Received: 28 November 2023 | Accepted: 20 August 2024

DOI: 10.1111/syen.12651

ORIGINAL ARTICLE

Systematic Entomology

Royal Entomological Society

Region-specific diversification dynamics and biogeographic history of one of the most diverse families of insects

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Funding information

The Spanish government (MINECO/MICIU/AEI); European Regional Development Fund (FEDER), Grant/Award Numbers: CGL2015-67849-P, PGC2019-XXXX-P; Australian Research Council, Grant/Award Number: DE190100805; Marie Skłodowska-Curie, Grant/Award Number: 642241; Departamento Administrativo de Ciencia, Tecnologa e Innovacin (COLCIENCIAS), Grant/Award Number: 756-2016; Swedish Research Council, Grant/Award Number: 2015-04441; Universidad de Sucre

Abstract

A long-standing question in evolutionary biology is how historical biogeographic processes have shaped the current diversity of organisms, especially for highly diverse groups. We study the diversification dynamics and biogeographic processes of one of the most diverse families of Lepidoptera, Geometridae, with over 24,000 described species and a worldwide distribution. Despite the cosmopolitan distribution of the family, most species of Geometridae have limited distribution ranges. We present the largest historical biogeography and diversification study on the current diversity patterns and distribution ranges of Geometridae. We use a multi-locus dataset of 1200 taxa to estimate the historical biogeography of Geometridae, implementing a Bayesian approach of the Dispersal-Extinction-Cladogenesis (DEC) model that incorporates palaeographic-based dispersal graphs with uncertainty in geological ages in RevBayes. We also implement a Bayesian time-variable, episodic birth–death model and a model that allows branch-specific speciation rates to estimate the diversification dynamics in the family. Our results suggest that the most recent common ancestor of Geometridae was distributed in the New World, with the Neotropics being the most likely ancestral area. An increase in diversification rates occurred circa 30–40 million years ago (Mya), coinciding with a time of a major global climate cooling in the Eocene. Clade-specific shifts in speciation rates also occurred around 10–15 Mya, coincident with another period of major climate change in the Oligocene. Our results point to different biogeographical and evolutionary histories per area to show the differences of the diversification rates in different biogeographical regions through time, showing the relative importance of each region in the diversification history of Geometridae.

KEYWORDS

branch-specific diversification, Geometridae, historical biogeography, Lepidoptera

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INTRODUCTION

Since the inception of natural sciences as a field at the end of the 18th century, the heterogeneity in the spatial distribution of biodiversity on Earth has fascinated scientists (Darwin, 1859; Hooker, 1854; Wallace, 1869, 1876). Many theories exist on the reasons behind these differences in biodiversity among different places. For example, the latitudinal diversity gradient (LDG) describes a general pattern in which the number of species of organisms increases from the poles to the equator. In this model, tropical regions are the most species-rich (Brown, 2014; Buzas et al., 2002; Fischer, 1960; Kinlock et al., 2017). The LDG has been partly explained by contemporary differences in environmental factors, such as temperature and precipitation, favouring higher productivity in these regions. However, there is growing consensus that historical processes such as the climatic and geological history of a landmass, driving lineage speciation and extinction rates, played a prominent role in shaping biodiversity patterns (Antonelli et al., 2009; Buerki et al., 2011; Condamine, Rolland, & Morlon, 2013; Linder, 2001).

The difference in diversity is not limited to different regions and habitats. Extant diversity also differs greatly among different groups of organisms. In insects, for example, Strepsiptera currently includes very few representatives (about 600 species), whereas their sister group (Coleoptera) exhibits species numbers that are orders of magnitude higher (more than 300,000 described species). Besides, present-day diversity is only a snapshot of the course of evolution. The vast majority of species have gone extinct, and numerous branches in the Tree of Life have not left any extant descendant, well known examples being the ammonites and trilobites (Payne & Clapham, 2012). Understanding the origin of present-day extant diversity is a challenging task, but reconstructing the extinct and unobserved diversity is even more complex (Meseguer et al., 2015; Purvis, 2008; Sanmartín & Meseguer, 2016). Initially, fossils and their associated stratigraphic ages were used for exploring hidden patterns of diversity in the past and the role of extinction in shaping these patterns (Simpson, 1944; Stanley, 1980). In recent decades, statistical methods have emerged that make use of molecular rates and phylogenetic information to elucidate the dynamics of diversification within a group of organisms (Hey, 1992; Morlon, Parsons, & Plotkin, 2011; Nee et al., 1992; Nee, Holmes, et al., 1994; Nee, May, & Harvey, 1994; Sanmartín & Meseguer, 2016). These methods require information about the times of divergence of extant lineages, often calibrated with fossil information or rates of molecular evolution from related groups. The power of such methods to estimate past diversification rates has been recently advanced by the development of more realistic models, permitting rates of diversification to change over time and across lineages, and the addition of Bayesian approaches to account for error in parameter estimation (Höhna et al., 2011; May et al., 2016; Morlon, Schwilk, et al., 2011; Sanmartín & Meseguer, 2016; Stadler, 2013). Fossils remain important to provide temporal calibration points or to inform on the magnitude or even direction of change, and it has been demonstrated that their inclusion can dramatically alter conclusions on the evolutionary history of a group, especially in deep time (Mao et al., 2012; Meseguer et al., 2015, 2018). However, the majority of organisms have highly incomplete fossil records, or even none, often due to poor fossilization rates.

One such group that lacks a reliable fossil record but still exhibits remarkable levels of diversity is the Geometridae moths. With nearly 24,000 described species (Rajaei et al., 2022; van Nieukerken et al., 2011), the family represents one of the major radiations within Lepidoptera, and insects in general. Yet fossil information is extremely scarce: thus far, only one fossil has been unambiguously assigned to the family (Fischer et al., 2019). Recently, Geometridae has been the focus of a series of phylogenetic studies, thanks to the publication of new extensive molecular datasets (Brehm et al., 2019; Murillo-Ramos et al., 2019, 2021; Sihvonen et al., 2020). The increase in taxon sampling, especially for higher level lineages, and the generation of well-supported multi-locus phylogenetic hypotheses, enables the investigation of diversification dynamics in the group.

Geometrid moths have a worldwide distribution and exhibit decreasing diversity levels from tropical to temperate areas (Beck et al., 2017). Western Palearctic species are by far the best studied, due to the work of many entomologists who have been observing and describing species since the 18th century. Currently, relatively few new species are being described from this region compared with tropical regions such as southeast Asia (Holloway, 1993, 1996, 1997), Africa (Tujuba et al., 2020) and the Neotropics (Brehm, 2018).

