Molecular Phylogenetics and Evolution 194 (2024) 108022

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

To and fro in the archipelago: Repeated inter-island dispersal and New Guinea's orogeny affect diversification of *Delias*, the world's largest butterfly genus

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ARTICLE INFO

Keywords:
Aposematism
Biogeographic stochastic mapping
Divergence dating
Indo-Australian archipelago
Lepidoptera
Sequence capture

ABSTRACT

The world's largest butterfly genus *Delias*, commonly known as Jezebels, comprises *ca.* 251 species found throughout Asia, Australia, and Melanesia. Most species are endemic to islands in the Indo-Australian Archipelago or to New Guinea and nearby islands in Melanesia, and many species are restricted to montane habitats over 1200 m. We inferred an extensively sampled and well-supported molecular phylogeny of the group to better understand the spatial and temporal dimensions of its diversification. The remarkable diversity of *Delias* evolved in just *ca.* 15–16 Myr (crown age). The most recent common ancestor of a clade with most of the species dispersed out of New Guinea *ca.* 14 Mya, but at least six subsequently diverging lineages dispersed back to the island. Diversification was associated with frequent dispersal of lineages among the islands of the Indo-Australian Archipelago, and the divergence of sister taxa on a single landmass was rare and occurred only on the largest islands, most notably on New Guinea. We conclude that frequent inter-island dispersal during the

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https://doi.org/10.1016/j.ympev.2024.108022
Received 13 August 2023; Received in revised form 20 January 2024; Accepted 28 January 2024
Available online 5 February 2024

Neogene—likely facilitated by frequent sea level change—sparked much diversification during that period. Many extant New Guinea lineages started diversifying 5 Mya, suggesting that orogeny facilitated their diversification. Our results largely agree with the most recently proposed species group classification system, and we use our large taxon sample to extend this system to all described species. Finally, we summarize recent insights to speculate how wing pattern evolution, mimicry, and sexual selection might also contribute to these butterflies' rapid speciation and diversification.

1. Introduction

Insects comprise more than half of all eukaryotic species (Grimaldi and Engel, 2005), and butterflies are perhaps the best-known group to serve as a model for studying insect biodiversity and biogeography (Kawahara et al., 2023; Pinkert et al., 2022). Many factors contribute to butterfly diversity, but the uniquely complex geography of the Indo-Australian Archipelago provides an opportunity to investigate the role of islands and tropical mountains on diversification.

The Indo-Australian Archipelago has a dynamic history. Approximately 23 Mya[2], the northern edge of the Australian plate began colliding with the Sunda shelf, resulting in the formation of islands in Wallacea via uplift and volcanism. Subsequent volcanic activity, driven by intense geothermal activity in the region, further shaped the landscape and added to the number and diversity of islands (Hall, 2009; Lohman et al., 2011). Episodic fluctuations in sea levels (eustasy) formed, fragmented, and isolated islands during the Plio-Pleistocene (Woodruff, 2010), in some cases leading to genetic differentiation and speciation of the biota inhabiting them. The diversification of multiple taxa may be associated with these sea level changes and corresponding changes in island connectivity and forest area (Condamine et al., 2015; Guo et al., 2015; Li and Li, 2018; Roberts et al., 2011; Sholihah et al., 2021).

Because of their variability in climate and microhabitats, tropical mountains are among the most diverse places on Earth, rich with endemic species (Rahbek et al., 2019a; Rahbek et al., 2019b). The central mountain range of mainland New Guinea exceeds 4800 m. It is likely that the tremendous elevational gradient from sea level to such high elevations set the evolutionary stage for the diversification of endemic bowerbirds, birds of paradise, tree kangaroos, various beetles, and other insects (Eldridge et al., 2018; Gregory, 2020; McCullough et al., 2022; Stelbrink et al., 2022; Toussaint et al., 2014; Toussaint et al., 2021). The island was formed from the geological changes caused by the northward collision of the Australian plate with the Pacific plate (Hall, 2001; Hall, 2002; Hill and Hall, 2003). As the two plates converged, New Guinea's mountains started forming around 5 Mya, and the central mountain range now has a dramatic elevational gradient with a mosaic of habitat types (Cámara-Leret et al., 2020). Prior to this point, "proto-New Guinea" likely existed as handful of ophiolitic or crustal islands that later accreted onto the northern edge of the Sahul plate to become the northern edge of what is now New Guinea (Hall, 2002; Toussaint et al., 2014). Variation in montane temperatures and precipitation are more pronounced over elevational gradients in the tropics (Janzen, 1967). These geologic and climatic features in New Guinea opened novel ecological niches to which species could adapt. Beginning *ca.* 5 Mya, the diversification of many animal taxa are temporally associated with the orogeny of the Central Highlands of New Guinea (Roycroft et al., 2022; Schweizer et al., 2015; Slavenko et al., 2020; Toussaint et al., 2014; Unmack et al., 2013). Mountain uplift is postulated to be the primary force diversifying habitats in New Guinea, providing a topographically complex landscape where organisms can evolve.

The butterfly genus *Delias* Hübner (Lepidoptera: Pieridae) is distributed throughout Asia, Australia, and Melanesia with numerous species endemic to individual islands or mountains. Their range is home to multiple biodiversity hotspots including Indo-Burma, Sundaland, the Philippines, and Wallacea (Myers et al., 2000). About half of the species are endemic to New Guinea (Yagishita et al., 1993), which is the second-largest island in the world. Although new species and subspecies continue to be described (Davenport and Grimaldi, 2019; Davenport et al., 2017), the alpha taxonomy and species distributions of this large, tropical insect group are likely better known than most other insect taxa in the region. These features make *Delias* particularly well suited for investigating the biogeography of diversification in the Indo-Australian Archipelago and neighboring areas.

Delias is currently regarded as the most diverse butterfly genus in the world with 251 described species that we consider valid (Table S1). These are organized into informal species groups for ease of discussion. The diversity of *Delias* is just ahead of *Arhopala* (Lycaenidae; 245 species), which is also distributed throughout Asia, Australia, and Melanesia, and *Acraea* (Nymphalidae; 235 species), which reaches its peak of diversity in Africa (Lamas, 2015). Most *Delias* larvae feed on hemiparasitic mistletoes in the order Santalales (Braby, 2006; Braby and Trueman, 2006). Dorsal wing surfaces are generally unremarkable in the visible color spectrum, but most species have yellow, red, or both colors on the ventral wing surfaces. The striking wing pattern diversity across the genus suggests that they are variegated red, yellow, white, and black signals to predators warning of unpalatable defensive chemicals (aposematism; Wee and Monteiro, 2017). Some *Delias* species form mimicry rings with other *Delias* (Morinaka et al., 2018) or other, presumably Batesian, mimics (Canfield and Pierce, 2010; Dixey, 1918). A mimicry ring is an assemblage of visually similar species with at least one aposematic species and other aposematic species or undefended Batesian mimics. For instance, *D. belisama*, *D. oraia*, and *D. sambawana* constitute a Müllerian mimicry ring in Bali, Indonesia, while *D. splendida*, *D. eileenae*, *D. lemoulti*, and *D. timorensis* form two other Müllerian mimicry rings in Timor (Morinaka et al., 2018). Müller et al. (2013) noted that most species in the *isse* species group mimic congeners from other groups, particularly the *nysa* and *hyparete* species groups. Multiple molecular phylogenetic studies support the monophyly of *Delias* (Braby and Pierce, 2007; Braby et al., 2007; Müller et al., 2013); however, prior studies only sampled a little over half of the species diversity and included too few markers to achieve adequate branch support at deeper nodes.

In this study, we addressed two main questions regarding the evolution of *Delias*: (1) Is the diversification of *Delias* corelated with the formation of New Guinea's Central Highlands during the past 5 Myr and dispersal events between islands of the Indo-Australian Archipelago during the Plio-Pleistocene? (2) Do morphologically defined species or species groups need to be revised in the light of increasing genetic data? We expanded the taxon and gene sampling of prior molecular phylogenetic studies to infer a robust, time calibrated tree with multiple samples of as many species as possible and calculated COI barcode genetic distances among samples. We used the tree to evaluate biogeographic and diversification models. Finally, we discuss several other factors that might have impacted diversification in this genus.

2. Material and methods

2.1. Taxon sampling

The alpha taxonomy of *Delias* is contentious. Because of their

[2] Abbreviations: m = meters; Mya = million years ago; Myr = million years

brightly colored wing patterns that can vary markedly between lineages, this genus has been favored by butterfly collectors for decades. As a result, new taxa have sometimes been described for small variants in wing pattern, often from few specimens, and rarely supported by other evidence. Consequently, the same taxon can be regarded as a species, a subspecies, a form, or a junior synonym by different authorities. To provide a taxonomic framework for this study, we list the 251 species, 621 subspecies (including monotypic species), and 275 junior synonyms that we co-authors collectively recognize (Tables S1–S3).

Adult butterflies were collected with aerial nets in the field and preserved in one of two ways before storage at −80 °C: wingless bodies were preserved in vials of 100 % ethanol or whole specimens were dried and stored in glassine envelopes. Wing vouchers of alcoholic specimens were kept in glassine envelopes at ambient temperature. Some dried samples were pinned museum specimens that were originally not preserved for genetic research. However, by adopting sequence capture via anchored hybrid enrichment, we were able to sequence the DNA of many old museum samples successfully (Nunes et al., 2022).

Our complete taxon sample consisted of 406 samples representing 212 *Delias* (ingroup) species and 15 outgroup species (Table S4). Unsampled *Delias* species are indicated in Table S1. The outgroup taxa include the two described species of *Leuciacria*, the sister genus to *Delias* (Braby and Pierce, 2007; Kawahara et al., 2023) and single specimens of other pierid taxa: *Catasticta philoscia*, *Mylothris rhodope*, *Prioneris thestylis*, *Pieris napi*, *Ascia monuste*, *Appias galba*, *Hebomoia glaucippe*, *Ixias pyrene*, *Pareronia anais*, *Colias alfacariensis*, *Gonepteryx taiwana*, *Eurema hecabe*, and *Dismorphia zaela*. We also created a dataset with a single specimen of each *Delias* species by selecting the sample with the most data and adding sequences from all outgroups.

