K**	**P**
Consensus tree							
Annual mean temperature	bio1	0.90	-228.34	-257.73	**<0.001**	0.75	**<0.001**
Temperature seasonality	bio4	1.00	-561.16	-601.84	**<0.001**	1.14	**<0.001**
Annual precipitation	bio12	0.85	-587.35	-608.53	**<0.001**	0.37	**<0.001**
Precipitation seasonality	bio15	0.54	-360.63	-372.80	**<0.001**	0.36	**<0.001**
Elevation	Elev	0.88	-649.13	-671.02	**<0.001**	0.60	**<0.001**
Posterior distribution of trees							
Annual mean temperature	bio1	0.9 [0.83,0.99]			**<0.001**	0.67 [0.26,0.87]	**0.005**
Temperature seasonality	bio4	0.99 [0.94,1.01]			**<0.001**	1.07 [0.56,1.32]	**<0.001**
Annual precipitation	bio12	0.83 [0.73,0.9]			**<0.001**	0.34 [0.02,0.62]	0.211
Precipitation seasonality	bio15	0.56 [0.47,0.66]			**<0.001**	0.31 [0.06,0.48]	0.156
Elevation	Elev	0.87 [0.81,0.95]			**<0.001**	0.53 [0.24,0.68]	**0.011**

Table 2. Overview of the climatic conditions and elevation at sites where species from the Asian clade and the European clades of the butterfly genus *Erebia* were recorded. Values of bioclimatic variables and elevation associated with individual occurrence records of all species, divided into the two clades, are summarised.

		Asian clade		European clade	
Variable	**Code**	**Mean**	**Range**	**Mean**	**Range**
Annual mean temperature	bio1	-6.88	-15.40; 10.31	4.77	-17.72; 15.83
Temperature seasonality	bio4	1375.00	531.79; 2334.81	742.27	327.55; 2334.81
Annual precipitation	bio12	350.13	129; 1545	857.82	99; 3057
Precipitation seasonality	bio15	55.71	6.48; 122.87	35.03	6.40; 120.03
Elevation	Elev	572.41	0; 3988	778.59	0; 5469

Table 3. Comparison of the fit of three models of trait evolution, Brownian Motion (BM), Ornstein-Uhlenbeck (OU), and Early Burst (EB) for the fivebioclimatic variables across the phylogeny of the genus *Erebia*. The rate parameter (σ^2) describes how fast the trait values change through time. θ is mean value of a trait, α describes the strength of attraction toward the mean value in the OU model, and a is the rate change parameter in the EB model. Models with the best fit (ΔAICc < 2) are highlighted in bold.

Variable	Model	σ^2	Θ	α	a	logL	AICc	Δ AICc
bio1	BM	2.20	-1.32	–	–	-232.31	468.77	5.18
	OU	**3.21**	**-0.89**	**0.060**	**–**	**-228.64**	**463.58**	**0.00**
	EB	2.20	-1.32	–	-0.000001	-232.31	470.92	7.34
bio4	**BM**	**6083.2**	**1069.7**	**–**	**–**	**-561.16**	**1126.47**	**0.00**
	OU	**6933.0**	**1060.7**	**0.017**	**–**	**-560.84**	**1127.98**	**1.51**
	EB	6083.3	1069.7	–	-0.000001	-561.16	1128.62	2.15
bio12	BM	21159.8	642.5	–	–	-612.89	1229.93	22.57
	OU	**37149.4**	**735.5**	**0.123**	**–**	**-600.53**	**1207.36**	**0.00**
	EB	21160.3	642.5	–	-0.000001	-612.89	1232.09	24.72
bio15	BM	75.8	53.1	–	–	-379.19	762.53	24.28
	OU	**149.4**	**46.3**	**0.150**	**–**	**-365.97**	**738.25**	**0.00**
	EB	75.8	53.1	–	-0.000001	-379.19	764.68	26.43
Elevation	**BM**	**54548.0**	**1525.5**			**-652.19**	**1308.53**	**1.94**
	OU	**73081.7**	**1547.7**	**0.043**		**-650.14**	**1306.59**	**0.00**
	EB	54549.1	1525.5		-0.000001	-652.19	1310.69	4.09

Table 4. Comparison of climatic and elevation niche width of species from the Asian clade and the European clade of the butterfly genus *Erebia*. Niche width was calculated for the total climatic niche based on PCA of four climate variables, for the four variables separately, and for the elevation. Mean niche width and standard error is shown for the two clades. Annual precipitation was $\log_{10}$-transformed prior to calculation of niche width. Results of generalised linear models (GLM) with Gaussian error distribution testing the difference of the climatic niche width between the European and Asian clades are shown. The number of observations (log-transformed) with climate data for each species was also included in the models to account for the potential confounding effect of the number of records on species' niche width. Significant differences in niche width between the Asian and the European clade are highlighted in bold.

		Asian clade		**European clade**				
Variable	**Code**	**mean**	**SE**	**Mean**	**SE**	**F**	**df**	**P**
Total climatic niche		0.030	0.015	0.014	0.011	2.11	1; 66	0.1515
Annual mean temperature	**bio1**	**10.092**	**1.380**	**7.380**	**1.022**	**6.90**	**1; 66**	**0.0107**
Temperature seasonality	**bio4**	**524.940**	**93.380**	**207.930**	**69.110**	**20.58**	**1; 66**	**<0.0001**
Annual precipitation	bio12	0.303	0.065	0.243	0.048	1.51	1; 66	0.2230
Precipitation seasonality	bio15	39.876	6.942	29.940	5.137	3.66	1; 66	0.0601
Elevation	Elev	1156.563	262.767	1470.416	194.461	2.55	1; 66	0.1152

Table 5 Comparison of mean niche overlap, indicated by Schoeners'D values, between sister species pairs and non-sister species pairs of the butterfly genus *Erebia*. Niche overlap was calculated for the total climatic niche based on the PCA of four climate variables, for each variable separately, and for elevation. Annual precipitation was $\log_{10}$-transformed. Two-tailed Mantel test was used to compare the values of niche overlap between sister and non-sister species pairs. The Schoeners'D values were calculated only for those species with > 5 distribution points; in total the analyses included 68 species.

		Sister species pairs		Non-sister species pairs			
Variable	**Code**	**mean**	**SD**	**Mean**	**SD**	**Mantel r**	**P**
Total climatic niche		0.309	0.232	0.123	0.170	0.089	**0.0001**
Annual mean temperature	bio1	0.465	0.258	0.278	0.249	0.062	**0.0016**
Temperature seasonality	bio4	0.471	0.214	0.194	0.245	0.093	**0.0001**
Annual precipitation	bio12	0.458	0.235	0.226	0.233	0.082	**0.0003**
Precipitation seasonality	bio15	0.428	0.307	0.237	0.239	0.065	**0.0012**
Elevation	Elev	0.470	0.222	0.292	0.237	0.062	**0.0010**