Despite the family's cosmopolitan distribution on all continents except Antarctica, most species of Geometridae are endemic to a single continent or biogeographic region, and many appear to be limited to small regions and/or narrow elevational bands, for example, in tropical mountains. The age of origin of the family has been dated to the Cretaceous in previous studies focusing on Lepidoptera (Kawahara et al., 2019; Wahlberg et al., 2013). This relatively ancient age and the endemic distribution patterns of extant species makes this group especially attractive for studying the historical processes that drive patterns of diversity over space and time. To date, there is no biogeographic study on the origin of geometrid moths, when and how they reached their current cosmopolitan distribution and excess levels of diversity. The large majority of works in Lepidoptera have focused on the butterfly families Nymphalidae (Aduse-Poku et al., 2009, 2015; Kodandaramaiah et al., 2018; Kodandaramaiah & Wahlberg, 2007, 2009; Matos-Maraví et al., 2013, 2014; Müller et al., 2010; Toussaint et al., 2020; Toussaint & Balke, 2016; Toussaint, Turlin, & Balke, 2019; Wahlberg & Freitas, 2007), Papilionidae (Condamine, Sperling, & Kergoat, 2013), Pieridae (Müller et al., 2013), Lycaenidae (Vila et al., 2011) and Hesperiidae (Toussaint, Vila, et al., 2019). A few studies have analysed the biogeography of other lepidopteran families (e.g. Rota et al., 2016), including one study on the geometrid tribe Boarmiini (Murillo-Ramos et al., 2021). Also, few works have studied patterns of speciation and extinction using statistical methods in butterflies (Chazot et al., 2019; Chazot et al., 2020; Condamine et al., 2012; Condamine, Rolland, et al., 2018; Toussaint & Balke, 2016). Many of these works highlight the major role played by global climate changes and past geography in the evolution of the extant diversity of Lepidoptera.

In this study, we used a published multi-locus phylogeny of Geometridae as a phylogenetic framework for inferring biogeographic and diversification patterns in the family. Specifically, we employed Bayesian statistical approaches to molecular dating, biogeographic reconstruction and diversification analyses to infer lineage divergence times, ancestral geographic ranges, changes in rates of migration, extirpation (local extinction) and lineage speciation and extinction over time. Our aim was to identify key time periods, with major climatic or geological changes, as well as biogeographic regions (landmasses), that played a significant role in the origin and evolution of the extant diversity of Geometridae.

MATERIALS AND METHODS

Taxon sampling and phylogeny

Our study is based on the most recent and comprehensive molecular dataset of the family Geometridae (Murillo-Ramos et al., 2019). This dataset includes 93 tribes and 1192 species, from a total of nearly 24,000 described species in the family, making it probably the best sampled dataset sequenced for 10 nuclear (*ArgK*, *Ca-ATPase*, *CAD*, *EF-1alpha*, *GAPDH*, *IDH*, *MDH*, *Nex9*, *RpS5* and *wingless*) and 1 mitochondrial marker (*COI*). The total length of the alignment was 7665 base pairs (bp). The details of phylogeny reconstruction can be found in the original study, but briefly, the phylogenetic reconstruction was obtained using a maximum likelihood approach, using the concatenated and partitioned alignments of all 11 genetic markers. It should be mentioned that some relationships were not well supported in the used phylogeny for example, the position of Sterrhinae. Nevertheless, in general, most nodes in this phylogeny received high support and thus constitute a robust phylogenetic framework to explore biogeographic and diversification patterns. The original phylogeny was rooted using taxa from the families Uraniidae, Pseudobistonidae, Epicopeiidae and Sematuridae, which are the closest relatives of Geometridae (Regier et al., 2009, 2013). Outgroup taxa were removed from this dataset before running the timing of divergence analyses to avoid incomplete taxon sampling biases, as outgroups were represented by only a few species. The trees were visualized using the R statistical framework (R Core Team, 2017) with package *ape* v. 5.2 (Paradis & Schliep, 2019).

Time calibration

To generate a time-calibrated phylogenetic tree, we used a relaxed log normal molecular clock model implemented in the Bayesian software BEAST2 (Bouckaert et al., 2014). The molecular dataset above was partitioned by gene, with independent molecular substitution models (Table 1) inferred by ModelFinder (Kalyaanamoorthy et al., 2017) implemented in the maximum likelihood inference software IQ-TREE 1.6.5 (Nguyen et al., 2015). Initial test runs failed to converge, probably due to the size and complexity of the dataset. To make the analysis computationally possible, we enforced the tree topology obtained by (Murillo-Ramos et al., 2019) by modifying the xml file manually and disabling operators for MCMC tree moves. A birth–death tree prior with incomplete sampling (Stadler, 2013) and a lognormal relaxed clock model (Drummond et al., 2006) were used. The clock and tree priors were linked across all partitions. Four calibration points based on secondary age estimates (Wahlberg et al., 2013), and a single node based on fossil (Fischer et al., 2019), were used to infer absolute divergence times. The following nodes were used in calibration: the most recent common ancestor (MRCA) of Geometridae; the MRCA of *Larentia* Treitschke and *Trichopteryx* Hübner; the MRCA of *Archiearis* Hübner and *Alsophila* Hübner; the MRCA of *Biston* Leach and *Alsophila*; and the MRCA of Ennominae. These nodes were chosen to represent the basal divergences of the crown clade of Geometridae (Murillo-Ramos et al., 2019; Murillo-

TABLE 1 Gene partitions and the substitution model as inferred by ModelFinder.

Partition	Markers	Length (bp)	Infor	Invar	Model
1	*ArgK*	388	192	152	GTR + F + I + G4
2	*Ca-ATPase*	444	176	221	SYM + I + G4
3	*CAD*	865	482	318	GTR + F + I + G4
4	*COI*	1476	802	502	GTR + F + I + G4
5	*EF1a*	1240	516	577	SYM + I + G4
6	*GAPDH*	691	324	290	SYM + I + G4
7	*IDH*	722	363	294	GTR + F + I + G4
8	*MDH*	407	209	161	SYM + I + G4
9	*Nex9*	420	241	138	GTR + F + I + G4
10	*RpS5*	603	259	265	SYM + I + G4
11	*wingless*	409	269	98	SYM + I + G4
Total		7665	3833	3016	

Abbreviations: Infor, number of parsimony-informative sites; Invar, number of invariant sites.

TABLE 2 Calibration points used to date the phylogeny of geometrid moths. The unit of age is in millions of years.

Dated nodes	Age (mean)	95% CI	Prior distribution	Prior sigma	Offset
Crown	71	61–82	Normal	6.6	0.3
Larentia and *Trichopteryx* ancestor	33	21–46	Normal	7.85	0.3
Archiearis and *Alsophila* ancestor	61	49–72	Normal	7	-
Biston and *Alsophila* ancestor	41	31–51	Normal	6.35	0.1
Ennominae crown	44–83	-	Uniform	-	-

Abbreviation: CI, confidence interval.

Ramos et al., 2023; Wahlberg et al., 2013). Normal distribution priors were used, with the mean and standard deviation spanning the 95% high-posterior-density (HPD) credibility intervals estimated by Wahlberg et al. (2013); see Table 2 for details on the value of parameters for these priors. A first analysis of one MCMC chain for over 1×10^8 generations was performed as burn-in to reach the stationary phase. Seven independent chains (with different seed numbers) were then run for 2×10^7 generations using the result of the first run as a starting point to sample all the parameters within the stationary phase. Three independent parallel analyses were run (with different seed numbers) and checked for convergence with the other runs to avoid the possibility of sampling in a local optimum. Each run was checked for adequate convergence and mixing using TRACER 1.6 (Rambaut et al., 2018), first independently and then together. All parameter ESS values scored higher than 200. Each of the 7 parallel runs yielded 2000 tree samples resulting in 14,000 trees. The software LogCombiner and TreeAnnotator (both available in the BEAST2 package) were used to merge the tree files from the independent runs and generate a maximum clade credibility (MCC) tree, representing the mean and 95% HPD interval for all nodal ages. The MCC tree is provided in the Supporting Information.