2.2. DNA extraction, anchored hybrid enrichment, and sequencing

DNA was extracted from the abdomens or legs following the protocol in Espeland et al. (2018) using an OmniPrep™ DNA extraction kit (gbiosciences.com). From the extracted DNA, 13 protein-coding loci were captured with the BUTTERFLY2.0 anchored hybrid enrichment (AHE) probe kit following the methods in Kawahara et al. (2018). This kit employs single-stranded DNA probes that capture a portion of one mitochondrial gene (cytochrome *c* oxidase subunit I, *COI*) and 12 nuclear genes: acetoacetyl-CoA thiolase (*AACT*), *CAD* (carbamoyl-phosphate synthetase 2, aspartate transcarbamylase, and dihydroorotase), catalase (*CAT*), dopa-decarboxylase (*DDC*), elongation factor 1 alpha (*EF1-a*), glyceraldehyde 3-phosphate dehydrogenase (*GAPDH*), hairy cell leukemia protein 1 (*HCL*), isocitrate dehydrogenase (*IDH*), malate dehydrogenase (*MDH*), ribosomal protein S2 (*RPS2*), ribosomal protein S5 (*RPS5*), and *wingless* (*wg*). A few specimens were sequenced with the BUTTERFLY1.1 AHE probe kit, which captures the same 13 loci plus many more (Toussaint et al., 2018). From these specimens, Arginine Kinase (*ArgKin*) was also included in the dataset because this locus is frequently Sanger sequenced and available on GenBank. Many of these loci were first used in butterfly phylogenetics by Wahlberg and Wheat (2008). DNA extracts quantitated with a Qubit 3 fluorometer (thermofisher.com) were sent to RAPiD Genomics (rapid-genomics.com) for anchored hybrid enrichment (AHE) and sequencing. Oligonucleotide fragments enriched through AHE were sequenced using the Illumina paired-end multiplexed sequencing protocol on an Illumina HiSeq 3000 (Breinholt et al., 2018).

2.3. Clean-up and data assembly

The reads were trimmed with Trim Galore! v0.4.0 (https://www.bioinformatics.babraham.ac.uk) before iterative baited assembly (Breinholt et al., 2018). Only sequences with both forward and reverse reads were assembled. The assembled reads were then used to identify orthologs of the 13 butterfly loci with a single hit threshold of 0.9 by blasting the reads against a *Danaus plexippus* reference genome in USEARCH (Edgar, 2010). Contaminated sequences were removed based on whether the sequences are 99 % identical across at least 95 % of the total sequence length in distantly related families.

2.4. Alignment and concatenation

AHE data were augmented with sequences from GenBank (Benson et al., 2013). Sequences of each locus were aligned with MUSCLE v3.8.425 (Edgar, 2004) implemented in AliView v1.28 (Larsson, 2014), and a few misaligned sequences/bases were manually adjusted. All loci are protein-coding, and open reading frames were determined in Aliview. SequenceMatrix v1.9 (Vaidya et al., 2011) was used to concatenate all 14 loci into a single data set.

2.5. Model selection, phylogenetic analyses, and divergence time estimation

All phylogenetic analyses were run on the CIPRES web server (Miller, 2019). ModelFinder (Kalyaanamoorthy et al., 2017) implemented in IQ-TREE 2.1.2 (Minh et al., 2020) was used to select the best-fitting likelihood models and data partitions for maximum likelihood (ML) and Bayesian inference (BI) using the TESTNEWMERGE command, which merges similar codon partitions followed by tree inference (Minh et al., 2020). The best-fitting models were selected under the corrected Akaike information criterion (AICc; Cavanaugh, 1997) or the Bayesian information criterion (BIC; Neath and Cavanaugh, 2012). IQ-TREE was used to infer the most likely tree using the complete dataset with all 421 ingroup samples. Ultrafast bootstrapping (UFboot; Hoang et al., 2018) and Shimodaira Hasegawa-like approximate likelihood ratio test (SH-aLRT; Ota et al., 2000) were used to estimate clade support with 1000 replicates each. In our taxon sample, *Dismorphia zaela* was specified as the most distantly related outgroup for rooting the phylogeny.

Bayesian inference (BI) was conducted in BEAST v1.10.4 (Suchard et al., 2018) using the reduced dataset with a single specimen per species of *Delias*. The XML file needed for the BEAST analysis on CIPRES was prepared in BEAUti v1.10.4 (Drummond et al., 2012). ModelFinderPro implemented in IQ-TREE was used to partition the data by codon and find appropriate substitution models using the BIC. Each data partition was assigned its own substitution model, but all partitions were linked into a single tree model. An uncorrelated relaxed clock (Drummond et al., 2006) with a lognormal distribution was used for each of the two clock models: one for the mitochondrial locus (*COI*) and another for the nuclear loci. Since some of the models selected with this program are not available in BEAUti, the available DNA substitution models closest to those inferred were selected for the partitions: TPM2 was substituted with TN93; TIM2 and SYM were substituted with GTR.

We estimated divergence times in two ways: maximum likelihood (ML) implemented in IQ-TREE; and Bayesian inference using BEAST. Lepidoptera are notorious for their unusually poor fossil record (de Jong, 2017; Sohn et al., 2015), and we therefore used the best available secondary calibrations that stem from fossil-informed age estimates on a large, comprehensive tree of butterfly genera (Kawahara et al., 2023). Three calibration points were used for both analyses, MRCA of: (1) Pierinae (49.1 Mya; 95 % HPD = 48.93–49.36 Mya; in BEAST, StDev = 0.066), (2) the split between *Delias* and *Leuciacria* (19.44 Mya; 95 % HPD = 18.60–20.30 Mya; StDev = 0.375), and (3) the MRCA of a subclade of *Delias* containing *D. henningia* and *D. descombesi* (13.54 Mya; 95 % HPD = 12.54–14.44 Mya; StDev = 0.41). IQ-TREE uses a least-squares dating method, which is considerably faster than Bayesian methods (To et al., 2016). The ML dating analysis followed the protocol described in the IQ-TREE 2.1.2 manual, including selection of partitions and substitution models using AICc (Crotty et al., 2019). Confidence intervals of the estimated node ages were generated with 100 replicates in which the starting seed of the analyses differed.

To investigate the effects of different priors in BEAST, we ran two stepping stone analyses: one with a Yule tree prior (Gernhard, 2008) and a second with a birth–death tree prior. Each of these had 100 path steps and chain lengths of 5 million, logged every 5000 generations. We also ran two full BEAST analyses; the Markov Chain Monte Carlo analyses (MCMC; Gamerman and Lopes, 2006) of each were run for over 1 billion generations (Drummond et al., 2006). Trees were sampled every 200,000 generations. After the analyses completed, the MCMC results were visualized using Tracer v1.7.2 (Rambaut et al., 2018) to confirm that all ESS values were greater than 200, and the final maximum clade credibility tree was generated using TreeAnnotator v1.10.4.

