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Title

Biogeographic patterns and diversification dynamics of the genus Cardiodactylus Saussure (Orthoptera, Grylloidea, Eneopterinae) in Southeast Asia

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Running title: Biogeography of Cardiodactylus crickets
Abstract
Southeast Asia harbors an extraordinary species richness and endemism. While only covering 4% of the Earth’s landmass, this region includes four of the planet’s 34 biodiversity hotspots. Its complex geological history generated a megadiverse and highly endemic biota, attracting a lot of attention, especially in the field of island biogeography. Here we used the cricket genus *Cardiodactylus* as a model system to study biogeographic patterns in Southeast Asia. We carried out molecular analyses to: (1) infer phylogenetic relationships based on five mitochondrial and four nuclear markers, (2) estimate divergence times and infer biogeographical ancestral areas, (3) depict colonization routes, and summarize emigration and immigration events, as well as *in situ* diversification, and (4) determine whether shifts in species diversification occurred during the course of *Cardiodactylus* evolution. Our results support the monophyly of the genus and of one of its species groups. Dating and biogeographical analyses suggest that *Cardiodactylus* originated in the Southwest Pacific during the Middle Eocene. Our reconstructions indicate that Southeast Asia was independently colonized twice during the Early Miocene (ca. 19-16 Million years ago), and once during the Middle Miocene (ca. 13 Million years ago), with New Guinea acting as a corridor allowing westward dispersal through four different passageways: Sulawesi, the Philippines, Java and the Lesser Sunda Islands. Sulawesi also served as a diversification hub for *Cardiodactylus* through a combination of high immigration and *in situ* diversification events, which can be accounted for by the complex geological history of the Wallacea region.

Keywords
Biogeography; climate change; crickets; diversification analyses; geological changes; molecular dating
1. Introduction

Southeast Asia (SEA) is considered as one of the most geologically dynamic regions of the planet (Lohman et al., 2011). It aggregates four major biodiversity hotspots (de Bruyn et al., 2014; Mittermeier et al., 2004; Zachos and Habel, 2011), which are divided by sharp, yet porous, biogeographic boundaries (Hearty et al., 2007; Morley et al., 2012; Wallace, 1860). The complex geological history of SEA generated a megadiverse and highly endemic biota that has attracted a lot of attention, especially in the field of island biogeography (Condamine et al., 2013, 2015; Hall, 2009a; Lohman et al., 2011; Metcalfe, 2006; Woodruff, 2010). In SEA, dynamic geological and climatic histories acted together to generate the world’s largest island complex, in which the spatial distribution of terrestrial habitats has been altered extensively through time (Bird et al., 2005; Hall, 1996, 2009a, 2011; Hall and Sevastjanova, 2012; Heaney, 1991; Metcalfe, 2006; Voris, 2000; Zahirovic et al., 2014). Volcanic uplifts and repeated sea-level fluctuations also promoted species diversification by providing countless opportunities for allopatric speciation (Heaney, 2000; Steppan et al., 2003; Jansa et al., 2006; Outlaw and Voelker, 2008). The interplay between the movement of tectonic plates, oscillations in the Earth’s orbit, and the variable configuration of landmasses and ocean currents also affected the climate of SEA (Morley, 2012). As a result, the vegetation and the distribution of habitats of SEA were profoundly modified through time (Heaney, 1991). Tropical rainforest in SEA greatly expanded during the Paleogene Period (66.0-23.0 Million years ago (Ma)) and the beginning of the Neogene Period, due to warmer temperatures and more humid climates. Tropical rainforests reached a peak during the mid-Miocene Climatic Optimum (MCO; 17-15 Ma), when their distribution extended further north to southern China and Japan (Heaney, 1991; Morley, 2012; Zachos et al., 2001). It is not until the Late Miocene and Early Pliocene that tropical rainforests started to decrease in range as a result of global cooling (Hall, 2012; Zachos et al., 2001). Lower sea levels, cooler temperatures, and modified rainfall patterns related with the development of continental glaciers during the Pleistocene (2.6-0.01 Ma) also had a great impact on SEA vegetation setting (Heaney, 1991). Studies of fossil pollen records from the Last Glacial Maximum (20,000 years ago)
indicate that SEA vegetation differed substantially from that of today, being characterized by an increase in the extent of montane vegetation and savannah, and by the presence of a continuous belt of evergreen rainforests across Sundaland (Bird et al., 2005). During the Last Glacial Period (110,000-11,700 years ago), short warmer interglacial periods also resulted in raises of the global sea level, which led to the fragmentation of some parts of the Sundaland into islands and peninsulas; for instance, the Thai-Malay Peninsula, Borneo, Sumatra and Java were separated from each other every time the sea level rose.