Diversification analyses

To study major changes or shifts in extinction and speciation rates over time that affected all lineages in the family simultaneously, we used time-variable, episodic birth–death (EBD) models implemented in the software RevBayes (Höhna et al., 2016). The EBD model is a Bayesian approach to the maximum likelihood discrete, episodic birth–death model implemented in TreePar (Stadler, 2011a, 2011b). In this model, time is divided into discrete time bins. The rates of speciation and extinction remain constant within each time slice but can vary between time slices according to a CPP (Condamine, Nabholz, et al., 2018). In our analysis, we evaluated three different values for the width of time bins: 2, 5 and 10 million-year (My) intervals. To account for incomplete taxon sampling in our phylogeny, we assumed that our taxon sampling was random and introduced a global sampling fraction parameter (ρ), which was set to a fixed value of 0.05. This was estimated as the number of tips in the phylogeny (1192) divided by the total number of described species in Geometridae (van Nieukerken et al., 2011), which is a conservative approach for the total number of species. Priors for speciation and extinction rates were modelled as lognormal distributions with the mean centred in the extant diversity (ln [N° extant species/2.0/Root age]) and the standard deviation set to place 95% uncertainty of one order of magnitude around the mean. The analysis was run for 6×10^4 generations, and the first 10^4 generations were discarded as the burn-in. The results were then visualized in R using the package RevGadget (Tribble et al., 2021).

To infer shifts in rates of diversification over time that affect only a given clade in the phylogeny, we used a branch-specific diversification (BSD) model implemented in RevBayes (Höhna et al., 2019). The model is a discretized approximation to the continuous-time clade-diversification approach implemented in BAMM (Rabosky, 2014). As in BAMM, a stick break-point process, Compound Poisson Process (CPP) is used to detect points in time where there is a significant change in diversification rates and to discriminate between different diversification regimes/scenarios; the model can account for incomplete taxon sampling. However, unlike BAMM, the BSD model properly accounts for the possibility of changes or shifts in speciation rates in unobserved, extinct lineages by using Maddison et al. (2007) numerical integration approximation accounting for all possible event change types in discrete, infinitesimal time bins (Höhna et al., 2019). Failing to do so has been shown to bias posterior estimates for shifts in diversification rates in BAMM (Meyer et al., 2018; Meyer & Wiens, 2018). As in BAMM, extinction rates are modelled as constant in BSD and only the magnitude and direction of shifts in speciation rates are inferred; accounting for both shifts in extinction and speciation rates can introduce unidentifiability of parameters and diversification regimes (Höhna et al., 2019). The rho parameter and all other priors were set as in the EBD analysis. We ran the analysis for 2×10^4 generations. Scripts to run these analyses are provided in the Supporting Information.

Biogeography

Biogeographic evolution was inferred using the Dispersal-Extinction-Cladogenesis (DEC) model (Ree et al., 2005; Ree & Smith, 2008) implemented in a Bayesian framework in RevBayes (Landis et al., 2018). An epoch, time-stratified DEC analysis was performed following the settings in the website tutorial (https://revbayes.github.io/tutorials/biogeo/biogeo_epoch.html). Following (Ree & Sanmartín, 2018), cladogenetic events were limited to narrow sympatry, peripheral-isolate speciation (subset sympatry) and vicariance (allopatry). We used seven

TABLE 3 Biogeographical areas (A) and time slices (B) used in the biogeography analysis.

A		B	
Areas	Code	Number	Timeframe
Neotropic	N	1	0–10 Mya
Afrotropic	F	2	10–30 Mya
Nearctic	A	3	30–40 Mya
Palearctic	P	4	40–50 Mya
Oriental	O	5	>50 Mya
Australia	S		
New Zealand	Z		
Antarctica	T		

Abbreviation: Mya, million years ago.

biogeographic regions as units for the analysis, corresponding to cratons or persistent landmasses since the Late Mesozoic and which harbour extant endemic species: the Afrotropics, Australia, Nearctic, Neotropics, New Zealand, Oriental and Palearctic. An eighth area, Antarctica, was included in the analysis, even if currently no geometrid species occur there because it potentially played an important role as a land bridge for dispersal in the southern continents over the Late Mesozoic and Cenozoic. The sampling effort in different regions were not homogenous. Nearctic, Palearctic and probably Neotropical regions have been better sampled than the other regions. On the other hand, the Oriental region is probably the region which is the most undersampled in our dataset. Nevertheless, the actual dataset is the most complete available for such studies. The rate of biogeographic change was modelled as a uniform distribution between 10E-4 and 10E-1/My^{-1}. The rate of extirpation was modelled as a log-uniform distribution with an expectation of one event per million year. The phylogeny was sliced into five consecutive time intervals or bins; each was assigned a different dispersal rate matrix, where the baseline migration rate (1.0) was multiplied by a relative ‘scaler’ value according to paleogeographical connectivity through time (Table 3). To define paleogeographical connectivity between our biogeographic units (cratonic landmasses), we used the EarthViewer application (www.hhmi.org/biointeractive/earthviewer), which is based on the Paleomap Project by Christopher R. Scotese (http://www.scotese.com). The connectivity was defined as five different subjective categories, 1, 0.9, 0.6, 0.3 and 0.01, where 1 was used when two land bodies are continuous without any water body separating them and 0.01 in cases where they are completely separated. We employed our own R script to extract and plot marginal probabilities for each geographic state as a pie chart on the nodes of the MCC tree. See Supporting Information for more details on area definition, dispersal rate scalers for the epoch model and the script used in the analysis.

To summarize the frequency of dispersal events between pairs of areas or regions over the reconstructed history of Geometridae, we used the R package qgraph (Epskamp et al., 2012). We made several assumptions to estimate the number of dispersal events. The source and sink regions for dispersal events were identified by comparing the most probable ranges at the upper and lower node of a branch. If at least one area was gained along the branch, we assumed at least one dispersal event took place. In cases where two or more areas could have been the source of the dispersal event, we used the time-stratified dispersal matrices implemented in the epoch model to choose the most probable source area. If two or more potential source areas had the same probability, we randomly picked one. Finally, a timing for the dispersal event was then randomly sampled along the branch. This procedure was repeated 1000 times and the sum of events between regions was calculated at each repetition and finally averaged.

Biogeography and diversification

To assess differences among biogeographic regions in lineage accumulation over time, we performed two different analyses. First, we estimated the relative frequency of lineages occupying a given region through time. To do so, we estimated the frequency of dispersal events and their timing, using a similar approach to the analysis above for counting the total number of events between regions. We then divided time into 1 My time bins, and for each time bin, we calculated the relative frequency of lineages in each region during that time period.

Second, we estimated the average rate of diversification in each region through time by combining the biogeographic ancestral state estimate and the BSD analysis, using a similar approach to (Chazot et al., 2020). From the DEC biogeographic analysis, we identified the dispersal events along each branch and randomly sampled its timing, following a similar procedure to the analysis above for counting the total number of dispersal events between regions. In addition, for each branch, we recovered the net diversification rate estimated by the BSD analysis. Hence, for each branch, we obtained the most probable biogeographic state (geographic range) and the net diversification rate. Finally, we divided time (the phylogenetic time scale) into 1 My time bins, and for each time, bin we calculated the mean diversification rate for all branches inferred as occupying a given a biogeographic state during that time interval. We repeated this procedure 1000 times. This allowed us to estimate the mean diversification rate per biogeographical area over time. To perform this analysis, we used dendextend (Galili, 2015), phyloch (Heibl, 2008), phylotate (Beer & Beer, 2019) and TreePar (Stadler, 2015) R packages and a custom script modified from the approach described in (Chazot et al., 2020).