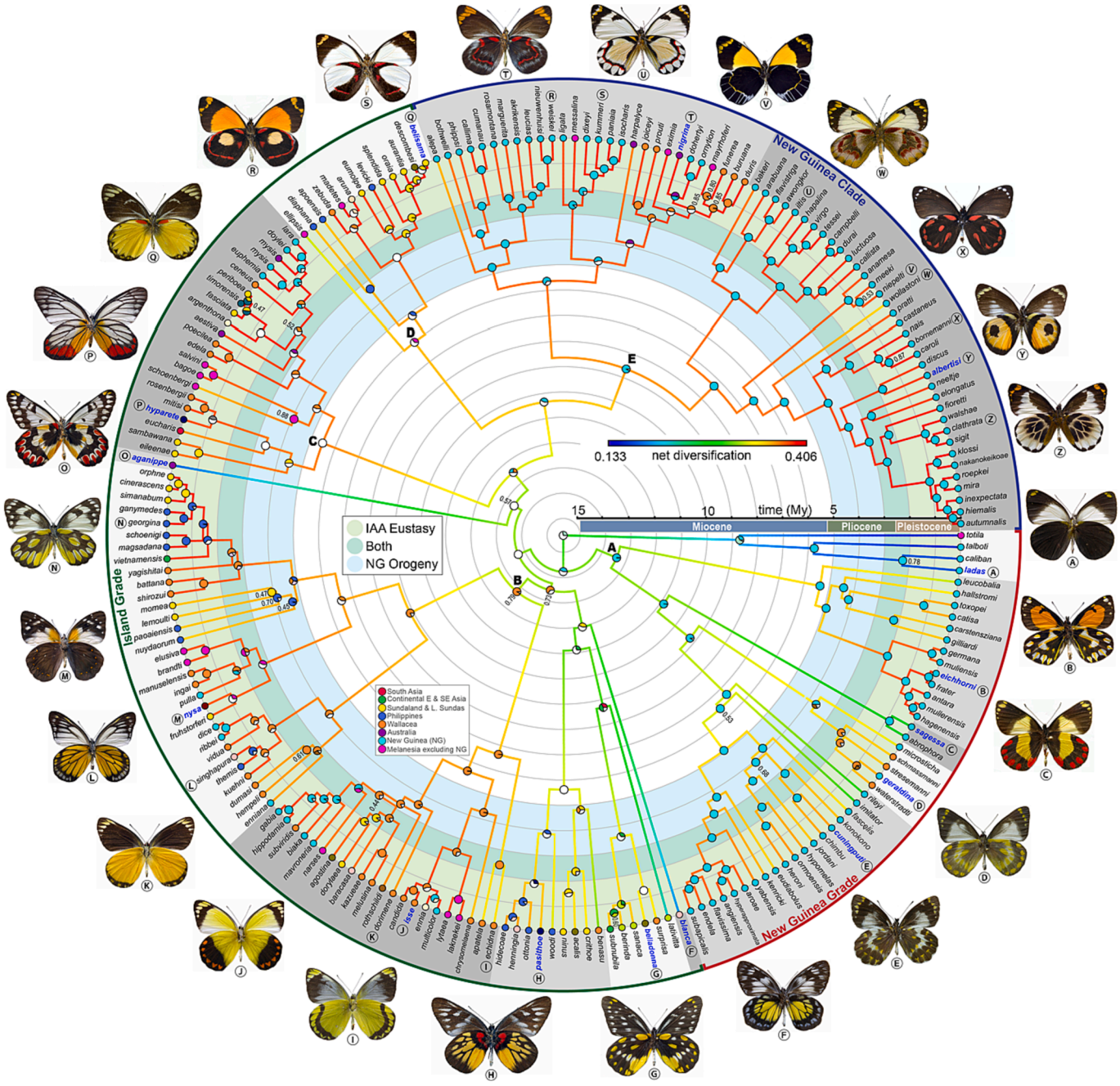


Fig. 1. Time-calibrated Bayesian phylogeny of 212 *Delias* species inferred with BEAST. Branch colors indicate net branch-specific diversification rates, and colored circles at the tips indicate the biogeographic region where the species is distributed as indicated by the inset legend and the map in Fig. 3. Tip colors not found in the legend represent combinations of different areas (Fig. S4). The complete distribution of each species and 95 % HPD intervals for divergence dates are provided in Figs. S1 and S2. Pie charts at internal nodes indicate the relative probabilities of possible ancestral distributions. Nodes with < 0.9 posterior probability support are labeled with their posterior values. The light blue ring around the phylogeny 3-5 Mya indicates the estimated peak of mountain building (orogeny) in New Guinea, and the partially overlapping light green ring indicates a period when drastic, cyclical sea level changes (eustasy) of >40 m below present caused some islands in the Indo-Australian Archipelago to fuse and separate. Gray boxes around the tip labels indicate species groups, and the species for which the group is named is indicated in bold, blue font. Select species, indicated with an encircled letter, are depicted with a ventral photograph of a male around the periphery. The New Guinea Grade, Island Grade, and New Guinea Clade—terms we use to discuss the group's biogeography—are indicated by a thin, colored ring outside the tip labels. Clades A-E are designated to facilitate discussion. Collection and voucher information for each sequenced specimen are provided in Table S1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.6. COI p-distance analysis

Since *Delias* diverged from its sister taxon *Leuciacria* ~19.44 Mya (Kawahara et al., 2023), the history of *Delias* has been relatively brief given its species richness. We hypothesize that some taxa regarded as different species might in fact be conspecific. To provide a benchmark of genetic differentiation among species, we calculated COI pairwise distances between all samples with sequence data for that locus. We also computed mean distances with standard deviations among 207 currently accepted species in our analysis (some samples lacked COI data). These analyses were performed in MEGA X (Molecular Evolutionary Genetics Analysis) (Stecher et al., 2020). ModelFinder indicated that a gamma distribution with invariant sites (G + I) was the best rate model, which we used for the distance analysis. The number of bootstrap replicates was set to 200.

2.7. Biogeographic analysis

The R package BioGeoBEARS v1.1.1 (Matzke, 2013) was used to infer the ancestral ranges and the historical dispersal of the taxon's ancestors using R v.4.1.2 (R Core Team, 2020). We ran three BioGeoBEARS analyses: one that considered only contemporary geography using a single set of adjacency and dispersal scalars; another that considered the changing geography of the region due to tectonic plate movements (Hall, 2001; Hall, 2002; Hill and Hall, 2003); and a third with no scalars or time stratification. The analyses were tested under six biogeographic models: DEC, DEC + *j*, DIVALIKE, DIVALIKE + *j*, BAYAREALIKE, and BAYAREALIKE + *j* (Matzke, 2013; Matzke, 2014), and the model with the best log-likelihood was chosen as the most strongly supported. We used the time-calibrated Bayesian Yule tree with one sample of each of the 212 *Delias* species in our larger dataset. We defined eight biogeographic areas occupied by *Delias* and scored whether each species was present or absent in one or more of these areas: South Asia; Continental East & Southeast Asia; Sundaland & the Lesser Sundas; Philippines; Wallacea including Sulawesi; Australia; New Guinea; and Melanesia excluding New Guinea (Table S5; Figs. 1 and 3). The adjacency scalars of these areas were determined by their relative positions on a map to ascertain whether each of the geographic areas shared a common border with the others (Table S6). Dispersal scalars were estimated using the Euclidian distance between each pair of areas to arrive at a relative probability of dispersal (Table S7). We used GPlates and its default dataset to estimate changes in area adjacency and dispersal probability through time (Müller et al., 2018). Because our Bayesian divergence dating analysis suggested that the crown age of *Delias* is *ca.* 16 Myr old, we estimated dispersal probabilities between all pairs of geographic areas at four time points less than 16 Mya: 12, 8, 4, and 0 Mya. Using the parameters from the best fitting model, time-stratified DEC + *j*, we conducted biogeographic stochastic mapping to estimate the number of dispersal events between the eight bioregions in BioGeoBEARS (Dupin et al., 2017). Using 100 pseudoreplicated biogeographical histories (100 BSMs × 1 posterior species tree), we followed Matos-Maraví et al. (2021) to calculate relative dispersal rates during different periods in the evolutionary history of *Delias*: 0–4 Mya, 4–8 Mya, 8–12 Mya, and 12–16 Mya. We visualized dispersal networks across its whole evolutionary history and for each time slice using the R package *qgraph* (Epskamp et al., 2012). We used different minimum dispersal values and cutoff values in *qgraph* to visualize dispersal networks for overall dispersal (min = 1, cut = 4) and for each time slice (min = 0.5, cut = 1).

2.8. Diversification analyses

We used two methods to estimate changes in diversification rates. Bayesian Analysis of Macroevolutionary Mixtures (BAMM) v2.5.0 (Rabosky, 2014) was first used to investigate the branch-specific diversification of *Delias* lineages. The program uses a birth–death model to infer diversification rates of different lineages within the tree and determine whether rate shifts occurred on a phylogeny. The configuration file to run BAMM, the R script required to generate priors, and the interpretation of output results were adapted from the online documentation. Using our ultrametric BEAST tree with a Yule tree prior, three priors–lambdaInitPrior, lambdaShiftPrior, and muInitPrior–were automatically determined with the R package BAMMtools v2.1.10 (Rabosky et al., 2014). Rate shifts were tested by running an MCMC analysis for 1,000,000 generations, and the log-likelihood of the tested hypotheses was sampled every 1000 generations. Bayes Factors for each shift hypothesis were calculated and compared to the null hypothesis of 0 shifts.

The accuracy of BAMM's diversification rate shift estimates have been called into question (Meyer et al., 2018; Meyer and Wiens, 2018; Rabosky, 2018; Rabosky et al., 2017), which prompted us to estimate rates shifts with a second method: Branch-Specific Diversification Rates (BSD) in RevBayes (Höhna et al., 2019; Höhna et al., 2016). RevBayes uses an approach similar to BAMM to estimate whether diversification rates vary among branches. The configuration script to run the BSD estimation with RevBayes was adapted from https://revbayes.github.io. RevBayes can approximate the continuous base distributions for the diversification-rate parameters by using a discrete rate category, similar to Yang (1994) and Drummond et al. (2006). Following the advice of Höhna et al. (2019), we selected a discrete rate category of 20, as this likely approximated the continuous diversification rate parameter distribution. Net diversification rates were estimated over 5000 MCMC generations with 2 runs and a tuning interval of 200. All other priors and parameters were left as default values.

Lineage-through-time (LTT) plots are another method to visualize changes in diversification over time, but this method has also been criticized for being unreliable (Louca and Pennell, 2020). We therefore estimated a deterministic lineage-through-time plot, which is shaped by changes in the pulled speciation rate over time (Helmstetter et al., 2022; Louca and Pennell, 2020). We used the R package *castor* v1.7.6 (Louca et al., 2018) function "fit_hbd_psr_on_grid". The "Ngrid" argument was set to 16, which is close to the estimated age of the genus in Myr. This value is a trade-off between computational accuracy and efficiency that allows *castor* to split the time range of the tree from the root to the tips into 16 portions before estimating the pulled speciation rate and the number of lineages for each portion independently. The "Nbootstraps" argument was set to 100 so that 100 trees could be generated to calculate confidence intervals around the pulled rates.

2.9. Species group taxonomy

Species groups are informal designations to facilitate the study and discussion of subgroups within large genera such as *Charaxes, Neptis*, *Hypochrysops*, and others (Ma et al., 2020). They are not recognized by the International Code of Zoological Nomenclature (ICZN, 1999) and thus the names are not subject to rules that apply to other higher taxa, such as typification, priority, etc. Talbot (1928–1937) first established species groups for *Delias* on the basis of androconia, genitalia, and wing patterns. Yagishita et al. (1993) made further changes on morphological grounds. Subsequent molecular phylogenetic work by Braby and Pierce (2007) and Müller et al. (2013) added the criterion of monophyly for the delimitation of species groups within *Delias* and reorganized their composition so that each group was monophyletic. Braby and Pierce (2007) recognized 24 species groups (including the monotypic *aganippe* group), but Müller et al. (2013) reduced this to 14 species groups in accordance with the topology of their tree with 131 *Delias* species. Among other changes, they reinstated Talbot's (1928–1937) *aroae* species group not recognized by Braby and Pierce (2007) and applied that name to species previously placed in the *cuningputi* group. It has long been acknowledged that the *aroae* and *cuningputi* groups are closely allied (Orr and Sibatani, 1985, 1986). With our expanded taxon sampling, we reexamined the species groups of Müller et al. (2013) to ensure that

they were monophyletic and to assign all species to groups.

3. Results

3.1. Phylogenetic inference

The log marginal likelihood of the stepping-stone analysis with a Yule prior was −179432.727, and −179413.781 with a birth–death prior. Thus, the Bayes Factor comparing the two was 18.95 (BF = log [ML_{BD}] − log[ML_{Yule}]), indicating support for the birth–death prior. Our time-calibrated BI phylogeny (BD Prior) of 212 *Delias* species (Fig. S2) illustrates that the genus diverged from its sister genus *Leuciacria* approximately 19.4 Mya (stem age) and suggests that it started to diversify around 15.15 Mya (crown age; 95 % HPD 13.98–16.38 Mya) (Table 1). Most nodes have high posterior probability values (>0.95) except for some deep nodes and nodes near the tips. The ingroup topology of the ML least-squares dated tree (Fig. S3) was similar to the undated ML tree (Fig. 2). Divergence times differed slightly depending on the inference method. Estimates with a Yule tree prior in BEAST were generally the oldest (Fig. 1 and S2), and ML estimates in IQ-TREE were the youngest (Fig. S3). Divergence dates with a birth–death tree prior in BEAST were intermediate (Table 1; Fig. S2). The confidence intervals were notably narrower in the ML dating analysis (Fig. S3). Since divergence dating with least-squares is relatively new and dating with BEAST has become the gold standard in systematics, we chose the BEAST tree for subsequent analyses requiring a dated, ultrametric tree. Diversification/biogeographic analyses and preparation of Fig. 1 used the tree with the Yule tree prior, as these (oldest) age estimates were viewed as the most conservative given the relative youth of the group in relation to its species diversity. Figure S2 compares the dated trees inferred with Yule or birth–death priors and demonstrates that the 95 % HPDs surrounding inferred median dates of the Yule and birth–death trees broadly overlap. The inferred relationships among species in our ML analysis with 421 specimens were highly congruent with the Bayesian tree. Further, the node support is similarly high (Fig. 2). There are several minor inconsistencies between trees inferred with the two methods. Within the *nysa* species group, *Delias pulla* is sister to the *D. elusiva* + *D. brandti* clade in the ML tree (SH-aLRT = 73.1; UFBoot = 63) but is sister to the *D. manuselensis* + *D. ingai* clade in the BI tree (PP = 0.631). Within the *singhapura* species group, *Delias dumasi* is sister to *D. enniana* in the ML tree (SH-aLRT = 16; UFBoot = 57) and BI (BD) tree (PP = 0.370), but sister to *D. hempeli* in the BI (Yule) tree (PP = 0.614). In the *georgina* species group, *Delias momea* is sister to *D. paoaiensis* in the ML tree (SH-aLRT = 52.3; UFBoot = 62), but sister to *D. lemoulti* in the BI tree (PP = 0.468). Within the *cuningputi* species group, *Delias fascelis* is sister to (*D. jordani* + *D. hypomelas* + (*D. ormoensis* + *D. heroni*)) in the ML tree (SH-aLRT = 13.4; UFBoot = 49). However, the divergence of *D. fascelis* is earlier in the BI tree, and it is sister to a larger clade containing *D. konokono*, *D. cuningputi*, *D. chimbu*, and the four species mentioned above (PP = 1). *Delias mayrhoferi* in the *nigrina* species group is sister to *D. eximia* in the ML tree (SH-aLRT = 90.9; UFBoot = 73) but sister to *D. funerea* in the BI tree (PP = 0.796). Perhaps the biggest difference between the ML and the BI trees is the placement of the taxon *Delias aganippe* (Figs. 1 and 2), which is a rogue, monotypic species that comes out in radically different places in the BI and the ML analyses.

3.2. Ancestral range reconstruction

The most likely biogeographic model for all BioGeoBEARS analyses was DEC + *j*, and the log-likelihoods with and without time-stratification were −348.498 and −348.476, respectively, and −362.349 in the analysis without scalars or time stratification. Addition of the founder effect speciation (*j*) parameter to each model made substantial improvements in likelihood (Tables 2 and S8). Log-likelihoods of the DIVALIKE + *j* model were quite similar to DEC + *j*: −348.860 and −348.972 with and without time stratification (Tables 2 and S8). However, biogeographic histories inferred under the DEC + *j* (Fig. 1) and DIVALIKE + *j* models (Fig. S4) were not noticeably different. Present-day New Guinea was formed by the accretion of multiple land masses, and one or more of these is the most likely ancestral area of the MRCA of *Delias*. Its sister genus *Leuciacria* is distributed entirely within the New Guinea region, and the MRCA of the two earliest diverging *Delias* lineages are likely to have been located on a landmass now considered to be part of New Guinea (Fig. 3C and D). These two lineages are the *ladas* group and clade A (Fig. 1), which includes the *eichhorni*, *geraldina*, and *sagessa* species groups. However, within the earliest diverging *Delias* lineages, the ancestor of *D. totila* dispersed to the Bismarck Archipelago, and the MRCA of the clade that includes *D. schmassmanni*, *D. stresemanni*, and *D. waterstradti* dispersed to Wallacea before the *D. geraldina* lineage subsequently dispersed back to New Guinea.

The geographic provenance of the ancestors of several major lineages cannot be determined with certainty (white node circles; Figs. 1 and S4). This is likely because these lineages are characterized by frequent dispersal between islands and by diversification on the Asian mainland (Fig. 3). Outside of New Guinea, insular sister taxa were rarely distributed on the same landmass (Fig. S1). The exceptions to this pattern include *D. battana* and *D. shirozui* on Sulawesi; *D. schoenigi* and *D. magsadana* on Mindanao; *D. prouti* and *D. joiceyi* on Buru; *D. apoensis* and *D. diaphana* on Mindanao; *D. henningia* and *D. hidecoae* on Mindoro; and *D. henningia, D. ottonia, D. pasithoe,* and *D. woodi*, which comprise a clade of species that co-occur on Mindanao. Some of these sister taxa are spatially separated by flying at different elevations, for example, *D. shirozui* (500–800 m) and *D. battana* (1600–2000 m) on Sulawesi (Yata and Morishita, 1985). Moreover, as discussed below, many of these co-occuring "species" pairs are so genetically similar that that they may be conspecific. The ancestor of clade E (Fig. 1) dispersed back to New Guinea and subsequently diversified, with ancestors of a few lineages dispersing to Australia, Wallacea, or Melanesian islands adjacent to New Guinea.

Biogeographic stochastic mapping demonstrates that dispersal played an important role in diversification, especially dispersal in and out of New Guinea. Dispersal events from Wallacea to Melanesian islands other than New Guinea and from the Philippines to Sundaland were also frequent (Fig. 3). Most dispersal events occurred within the past 4 Myr, which could reflect the increased amount of subaerial land in New Guinea, Wallacea, and the Philippines; Pleistocene eustasy that periodically decreased inter-island distances likely played a role, too. There was no dispersal network for the 12–16 Myr time slice resulting from our analysis because none of the dispersal rates reached the threshold values that were specified to visualize the networks.

Table 1
Comparison of stepping-stone log marginal likelihoods (ml) for birth–death and Yule tree priors along with estimated ages of key nodes in all three dating analyses. Ranges are 95% HPD (BI) or 95% CI (ML).

Criterion	log (ml)	BF	*Delias* stem (Myr)	*Delias* crown (Myr)	*hyparete* species group crown (Myr)
BI BD	−179413.78	18.95	19.41 (18.71–20.12)	15.15 (13.98–16.38)	4.65 (3.72–5.70)
BI Yule	−179432.73		19.42 (18.74–20.15)	15.67 (14.55–16.96)	5.48 (4.45–6.64)
ML			19.44 (19.44–19.44)	14.08 (13.54–14.54)	3.07 (2.66–3.49)