RESULTS

Time calibration

Based on our calibration, first split within the extant radiation of Geometridae (i.e., the crown age of the family) occurred at 67.2 million years ago (Mya) (61.1–73.9), separating the subfamily Sterrhinae from the rest of the family. The other subfamilies diverged during the Early Cenozoic, with ages ranging between 6 and 50 My (Figure 1). The

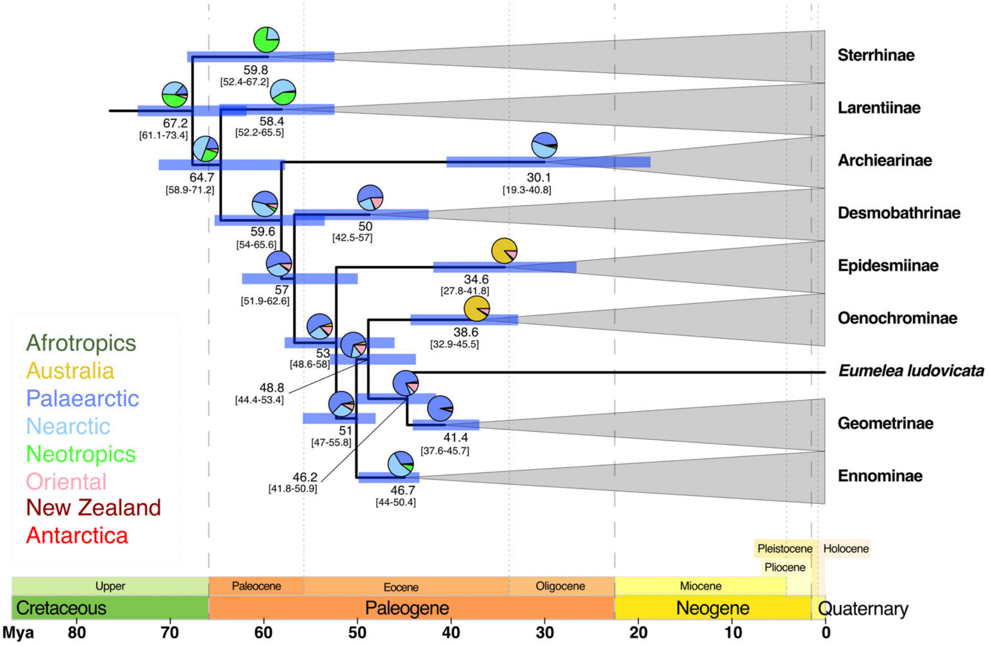

FIGURE 1 Times of divergence of the major lineages (subfamilies) within Geometridae and their inferred distributions. The age of each node is shown in million years with its 95% credibility interval. Pie charts show the sum of the marginal probability of each inferred biogeographical state.

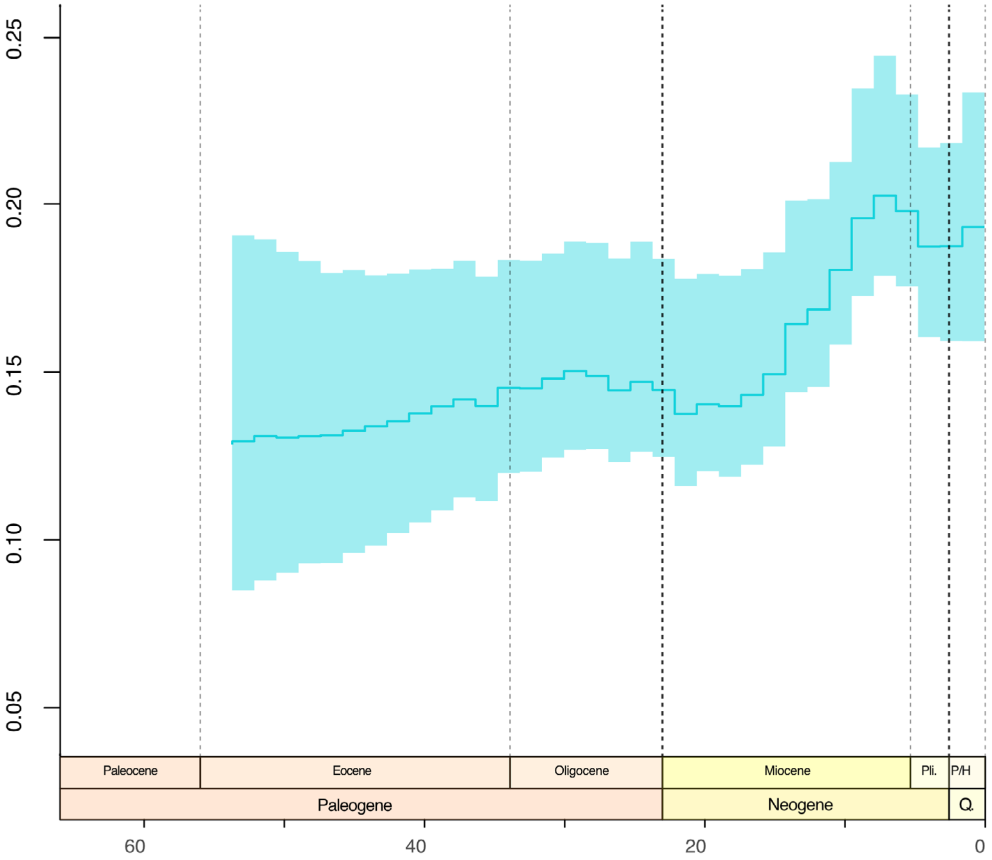

FIGURE 2 Net diversification rate over time in Geometridae inferred with the episodic birth death (EBD) model in RevBayes, showing the upward rate shifts at 30 and 8 million years ago (Mya). The hard blue line represents the mean value, and the blue coloured contour the 95% confidence intervals. The scale on the *x* axis is on Mya and that of the *y* axis indicates the net diversification rate. P/H, Pleistocene/Holocene; Pli, Pliocene; Q, Quaternary.

start of lineage diversification within each subfamily was also diverse, with Sterrhinae being the oldest (60 Mya) and Archiearinae the youngest (30 Mya, Figure 1).

Diversification

The EBD analysis (Figure 2) supports an overall increase in the net diversification rate over time in Geometridae. However, we can identify two periods of gradual increase in the diversification rate during the Eocene and the Miocene. Between these two periods of time, during the Oligocene, we infer a slightly decreasing diversification rate.

The BSD analysis (Figure 3) reveals a homogeneous net diversification rate for a major part of the tree, with independent increases in the rate of diversification for several clades within subfamilies. In Larentiinae, a nearly threefold increase in diversification rates is estimated at 35 Mya in the clade comprising Scotopterygini, the Euphyiini-Xanthorrhoini complex and the Larentiini complex (Brehm et al., 2019) (Figure 3a). Two further shifts towards higher diversification rates have been detected around 15 and 10 Mya at the root of Triphosini and a subclade within the genus *Eupithecia* Curtis (Figure 3b,c). In the subfamily Geometrinae, the tribe Geometrini also presents a pronounced increase in diversification rates dated circa 15 Mya (Figure 3d).