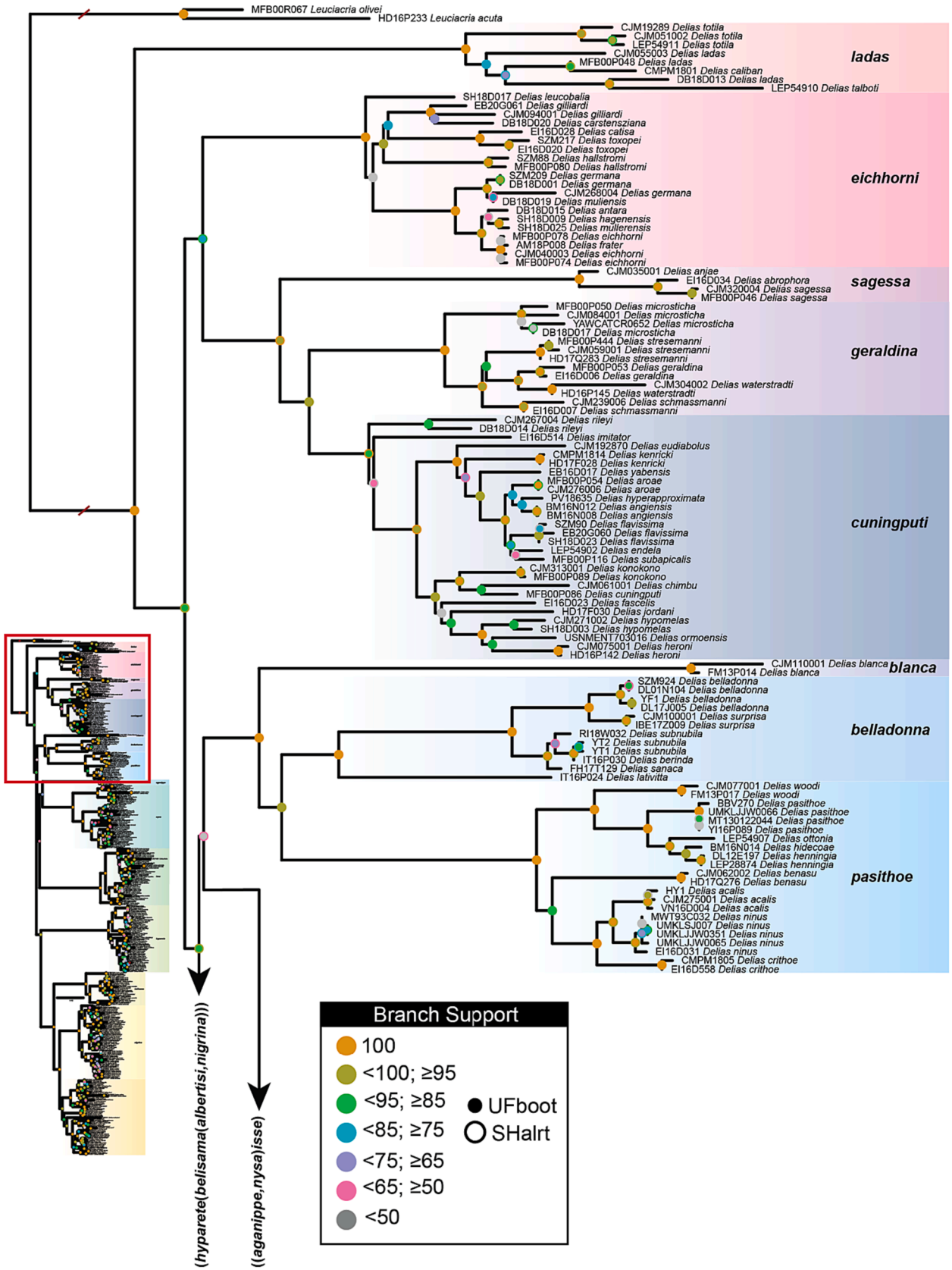


Fig. 2. Maximum Likelihood phylogeny of 406 specimens of 212 *Delias* species with two *Leuciacria* spp. as outgroups. SH-aLRT and ultrafast bootstrap supports are indicated by the outer and the inner portions, respectively, of the circles at the nodes. Red slashes indicate long branches that were shortened for cosmetic reasons. The portion of the larger tree depicted in each panel is indicated with a red box around the inset figure. Species groups recognized in this work are indicated with colored blocks. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

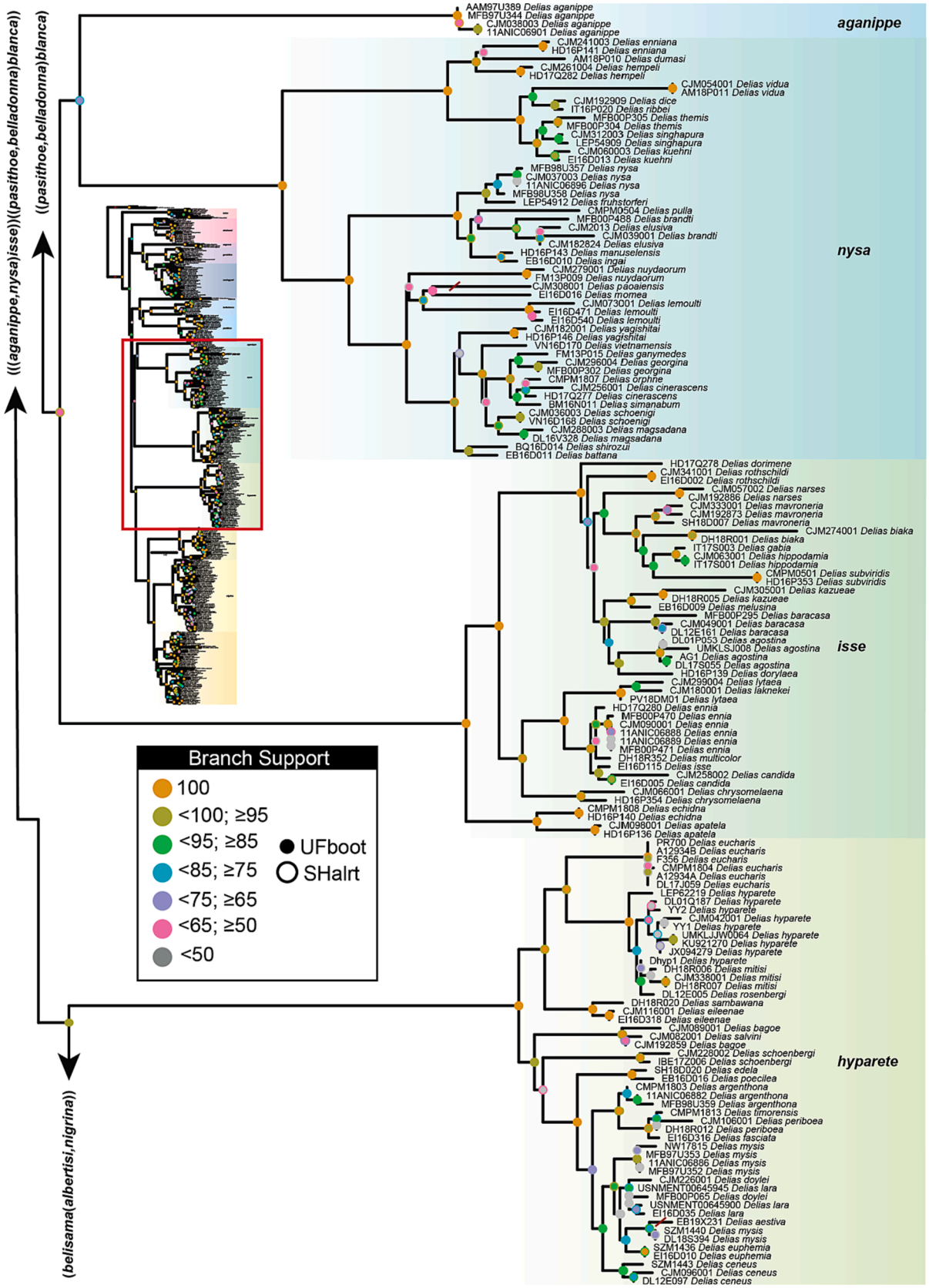


Fig. 2. (*continued*).

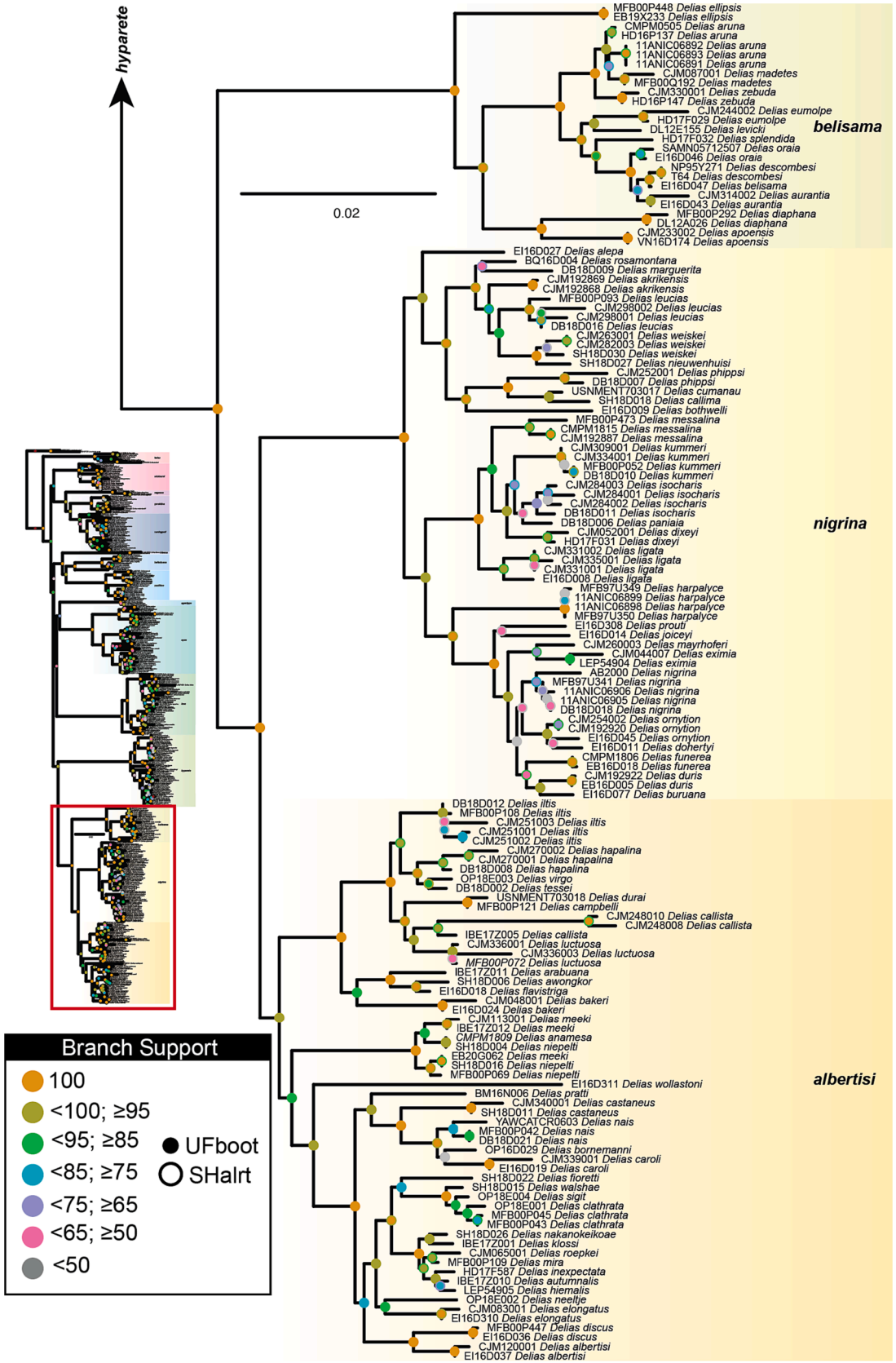


Fig. 2. (*continued*).

Table 2
Log likelihoods for alternative biogeographic models describing the extant distribution of *Delias* given their phylogeny. These estimates come from an analysis with dispersal scalars and adjacency scalars with no time stratification. The best log likelihood value is in bold.

	LnL	d	e	*j*	AICc
DEC	−395.17523	0.03221306	0.0119262	–	794.407875
DEC + *j*	**−348.47586**	1.56E-02	1.00E-12	0.02514731	703.067101
DIVALIKE	−385.86067	0.03708772	0.0047638	–	775.778765
DIVALIKE + *j*	−348.97235	1.94E-02	1.00E-12	0.02118569	704.060083
BAYAREALIKE	−489.17522	0.03952282	0.1554935	–	982.40785
BAYAREALIKE + *j*	−357.90779	0.01059493	0.00193205	0.03198221	721.930968

3.3. Diversification estimation

The BAMM analysis suggests no rate shifts on the tree, with the net diversification of *Delias* slowly increasing across all lineages (Fig. S5). However, the branch-specific diversification (BSD) estimation of RevBayes suggested high net diversification rates across the phylogeny with a few lineages that have substantially slower diversification (Fig. 1). The net diversification rate of the early diverging *ladas* species group began to decrease around 9 Mya. Early diverging members of the *eichhorni* species group also have lower diversification rates than younger branches. The *sagessa* and monotypic *aganippe* and *blanca* species groups also have lower than average diversification rates.

The pulled speciation rate (PSR) was initially high early in the genus' diversification but dropped quickly (Fig. S6A). Around 13–14 Mya, the rate again increased dramatically and then decreased again. Thus, the number of lineages also increased steeply from the genus' crown age of 13–16 Mya. Although the tree topology near the root is not strongly supported (Figs. 1, 2, S1 and S2), this should not affect the diversification rate shift estimate. Our inability to resolve the branching order of the oldest lineages along the backbone (>10 Myr) with high confidence is likely due to short internodes likely caused by rapid diversification. After 13 Mya, the PSR is relatively low until 7 Mya. From 7 Mya, the PSR increased slightly and mildly fluctuated, decreasing to 0 at the present. In the deterministic lineages through time plot, the slope for lineage number is initially large, but it is lower from 13 Mya to 7 Mya, and then increases again after 7 Mya (Fig. S6B), which is roughly coincident with the orogeny of the New Guinea Central Highlands.

3.4. Taxonomy

We included multiple individuals of 120 species in the ML tree, and, of those species represented by two or more specimens, 17 species were not recovered as monophyletic. *Delias ladas* was paraphyletic in relation to *D. caliban* and *D. talboti*; *D. gilliardi* was paraphyletic in relation to *D. carstensziana*; *D. germana* was paraphyletic in relation to *D. muliensis*; *D. eichhorni* was paraphyletic in relation to *D. frater*; *D. meeki* and *D. niepelti* were polyphyletic in relation to *D. anamesa*; *D. ornytion* was paraphyletic in relation to *D. dohertyi*; *D. aruna* was paraphyletic in relation to *D. madetes*; *D. doylei* and *D. lara* were polyphyletic in relation to each other; *D. timorensis* is in a polytomy with *D. periboea*; *D. salvini* is paraphyletic with *D. bagoe*; *D. mitisi* and *D. rosenbergi* are nested within *D. hyparete*; *D. laknekei* is paraphyletic with *D. lytaea*; *D. elusiva* and *D. brandti* samples were polyphyletic; and our only *Delias orphne* sample (CMPM1807) was recovered in a polytomy with *D. cinerascens*. Interestingly, *Delias mysis* from Australia and Aru were in separate, non-sister clades (Figs. 2 and S2), with Australian *D. aestiva* sister to *Delias mysis aruensis*, suggesting the latter taxon is either a distinct species or conspecific with *aestiva*.

Many *Delias* taxa considered to be separate species were genetically similar or identical at the COI DNA barcoding locus. Pairwise comparisons were conducted for 207 species in the ML tree. Out of the 21,321 comparisons (Table S9), 146 differ by less than 2 % (Table S10). Interestingly, there were three sister species pairs in which one species is considered endemic to New Britain (NB) and the other to New Ireland (NI). In all cases, we found that one or both species in each pair was not reciprocally monophyletic (Fig. 2) and the average COI pairwise distance between all pairs was <2 %: *Delias elusiva* (NB)/*D. brandti* (NI); *D. lytaea* (NB)/*D. laknekei* (NI); and *D. salvini* (NB)/*D. bagoe* (NI). Different species in these closely related pairs are morphologically distinctive.

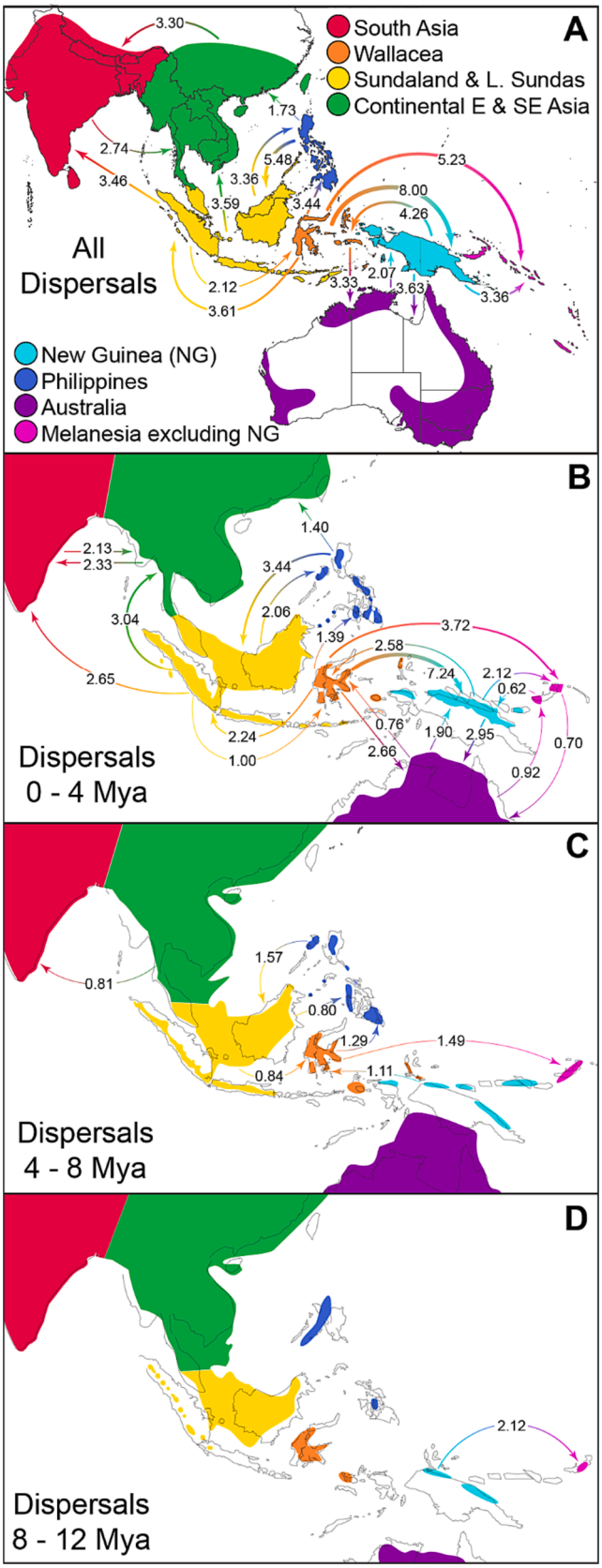
Our taxon sample is 50 % larger than that of Müller et al. (2013), and we found that their species groups are stable and monophyletic with a single exception. *Delias blanca* was on a long branch that was strongly supported as sister to the *pasithoe* and *belladonna* species groups. Its inclusion with one of these groups makes the other paraphyletic, so we considered it to be in the monotypic *blanca* species group. We made one additional change to species group affiliations. Müller et al. (2013) did not recognize the *cuningputi* species group, named after *D. cuningputi* (Ribbe, 1900, p. 308), and placed these species in the *aroae* species group along with some of Braby and Pierce's (2007) *geraldina* group species. However, the *D. aroae* (Ribbe, 1900, p. 346) is not the oldest name, and the clade is more commonly called the *cuningputi* group (rejecting Müller et al.'s [2013] change in terminology). We propose these taxa to be placed in the *cuningputi* species group. All species group affiliations are noted in Table S1. Thirty-nine *Delias* species were not sampled in the current analysis, so their species group placement cannot be verified. Nonetheless, we have attempted to place these in the revised framework based on their morphological similarity to species that we sampled (Table S1). For example, we did not sample *D. akikoae* Morita, 2001, which has recently been considered a subspecies of *D. enniana* Oberthür, 1880 (Pequin, 2023). We consider the former species to belong to the *nysa* group along with the latter. All species groups are monophyletic with >95 % ultrafast bootstrap and >95 % SH-aLRT support. A few deep nodes and some nodes near the tips do not have high support (bootstrap and SH-aLRT <65 %), but instability at these weak nodes would not affect species group memberships. The topologies of both the ML and the BI trees agree on the membership and relationships among all 14 species groups with the exception of the rogue taxon *D. aganippe*.

4. Discussion

4.1. Historical biogeography

Early hypotheses from the 20th century proposed that *Delias* evolved in Asia before colonizing Australia and Melanesia (Holloway, 1974; Holloway, 1986; Talbot, 1928–1937). However, Braby and Pierce (2007) and Braby et al. (2007) proposed an 'Out-of-Australia' hypothesis for the origin of *Delias* based on their molecular phylogenetic evidence. The phylogeny of Müller et al. (2013), which was more extensively sampled than that of Braby and Pierce (2007), further supported this alternative hypothesis. Our study also provides stronger evidence in support of hypothesis that *Delias* originated in the Australian region.