The subfamily Ennominae harbours more than half of the total known diversity of Geometridae. Increases in net diversification rates are detected in two independent lineages around 35 Mya: one clade comprises mainly the tribe Ennomini, and the other one is located within the tribe Boarmiini (Figure 3e,f). A more recent upward shift in diversification rates is found within this subfamily, at 15 Mya, affecting species within genus *Cleora* Curtis (Figure 3, shown in red in clade F). The diversification dynamics of the tribe Boarmiini have been investigated in more details by Murillo-Ramos et al. (2021).

Biogeography

Our results suggest that the MRCA of Geometridae (Figure 1) was distributed on the American continents, most probably in the Neotropics (marginal posterior probability, $pp = 0.43$). The MRCA of the subfamily Sterrhinae (59.8 Mya) shares the same Neotropical ancestral distribution ($pp = 0.74$). The ancestor of Larentiinae and the other

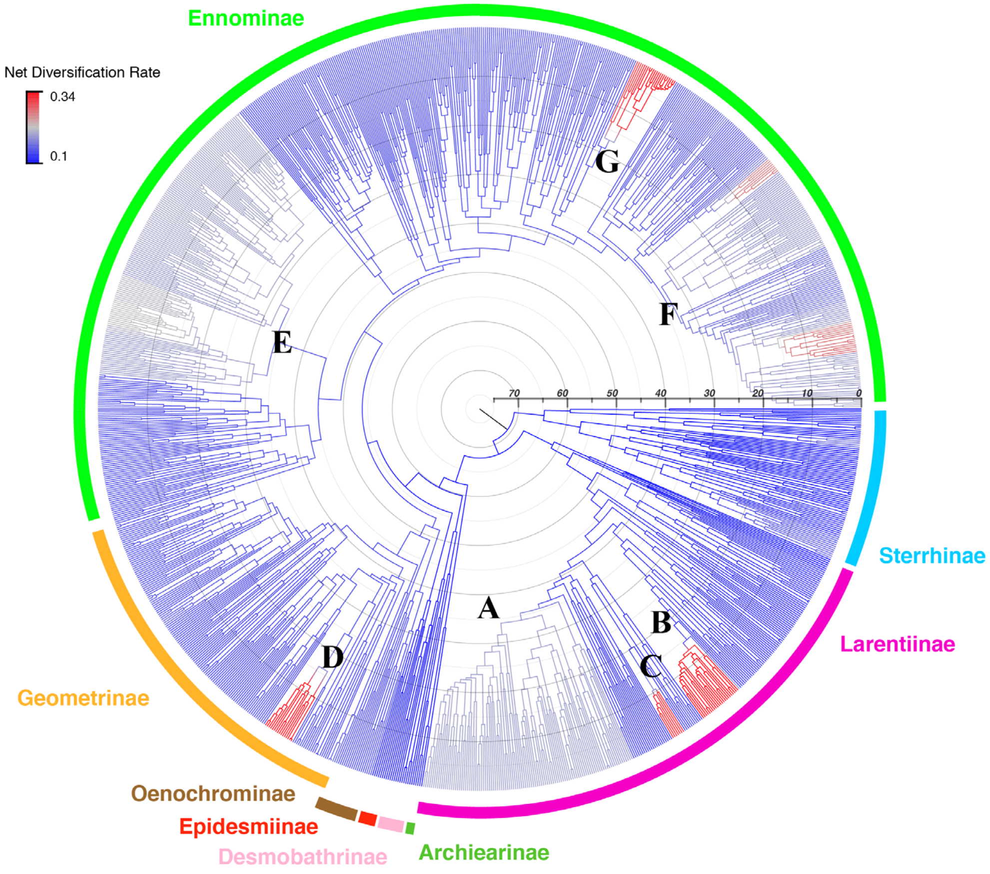

FIGURE 3 Diversification rate variation across Geometridae subfamilies identified with the branch-specific diversification (BSD) analysis in RevBayes. The numbers on the time scale are in million years before present. The letters A–G represent lineages discussed in the text.

subfamilies (64.7 Mya) is reconstructed as Nearctic (*pp* = 0.51), although the Neotropics is the second most probable option. The MRCA of Larentiinae (58.4 Mya) is inferred to have originated in the Nearctic region (*pp* = 0.55). The MRCA of the remaining subfamilies (59.6 Mya) was probably distributed in the Holarctic, with the Palearctic and Nearctic regions receiving similar marginal posterior probabilities (*pp* = 0.4 or 0.37, Figure 1). The MRCA of Archiearinae (30.1 Mya) is inferred to be distributed in the Nearctic (*pp* = 0.51) or the Palearctic region (*pp* = 0.37). The subfamily Desmobathrinae likely originated in the Palearctic region (*pp* = 0.52), with the Nearctic and Oriental regions as alternative ancestral ranges. The MRCAs of Epidesmiinae and Oenochrominae are inferred to be distributed in the Australian region with high probability (*pp* = 0.86 and *pp* = 0.88, respectively); their extant distribution is inferred to have resulted from independent dispersal events from the Palearctic region (possibly via the Oriental region; see discussion below). Finally, the MRCAs of subfamilies Geometrinae and Ennominae are inferred to be Palearctic (*pp* = 0.75) and Nearctic (*pp* = 0.51), respectively.

Estimates of the frequency of dispersal events between pairs of regions (Figure 4) show that the large majority of dispersal events occurred between geographically adjacent regions, as expected from the model (277 adjacent dispersal events, Figure 4; Supporting Information). Long distance dispersal events between regions that were not connected by landmass are present (Figure 4) but are less common (46 long distance events, Supporting Information). Another observation is the dominance of dispersal events between the Palearctic, Nearctic, Neotropical and Afrotropical regions, and the relative isolation of the Australian and Oriental regions. In particular, the Palearctic region appears as the source area with the highest number of dispersal events, mostly towards the Afrotropical and Oriental regions (Figure 4). A high rate of dispersal towards the Nearctic is also inferred; however, dispersal in the opposite direction, from the Nearctic to the Palearctic, appears more frequent in our estimation. The Nearctic, indeed, is inferred as the second most important hub of dispersal events, mainly towards the Palearctic and Neotropical regions (Figure 4). New Zealand is reconstructed as the sink of some dispersal events, with no 'outwards' dispersal (Figure 1).

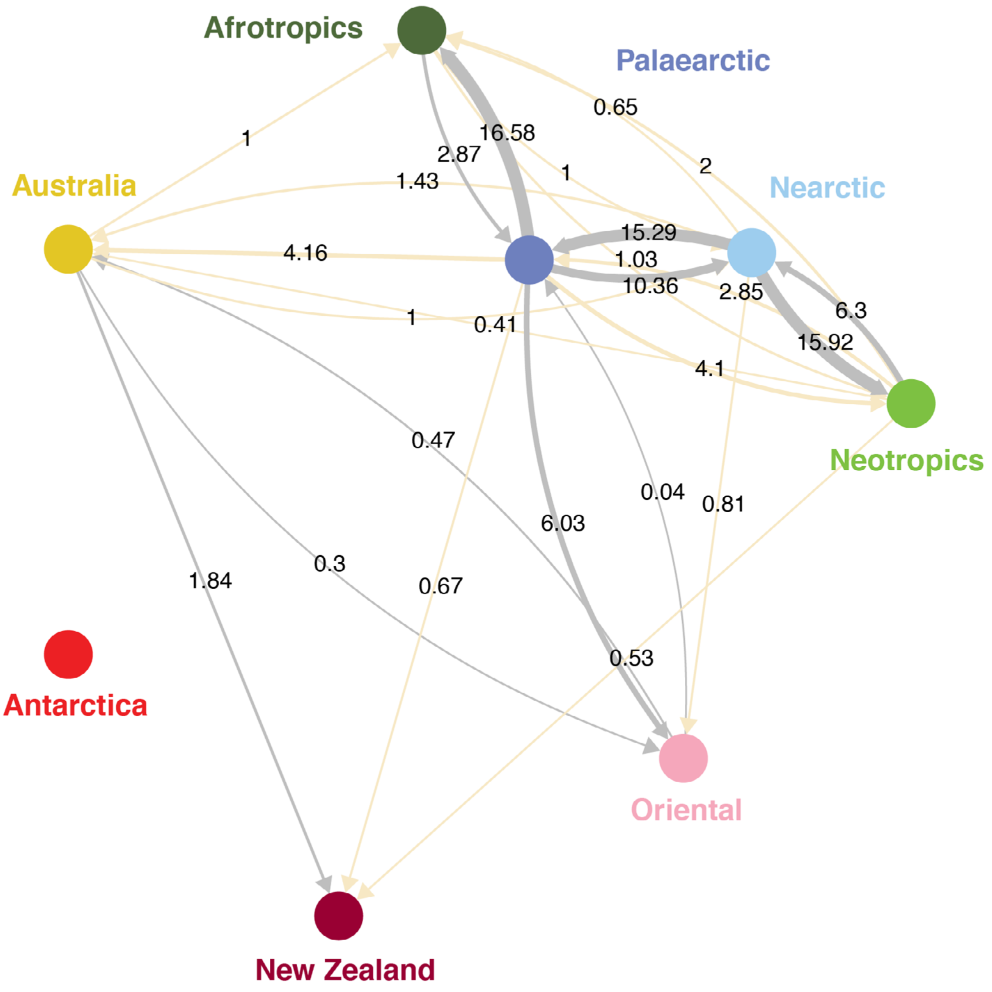

FIGURE 4 Number of dispersal events between the different biogeographical areas without considering the last 20 My. Adjacent dispersals between landmasses or continents that showed paleogeographical connectivity are shown with grey arrows and long-distance dispersals with yellow arrows.

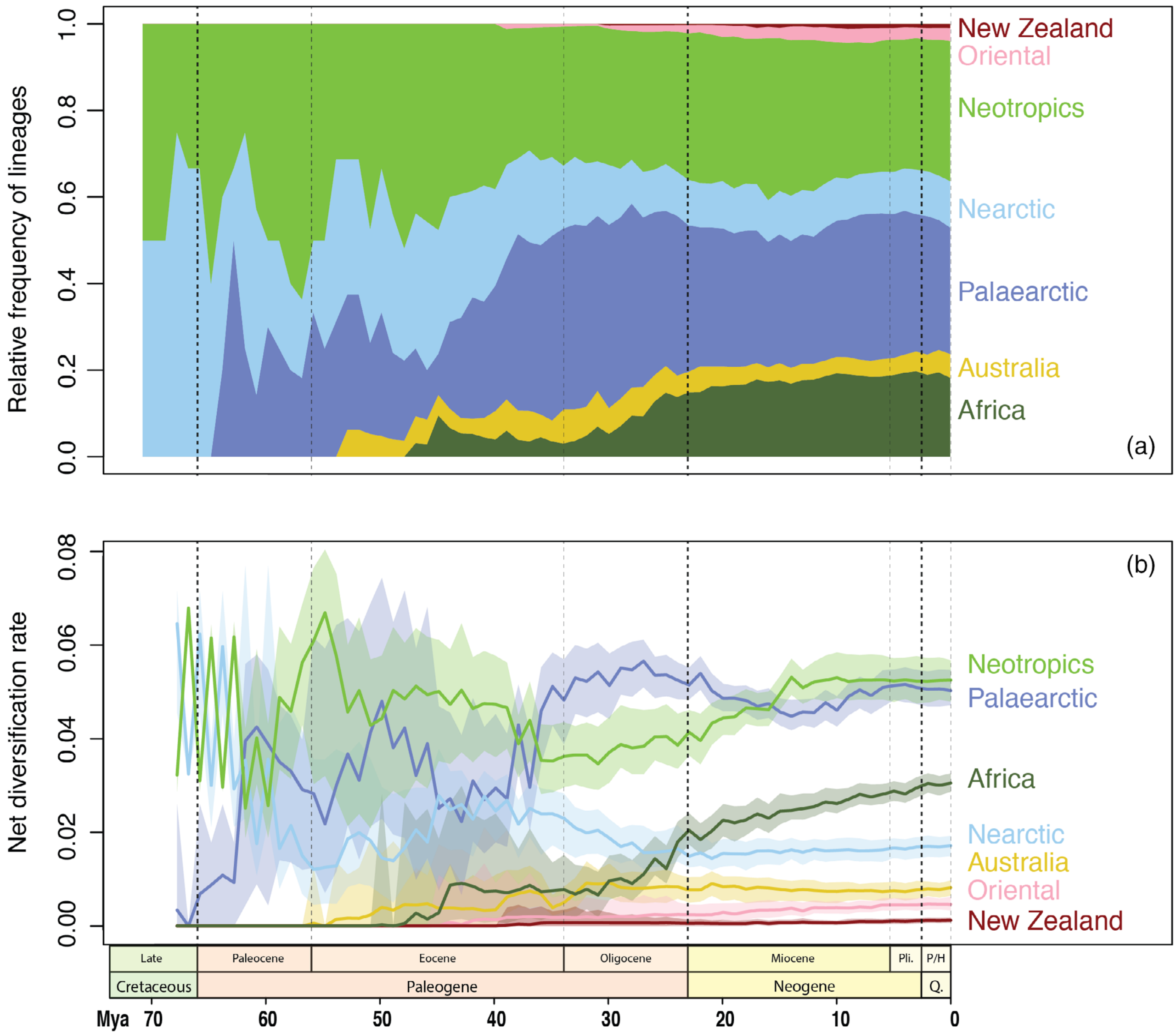

FIGURE 5 (a) Relative frequency of lineages in each biogeographic region through time. (b) Net diversification rate variation through time per biogeographic region. Shaded polygons are the distributions of 1000 mean net diversification rates in each biogeographic region. The bold line is the mean of that distribution. P/H, Pleistocene/Holocene; Pli, Pliocene; Q, Quaternary.

Figure 5 shows estimates of the relative frequency of lineages occurring in each biogeographic region through time (Figure 5a), and the variation in the net diversification rate per region over time (Figure 5b). Both estimates show a similar pattern, in accordance with the ancestral range estimation (Figure 1). The Neotropic and Nearctic regions show the highest frequency and net diversification rate closer to the root of the tree, being gradually replaced by the Palearctic region, once this landmass was colonized during the Early Palaeocene. Net diversification was highest in the Neotropics during the Eocene and the Miocene. At the end of the Eocene, however, the Palearctic region started becoming the main cradle of diversification, and during the Oligocene became the fastest diversifying region combined with a rise in the relative frequency of lineages (Figure 5a,b). At the end of the Oligocene, diversification rate decreased again in the Palearctic. Diversification in Africa, the Oriental region and Australia only started during the middle Eocene. While the net diversification rate in Africa increased over time, especially during the Miocene, the other two regions exhibit a low and nearly flat pattern of diversification (Figures 1 and 5a,b).