Delias and its sister genus *Leuciacria* diverged from each other on islands that now constitute part of New Guinea around 19.42 Mya (stem age), and the oldest extant lineage—the *ladas* group—diverged an estimated 15.67 Mya (*Delias* crown age; Figs. 1, S1-S3). The crown age inferred by Müller et al. (2013) was older at *ca.* 24 Mya, and their tree topology is also radically different from ours. These authors used two



(caption on next column)

Fig. 3. Geography of *Delias* distribution and dispersal. (A) The eight biogeographic regions in which *Delias* is currently distributed. These areas were designated for the BioGeoBEARS analyses, and the colored circles at the tree tips in Fig. 1 indicate where the species are distributed with reference to this map. Arrows indicate total dispersal counts between regions from 16 Mya to present. (B–D) Dispersal counts during different periods of *Delias* evolution as inferred by biogeographic stochastic mapping in BioGeoBEARS. Maps reflect the changing geography over time. Outlines indicate the approximate position of present-day land masses during that period, but only colored areas are thought to have been subaerial (not submerged). Arrows indicate movement from one biogeographic region to another; there is no significance to the precise placement of each arrow within a region. Maps are adapted from Hall (1998).

calibration points in their divergence dating analysis: the *Delias-Leucia cria* split from Braby et al. (2006) and the crown age of *Delias* taken from Braby and Pierce (2007). Our secondary calibration points came from the most comprehensive butterfly phylogeny to date (Kawahara et al., 2023). It was inferred using 391 genetic loci from *ca.* 2300 species representing >90 % of valid butterfly genera, and multiple calibration schemes with sensitivity analyses were conducted to arrive at the most plausible divergence estimates (de Jong, 2017; Sohn et al., 2015). Müller et al. (2013) sampled 131 species and sequenced up to three loci, though most samples had only a single DNA barcode. The monophyly of the genus was strongly supported, but the PP branch support values along the backbone ranged from 0.09 to 0.67. By increasing the taxon sample, sampling multiple individuals per species (including all of the data from that study), and sequencing many more genetic markers per sample, we have been able to arrive at a stable and reasonably well-supported topology that allows us to make stronger and more nuanced conclusions than previous molecular phylogenetic studies of *Delias* (Braby and Pierce, 2007; Morinaka et al., 2017; Morinaka et al., 2002; Müller et al., 2013; Ni et al., 2010; Sbordoni et al., 2018). For example, Müller et al. (2013) proposed that early diversification of *Delias* occurred in Wallacea and the Oriental region of Southeast Asia, but our more robust phylogeny contradicts this assertion.

Biogeographically, the group's evolutionary history can be divided into three phases. First, the two earliest diverging lineages, which we call the 'New Guinea Grade' (Fig. 1) diversified primarily within New Guinea. Second, around 14 Mya, the ancestor of a lineage that we call the 'Island Grade' dispersed out of New Guinea and diversified by repeated dispersals between the islands of the Indo-Australian Archipelago (including dispersal back to New Guinea) or diversification on the Asian mainland (Fig. 3). Finally, around 8.5 Mya, a lineage dispersed back to New Guinea and again diversified extensively on the island in what we have called the 'New Guinea Clade.'

The extraordinary species diversity of *Delias* arose relatively recently (Figs. 1, S1–S3), and several factors likely contributed to its diversification, namely: (1) the orogeny of New Guinea's Central Highlands within the past 5 Myr; (2) island-hopping around the Indo-Australian Archipelago in the Plio-Pleistocene when fluctuating sea levels affected the connectivity and dispersal distance among islands; (3) their unusual ecology as hyperparasites of hemiparasitic mistletoe host plants; and (4) the rapidity of wing pattern evolution in allopatrically distributed aposematic taxa, which could maintain differentiation upon secondary contact of formerly isolated populations (Lukhtanov et al., 2005). We discuss below each of these four factors below.

4.2. Orogeny of New Guinea Central Highlands

More than half of all *Delias* species live on the island of New Guinea. After the genus diverged from its sister genus, the group diversified in and around New Guinea (the New Guinea Grade, Fig. 1) before dispersing elsewhere around 13.7 Mya. At least six lineages subsequently dispersed back to New Guinea, including one that arrived around 8.6 Mya and diversified to become the New Guinea Clade, comprising nearly one-third of the species richness (Fig. 1). New Guinea

straddles the Australian and Pacific tectonic plates, and ongoing collision between the two contributes to the uplift of the Central Highlands, which reach >4800 m in elevation (Toussaint et al., 2021). Although subaerial land existed in the vicinity of New Guinea long before, the uplift of this cordillera is thought to have begun just 5 Mya, and much of the land north of the central mountain range is thought to have been ancient island arcs (on which species could have diversified in isolation) that were pushed into the northern margin of the Australian plate by tectonic forces (Hall, 2001; Hall, 2002; Hill and Hall, 2003). This orogenic event established diverse montane elevations and habitats, potentially creating climatic barriers that isolated populations. Although the uplift is ongoing, the process is believed to have been most rapid between 3 and 5 Mya. This period is highlighted with a ring of light blue shading in Fig. 1, and most of the diversification events on New Guinea occurred during this period or more recently. Multiple studies investigating the evolution of animals and plants on New Guinea conclude that this recent mountain-building is the leading cause of New Guinea's high biodiversity and endemism (Roycroft et al., 2022; Schweizer et al., 2015; Slavenko et al., 2020; Toussaint et al., 2014; Unmack et al., 2013). The many opportunities for isolation and divergence afforded by these mountains contributed both to its exceptionally rich flora—the most diverse of any island (Cámara-Leret et al., 2020)—as well as its human languages. The island's 820 languages represent about 10 % of the planet's total linguistic diversity (Kik et al., 2021).

4.3. Island hopping facilitated by eustasy

Many *Delias* species are endemic to islands or island groups, and most of these evolved in the the Island Grade (Fig. 1). Speciation is assumed to be allopatric (Futuyma and Mayer, 1980), and archipelagoes provide ample opportunities for isolation. This is particularly true of the Indo-Australian Archipelago, which comprises 20,000 islands, primarily in Indonesia and the Philippines. This region underwent dramatic changes throughout the Cenozoic, including volcanism, rapid movement of terranes, and eustasy driven in part by glaciation near the poles (Lohman et al., 2011). The Earth experienced many sea level fluctuations over the past 9 million years (Miller et al., 2005). Eustasy has driven diversification of multiple Southeast Asian taxa during this period (Guo et al., 2015; Li and Li, 2018; Roberts et al., 2011; Sholihah et al., 2021), and was ongoing throughout the Plio-Pleistocene. However, the minima became more pronounced around 3 Mya, with sea levels reaching 40 m below present. The amplitude of these repeated episodes of high and low sea level increased, with lows plummeting to 120 m below their current levels during the last glacial maximum *ca.* 20 Kya (Naish and Wilson, 2008; Woodruff, 2010). These pronounced changes exposed the shallow sea floor between adjacent islands, creating land bridges that provided opportunities for dispersal, followed by isolation when rising seas again separated the islands with seawater (Brown et al., 2013). Thus, "island-hopping," or dispersal from island to island and potentially followed by differentiation (founder-effect speciation), might have been facilitated by sea level change (Condamine et al., 2015; Toussaint and Balke, 2016). Studies investigating the influence of sea-level changes in Southeast Asia on diversification have found similar patterns in spiders, slipper orchids, and flying lizards (Guo et al., 2015; Li and Li, 2018; Reilly et al., 2022). These studies indicate an increase in diversification after 10 Mya. In Fig. 1, we note that many divergences within the Island Grade occur during this period of dramatic eustasy, which is highlighted with light green shading from 3 Mya to the present. This hypothesis is further supported by biogeographic stochastic mapping (Fig. 3), which demonstrates that most dispersal events happened in the past 4 Myr. We further note that addition of the *j* parameter modeling founder-effect speciation substantially increases the fit of various biogeographic models to the data (Tables 2 and S8). Even accounting for the possibility of artificially inflated parameter values (Ree and Sanmartín, 2018), the improvements to the log likelihoods are substantial (>10 %), and the process being modeled by the *j* parameter–dispersal followed by genetic differentiation–intuitively seems likely in the Indo-Australian Archipelago. Matzke (2022) argues that inclusion of this parameter is valid and tantamount to other recommended models. It seems that reciprocal dispersal ("island hopping") between (1) New Guinea and Wallacea; (2) New Guinea and Australia; (3) the Sunda shelf and Wallacea; and (4) the Sunda shelf and the Philippines, were particularly important for the diversification of *Delias*, particularly in the Island Grade. Counter to the assertions of Treadaway and Schroeder (2012) that the Philippines are primarily a biodiversity "sink" that accumulates taxa that dispersed from Sundaland, Wallacea, Taiwan, and New Guinea, we find that they are also a "source" of taxa that dispersed out of the archipelago to Sundaland and continental Asia (Fig. 3). In contrast, dispersal to Melanesian islands east of New Guinea seems to be a biogeographic dead end—few *Delias* lineages have dispersed out of that region (Fig. 3).

4.4. Delias are hyperparasites that feed on mistletoes

Herbivorous parasites like *Delias* butterfly larvae typically consume their hosts without killing them (Price, 1997). Nearly all *Delias* larvae feed on the leaves of mistletoes in the order Santalales, which are hemiparasites of other plants (Braby, 2006). There are only three known exceptions to this specialization on Santalales. Braby (2012) documented that *D. aestiva* in Australia feeds on the mangrove *Excoecaria ovalis* (Euphorbiaceae), Kitamura (1999) reared *D. henningia* on *Glochidion subfalcatum* (Euphorbiaceae) in Palawan, and Bao et al. (2014) reported that *D. pasithoe* consumes leaves of *Sonneratia caseolaris* and *S. apetala* (Lythraceae) in southern China. Mistletoes are especially diverse in New Guinea (Barlow, 1997), and, like other parasites, mistletoes do not colonize all possible hosts. They show varying degrees of host preferences (Milner et al., 2020). Thus, *Delias* and other mistletoe-feeding insects can be viewed as hyperparasites: parasites of parasites (Poelman et al., 2022). This dual layer of ecological specialization is likely to increase genetic divergence and genetic isolation-by-distance (Schär et al., 2018).