DISCUSSION

Our results are contingent on the phylogenetic hypothesis that we used, which is the most comprehensive hypothesis available at the moment (Murillo-Ramos et al., 2019). Despite the uncertainties associated with the relationships of a few groups (see e.g. Murillo-Ramos et al., 2023), we feel the tree is robust enough to investigate patterns of diversification in this megadiverse family over its evolutionary history.

Given our calibration of the age of the crown group of Geometridae in the Maastrichtian (Late Cretaceous), we find that early divergence of subfamily lineages (Figure 1) took place during the Palaeocene and Eocene, much like in the butterflies (Espeland et al., 2018; Heikkilä et al., 2012). Many family lineages in Lepidoptera are inferred to have diverged from each other mainly before the KT event, while diversification within families happened during the Cenozoic (Wahlberg et al., 2013). The age estimate obtained for the root of the family is very close to the root age obtained in Kawahara et al. (2019), in which seven species represent Geometridae and the crown age for the family is recovered to be slightly older than 65 Mya. Although some lineages of Lepidoptera are known to feed on detritus, algae, ferns and non-plant-based food sources, it is likely that the diversification of the major Lepidoptera lineages is connected to the diversification of their major host plants, the angiosperms (Davis et al., 2005; Wahlberg et al., 2013).

Our EBD diversification rate analyses inferred two periods of increase in net diversification—the Eocene and from the mid-Miocene onwards—while diversification slowed down during a period spanning the end of the Eocene and the Oligocene until the mid-Miocene (Figure 2). We identified seven clade-specific changes in diversification rate that may explain these global variations within different subfamilies of Geometridae and dated around 40–30 Mya (three lineages) and between 10 and 15 Mya (four lineages; Figure 3). Nevertheless, we also identified major differences in rate variation through time between biogeographic regions.

The Neotropics exhibit the highest diversification rate among regions during the Eocene and from the mid-Miocene onwards, with a period of slower diversification in between, a pattern that closely resembles variations identified globally from our EBD analyses. The Oligocene, however, was dominated by an increased diversification rate in Palearctic. Thus, we found the Eocene–Oligocene transition period to be associated with both decreasing Neotropical diversification rate and increasing Palearctic diversification rate. The relative diversification rate between the Neotropics and the Palearctics inverted again around the mid-Miocene. This pattern matches remarkably in both space and time with the results obtained by Chazot et al. (2020) for Nymphalidae butterflies. Geographically, the mid-Miocene increase in diversification rate appeared to be mainly explained by increasing diversification in both the Neotropics and Afrotropics, all other regions showing little to no variation through time. As in Chazot et al. (2020), we suggest that these major modifications in the dynamics of diversification resulted primarily from climatic events that happened globally but affected regions and groups in a different way.

The global cooling event at the end of the Eocene, known as the Terminal Eocene Event (TEE) (Meseguer et al., 2015; Sanmartín et al., 2001; Tiffney, 1985) or the Late Eocene-Early Oligocene cooling event (Crisp & Cook, 2007; Zachos et al., 2008), dated between 35 and 32 Mya, is considered as one of the most influential climatic events of the Cenozoic. Temperatures dropped nearly 10°C worldwide—accompanied by a major drop in CO_2 concentrations (Beerling et al., 2009)—followed by major changes in vegetation and associated fauna (Morley, 2000; Plana, 2004; Sanmartín et al., 2001; Tiffney, 1985). The event was caused, among others, by the opening of the Drake Passage between South America and Antarctica and the onset of the Circum-Antarctic Current. In the Holarctic, the closing of the Turgai Strait between Europe and Asia (c. 30 Mya) brought about a more continental climate into the Western Palearctic (Sanmartín et al., 2001). The TEE has been associated to widespread extinction in flowering plant (angiosperm) families (Antonelli & Sanmartín, 2011; Crisp & Cook, 2007;Pan et al., 2006; Plana, 2004). A warm-adapted boreotropical flora was replaced across the Holarctic continents, Eurasia and North America, by the temperate mixed-mesophytic forest (Meseguer et al., 2015; Tiffney, 1985); in Africa, humid tropical forests were replaced by more xeric vegetation (Pan et al., 2006; Plana, 2004). A long-term cooling trend, punctuated by warming events, started with the TEE, which saw the expansion of C4 grasses in temperate and subequatorial regions, and the rise to dominance of coniferous forests in the boreal Holarctic regions (Kergoat et al., 2018; Meseguer et al., 2015). These changes in vegetation composition were concomitant with changes in the associated fauna (Kergoat et al., 2018; Sanmartín et al., 2001), with expansion and adaptation of insect families to the new grassland biomes, boreal and tundra forests, etc., but also events of widespread extinction. Such climatic and biotic changes appear as likely explanations for both the decreasing diversification in the Neotropic towards the end of the Eocene and the Oligocene and the concomitant increase in diversification rate in the Palearctic. As in Chazot et al. (2020), this dynamic of diversification in the Palearctic may correspond to the appearance and early diversification of the more modern Palearctic fauna that evolved in response to the new environmental conditions following the retreat of tropical biomes from higher latitudes. This process has created new habitats, and fragmented already stablished ones which could explain, at least partly, the observed diversification patterns.

The second period of increasing diversification rate in Geometridae, c. 15 Mya (Figure 3), coincides with another event of rapid global change and biotic extinction. The Mid-Miocene Climate Optimum (MMCO) at 17–14 Mya (Zachos et al., 2008) was a dramatic warming event, which saw increases in temperature close to 5°C worldwide (Bohaty & Zachos, 2003; Steffen et al., 2018). In the Holarctic and temperate areas, the MMCO was accompanied by range expansion of dryland floras worldwide (Edwards et al., 2010; Spriggs et al., 2014), and the colonization of tropical mountain regions by temperate lineages (Meseguer et al., 2015). In tropical regions like Africa, warmer and drier climates led to appearance of xeric-adapted floras and the extinction of humid-adapted, subtropical lineages (Morley, 2000; Pan et al., 2006; Plana, 2004; Pokorny et al., 2015). This warming trend was brought about by regional and global tectonic events, such as the closing of the eastern arm of the Tethys Seaway that connected the Indian and Atlantic Oceans, around 15 Mya; the rapid uplift of the Eastern African Plateau (∼17 Mya, Sepulchre et al., 2006) and the Tibetan Plateau (Yin & Harrison, 2000) and the continental collision of the Australian and Eurasian plates, which led to the aridification of central Australia (∼15 Mya, Crisp & Cook, 2007).