4.5. Aposematism and mimicry

Delias have all the hallmarks of being chemically defended, but no defensive compounds have yet been identified. The undersides of their wings are brightly colored, the larvae are gregarious, and they can be observed flying slowly in full sun, apparently unafraid of predators (Braby and Nishida, 2010; Braby and Trueman, 2006). Orr (1999) observed that *Delias* are avoided by predators in the field, and Morinaka and coauthors performed palatability trials with caged birds demonstrating that birds seldom consume them (Morinaka et al., 2019; Morinaka et al., 2018). Unpalatability seems to be signaled to non-naïve predators by red and yellow wing markings, at least in *D. hyparete* (Wee and Monteiro, 2017). *Delias* also participate in mimicry rings. For example, Brassicales-feeding *Prioneris sita* (Pieridae) is an excellent mimic of *Delias eucharis* in the Western Ghats of India (Dixey, 1920; Joshi et al., 2017; Nitin et al., 2018), and multiple *Delias* species comprise distinctive mimicry rings in Timor and Bali (Morinaka et al., 2018). Several day-flying moths, especially Zygaenidae, mimic various *Delias* species throughout East and Southeast Asia (Yen et al., 2005). Host plant-derived chemical defense is the underlying deterrent of most aposematic butterflies, but putative defensive compounds have yet to be identified in *Delias* butterflies or in the Santalales host plants they consume (Moghadamtousi et al., 2013; Muhammad et al., 2019; Rutz et al., 2022). Braby and Trueman (2006) postulated that *Delias* might synthesize noxious defensive compounds from innocuous, host plant-derived precursor molecules.

If *Delias* are indeed aposematic, as is widely presumed (Dixey, 1920; Parsons, 1998; Talbot, 1928–1937; Yata and Morishita, 1985), this, too, might contribute to their rapid diversification. Aposematic coloration and mimicry have been recognized for decades as key mechanisms promoting speciation in butterflies (Mallet and Joron, 1999). Basu and

colleagues (2023) recently demonstrated that the wing patterns of aposematic butterflies evolve more quickly than those of Batesian mimics and non-mimics. This accelerated rate of phenotypic evolution might have reduced the chance that populations differentiating in isolation during periods of high sea level would interbreed with other populations when they were reunited during periods of low sea level. Wing patterns are under sexual selection (Rossato et al., 2018), which might hasten differentiation in isolation; reproductive character displacement might also play a role in preventing hybridization between differentiating species (Brown and Wilson, 1956).

4.6. Sister species are (almost always) allopatric

It is striking that many land masses are home to multiple, co-existing endemic species, but—with the exception of New Guinea—virtually none of these are close relatives. For example, Australia has 10 *Delias* species. Only *D. aestiva* and *D. argenthona* are close relatives, as are *D. mysis* and *D. lara*, though neither pairs are sister species. This suggests that at least eight independent lineages dispersed to Australia from elsewhere. Seram is home to 10 *Delias*, but none of the nine we sampled are closely related (Fig. S1). With few exceptions, closely related *Delias* are distributed allopatrically, either on different islands, or (presumably) at different elevations on New Guinea (Fig. S1 provides the entire known distributions of each species we sampled, and Table S1 provides the distributions of the rest). Unfortunately, lack of elevation data for most species precluded a formal analysis. There are a few sister species pairs found on the same island that seem to contradict this general pattern. However, these may be cases of questionable taxonomy resulting in overly exuberant splitting: the co-occurring species may in fact be conspecific. *Delias magsadana* is endemic to Mt. Hamiguitan in Mindanao and is sister to *D. schoenigi*, which is found on several other mountains in Mindanao. Although our two samples of each species are reciprocally monophyletic (Fig. 2), the average pairwise COI distance between them is low: 0.42 % (±0.24 % SE) (Table S9 and S10). Other examples include *D. battana* and *D. shirozui* on Sulawesi (0.51 ± 0.28 %); *D. hidecoae* and *D. henningia* on Mindoro (0 %). For comparison, Hebert et al. (2003) found that congeneric Lepidoptera are on average 6.6 ± 2.2 % divergent, while Meier et al. (2008) measured 6.2 ± 2.7 % mean interspecific variability, and the smallest observed interspecific distances in Lepidoptera were 1.9 ± 2.9 %. However, in reviewing more than a decade of DNA barcoding results from a large, tropical insect fauna, Janzen and Hallwachs (2016) note several examples of shallow (0.1–1.5 %) COI barcode distances between morphologically distinctive sympatric species, and the examples they discuss generally involve closely related species in different mimicry complexes.

We do not believe that taxonomic decisions should be made solely on genetic divergence at a single locus, but COI genetic distances can be invaluable for integrative taxonomic approaches (Riedel et al., 2013), particularly for mimetic taxa like *Delias* that can rapidly evolve convergent or divergent wing patterns (Basu et al., 2023; Morinaka et al., 2018). The 25 non-monophyletic species (Figs. 2 and S3) and 146 interspecific COI distances smaller than 2 % (Table S9 and S10) that we found, together with similar findings in previous studies (Morinaka et al., 2017; Morinaka et al., 2002), suggests that a holistic re-appraisal of *Delias* species delimitation is warranted. If these low, interspecific COI distances are indicative of truly conspecific taxa that should be synonymized, the species richness of the genus would decrease, the number of endemic species would decrease, and the magnitude of our inferred diversification rate shifts would change.

It is likely that closely related species on the island of New Guinea are also allopatric, but there are insufficient data to quantify this. Most species inhabit cool, montane forests with temperate climates at tropical latitudes (Braby and Pierce, 2007). In New Guinea, few species live below 1200 m in elevation (Parsons, 1998; Roepke, 1955; van Mastrigt, 2001). Most live between 1600 and 2000 m with some extending to 3600 m (Braby and Pierce, 2007; Parsons, 1998). Most specimens from New Guinea lack elevation and GPS coordinate collection data, which makes it challenging to evaluate this hypothesis rigorously. However, there are several examples with good data. *Delias discus*, for example, can be sampled from elevation as low as 600 m, while *D. walshae* in the same species group is found as high as 1800 m (Yagishita et al., 1993). Morinaka et al. (2001) documented co-existing *Delias* species at six sites in New Guinea. Inspection of the phylogenetic position of these syntopic species suggests that they are rarely if ever close relatives. In addition to elevational differences, the complex geological history of New Guinea means that the north, Central Highlands, and south of the island have different origins and ages. Thus, lineages distributed in different parts of New Guinea likely experienced different selective pressures and genetic drift in isolation, leading to high differentiation on the island (Toussaint et al., 2014; Toussaint et al., 2021).

5. Conclusions

The broad- and fine-scale topology of our tree differs markedly from those of Müller et al. (2013) and Braby and Pierce (2007), and our phylogeny is more robustly supported. Further, our tree does not have polytomies above the species level that complicate inferences about species group membership or biogeographic inference. Although the inferred relationships among most species groups are congruent in our BI and ML trees, the two trees don't agree on the position of the *aganippe* group, which is monophyletic and monotypic as first suggested by Ford (1942). Our 14 loci are unable to resolve the true position of *D. aganippe*; genome-scale data might be helpful in resolving its evolutionary affinities. Dispersal between islands followed by differentiation, founder-effect speciation, and the orogeny of the Central Highlands of New Guinea, have played important roles in the diversification of this group. In addition, the presumed aposematism and mimicry of *Delias*, as well as their hyperparasitic lifestyle as herbivores of plant hemiparasites, might have contributed to their rapid divergence.

6. Data statement

NCBI BioProject, BioSample, and GenBank accession numbers can be found in Table S4.

CRediT authorship contribution statement

Weijun Liang: Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Renato Nunes:** Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Jing V. Leong:** Formal analysis, Writing – original draft, Writing – review & editing. **Ana Paula S. Carvalho:** Formal analysis, Writing – review & editing. **Chris J. Müller:** Resources, Writing – review & editing. **Michael F. Braby:** Resources, Writing – review & editing. **Olivier Pequin:** Resources, Writing – review & editing. **Sugihiko Hoshizaki:** Resources, Writing – review & editing. **Sadaharu Morinaka:** Resources, Writing – review & editing. **Djunijanti Peggie:** Resources, Writing – review & editing. **Jade Aster T. Badon:** Resources, Writing – review & editing. **Alma B. Mohagan:** Resources, Writing – review & editing. **Ethan Beaver:** Resources, Writing – review & editing. **Yu-Feng Hsu:** Resources, Writing – review & editing. **Yutaka Inayoshi:** Resources, Writing – review & editing. **Alexander Monastyrskii:** Resources, Writing – review & editing. **Petr Vlasanek:** Resources, Writing – review & editing. **Emmanuel F.A. Toussaint:** Formal analysis, Writing – review & editing. **Hugo A. Benítez:** Formal analysis, Writing – review & editing. **Akito Y. Kawahara:** Funding acquisition, Resources, Writing – review & editing. **Naomi E. Pierce:** Funding acquisition, Resources, Writing – review & editing. **David J. Lohman:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We are grateful to Danny Burk (deceased), Jacques Lamy, and Robert Siby for providing tissues of rare species, Chris Davenport for providing pictures of specimens in his collection and commenting on the manuscript, Thang Nguyen for help with figure preparation, and Yi-Kai Tea for permission to use his photographs in the graphical abstract. In addition, we thank Y-Lan Nguyen and Kelly Dexter for assisting with lab work, Caroline Storer for bioinformatic processing, and Ana C. Carnaval for comments on a previous version of this paper. This work was funded by US NSF grants to AYK (DEB-1541500), DJL (DEB-1541557), and NEP (DEB-1541560). A Fulbright ASEAN Research Award to DJL and grants 9285-13 and WW-227R-17 from the National Geographic Society to DJL funded field work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2024.108022.

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