The expansion of grassland biomes after the MMCO has been argued as a diversification driver in herbivore lineages, such as mammals (MacFadden, 2005; Stebbins, 1981), beetles (Micó et al., 2009) and Satyrinae butterflies (Peña & Wahlberg, 2008); in contrast, Kergoat et al. (2018) did not find evidence of synchronous diversification in stemborer moths (Noctuidae) (Chazot et al., 2020) and our results support an increase in net diversification rates in Nymphalidae and Geometridae around the MMCO, respectively; yet, this shift was not general, affecting some clades within different subfamilies, and we did not test for a causal connection. In Nymphalidae, the pattern is most probably driven by Satyrinae which are mainly grass feeder specialists. However, Geometridae very rarely feed on grasses; they are usually feeding on other angiosperms. However, the spread of grasslands probably also implied increasing habitat fragmentation and appearance of gene flow barriers to the mostly forest-dwelling Geometridae. The expansion of grasslands and the fragmentation of the African tropical mesic forests (Paun et al., 2005; Plana, 2004) especially, could explain the increasing diversification rate in the Afrotropics since the Late Oligocene (Figure 5b).

Like the Palearctic, the Nearctic is a relatively well studied region, and it probably played an important role in the divergence of many of the deepest lineages of Geometridae, as a bridge between the Neotropics and the Palearctic (Figure 1; see also Brehm et al., 2019). Interestingly, although the Nearctic mirrors the Palearctic in the relative frequency of lineages (Figure 5a), the net diversification rate of this region over time has decreased in the last 40 Mya compared with other regions (Figure 5b) (Chazot et al., 2020) also found a similar pattern in the family Nymphalidae, with a low relative diversity in the Nearctic region since the Eocene. The reason for this could be related to the differential effect of Pleistocene glaciations, which hit the Eastern Nearctic region harder, where most geometrid moth species are endemic, compared with the Palearctic region, especially the eastern (Asian) parts (Sanmartín et al., 2001).

A general increase in the diversification rate towards the present is seen in all biogeographic regions, except Australia (Figure 5b). In Nymphalidae, the Australian region exhibits a relatively low diversification rate compared with other regions (Chazot et al., 2020). In Geometridae (Figure 5a,b), the Australian region shows a constantly low relative diversity compared with the Afrotropics since its colonization in the Early-Mid Cenozoic (Figures 1, 5a), and the net diversification rate slightly decreases in the last 20 Mya (Figure 5b). However, we treated New Zealand as a different region from Australia, but it has been considered as part of the same region in other studies. Thus, it might be that the Australian region harbours a relatively higher diversity than represented in our study.

We need to consider here, however, that some of these patterns might be a consequence of the different level of sampling of these regions in our dataset. The Neotropics and the Palearctic regions have been historically better studied and/or are better sampled in our study, than the Oriental region, Australia and the Afrotropics. Towards the present, those regions that are historically better studied and sampled will have comparatively a better representation of younger clades (i.e., genera, species); we, therefore, expect them to exhibit higher diversification rates towards the present compared with the other regions. Similarly, the fact that the net diversification rates in most regions stabilizes towards the present (Figure 5a,b) is most likely due to the effect of incomplete taxon sampling (i.e., missing taxa), which affects more younger clades than clades with deeper divergences (i.e., subfamilies, tribes).

Even taking these possible constraints into consideration, the role of the Neotropics as a region that has historically harboured a higher diversity than other regions is apparent in Geometridae. This agrees with the higher relative diversity observed in other Lepidoptera families (Chazot et al., 2020; Vila et al., 2011). However, unlike Nymphalidae, where the Neotropics show a higher relative diversity only after the Eocene, in Geometridae, this region had a high relative diversity since the crown diversification in the Late Cretaceous (Figures 1 and 5).

In general, our biogeographic analysis supports very few ancestral range states including more than one region. This is in line with our observation of extant species being endemic to a single region, probably due to their limited dispersal abilities/capacities. Most dispersal events are inferred to have occurred between geographically adjacent regions (Figure 4; Supporting Information). Moreover, many the inferred long-distance dispersal events (Supporting Information) could be the result of undersampling in the Asian and Afrotropical regions. This is probably the case for the unexpected long-distance jumps between Australia and the Palearctic regions (Figure 4). The Oriental region—which serves as a bridge between these two regions—is severely underrepresented in our study. On the other hand, the high frequency of dispersal events between the Neotropics and the Nearctic region, or between the Nearctic and Palearctic regions, and between the Palearctic and Afrotropical regions (which are very common in both directions) are in agreement with paleogeographic scenarios, supporting the presence of current or past connections among these regions, for example, the trans-Atlantic and Beringian land bridges between both halves of the Holarctic (Peña et al., 2010; Sanmartín et al., 2001; Vila et al., 2011).

CONCLUSION

Using the most complete and up to date phylogeny of Geometridae, we studied for the first time, the diversification patterns and biogeographical history of this hyper-diverse family. We reveal a high number of dispersal events between Afrotropic, Nearctic, Neotropic and Palearctic regions that have shaped the actual distributional ranges of the family. The Neotropical region has the highest recent diversity of the family. This appears to be a result of higher relative diversification rates and the early presence of the family in this region. The Palearctic region also presents a relatively high diversification rate and similarly high diversity. Most of the dispersal events are recorded between adjacent regions. Doubtlessly, a better and more even taxon sampling across all regions, in particular the African and Oriental regions, is desired in future studies.

In general, we show that it is possible to investigate the evolutionary history of a megadiverse clade, despite the challenges of taxon sampling across wide geographic regions, and broad phylogenetic diversity. Our analyses give a basic understanding of how the clade has evolved through time and space and identifies the problematic areas that need more work. Highly diverse groups are common among the insects, and we hope that our approach inspires more in-depth studies of such groups and facilitates the development of methods to deal with large phylogenetic hypotheses that have relatively poor taxon sampling.

AUTHOR CONTRIBUTIONS

Hamid Reza Ghanavi: Conceptualization; writing–original draft; methodology; visualization; formal analysis. **Nicolas Chazot**: Methodology; visualization; formal analysis; writing–review & editing. **Isabel Sanmartín**: Writing–review & editing; conceptualization; formal analysis. **Leidys Murillo-Ramos**: Conceptualization; writing–review & editing; data curation. **Sebastián Duchêne**: Methodology; writing–review & editing; formal analysis. **Pasi Sihvonen**: Writing–review & editing; Data curation. **Gunnar Brehm**: Data curation; writing–review & editing. **Niklas Wahlberg**: Writing–review & editing; conceptualization; funding acquisition; resources; supervision.

ACKNOWLEDGEMENTS

Hamid Reza Ghanavi received funding from the European Union's Horizon 2020 research and innovation program under the Marie Sklodowska-Curie grant agreement No. 642241. Niklas Wahlberg acknowledges funding from the Swedish Research Council (Grant No. 2015-04441). Leidys Murillo-Ramos acknowledges funding from Colciencias, 756-2016 and Universidad de Sucre, Colombia. Isabel Sanmartín was funded by the Spanish government (MINECO/MICIU/AEI) and the European Regional Development Fund (FEDER) through projects CGL2015-67849-P and PGC2019-XXXX-P. Sebastián Duchêne was supported by the Australian Research Council (DE190100805).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data in the Supporting Information, the alignment (XML file), the script files and the results can be downloaded from the GitHub repository: github.com/Hamidhrg/Geometridae and Zotero repository: 10.5281/zenodo.13315644

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Supporting Information.

How to cite this article: Ghanavi, H.R., Chazot, N., Sanmartín, I., Murillo-Ramos, L., Duchêne, S., Sihvonen, P. et al. (2025) Region-specific diversification dynamics and biogeographic history of one of the most diverse families of insects. *Systematic Entomology*, 50(1), 206–220. Available from: https://doi.org/10.1111/syen.12651