The complex geological and climate history and the fragmented island habitats have raised many questions on the origins of the current biota of SEA. In a comprehensive study, de Bruyn et al. (2014) reviewed previous biogeographical works by conducting meta-analyses of geological, climatic and biological data. Based on inferences of colonization routes and ancestral areas derived from meta-analyses of phylogenetic data, they inferred that Borneo and Indochina acted as major evolutionary hotspots during the Cenozoic. One of the reasons invoked is the length of their emergent histories (more than 80 million years), which surpasses by far those of other regions in SEA. De Bruyn et al. (2014) also found out that within-area diversification (in situ diversification) and subsequent emigration played a major role in Borneo and Indochina, especially during the course of the Neogene and Quaternary sea-level fluctuations.

To investigate biogeographic and species diversification patterns in SEA, we use a species-rich clade of crickets from the subfamily Eneopterinae, the genus *Cardiodactylus* Saussure, as a model system. Eneopterinae crickets are mostly distributed in tropical areas (Vicente et al., 2017) and are characterized by a diversity of traits in relation with acoustic communication (e.g., Robillard et al., 2007, 2013; ter Hofstede et al., 2015). With 82 known species, *Cardiodactylus* is currently the most speciose eneopterine genus. It is also the most widespread one, as its distribution runs from Japan (northern Ryukyu Islands), to the coasts of Southeast Asia, Northern Australia and the archipelagos of the Western Pacific across the Caroline Islands, Fiji, Indonesia, New Caledonia, Palau, Papua New Guinea, the Philippines, the Samoan Islands, the Solomon Islands, the Mariana Islands, Tonga, Vanuatu and Wallis
The genus is subdivided in two species groups, *Efordi* (22 known species) and *Novaeguineae* (60 known species), which show contrasted patterns of geographical distributions. Only one species of the *Efordi* group is distributed in SEA; the other species are distributed in New Guinea and in archipelagoes of the Southwest Pacific. In contrast, the *Novaeguineae* species group has a wider distribution, and is well diversified in SEA (35 species are found in SEA: Dong and Robillard, 2016; Robillard et al., 2014). Interestingly, the distribution map of the *Novaeguineae* group indicates that species richness is inconsistent with landmass sizes (see details in Figure 1). For example, only one species occurs in the northern part of Indochina (*Cardiodactylus guttulus*, distributed from Japan to Northern Vietnam), while four species are endemic to Sulawesi. Some species are not endemic to a single island; for example, *C. empagatao* is found in the Philippines and Sulawesi, and *C. borneoe* is widely distributed in Borneo and in the Thai-Malay Peninsula. Disentangling the origin of such diverse distribution patterns thus calls for the need of a thorough biogeographical study of the genus.

According to the study of Vicente et al. (2017) on Eneopterinae the genus *Cardiodactylus* did not originate in SEA but in the Southwest Pacific; however, this inference was potentially biased by the settings of the analysis in terms of time slices, and by the fact that it relied on a sparse sampling for the genus (only six *Cardiodactylus* species were sampled). Here, we use a more comprehensive sampling (41 *Cardiodactylus* species) for the genus and more appropriate time slices to infer the biogeographic patterns and diversification dynamics of the genus using a time-calibrated species tree. This allows us to assess with more precision the dynamics of diversification of the genus, and to determine whether Borneo and Indochina played a major role in its diversification.

2. Materials and methods

2.1. Taxon sampling

The taxon sampling of *Cardiodactylus* is focused on species distributed in SEA, but also includes representatives of the whole distribution and taxonomic diversity of the genus. In
this study, we sampled 113 individuals representing 41 species of *Cardiodactylus* crickets, including 28 species from SEA and 13 species from New Guinea and Southwest Pacific archipelagoes (New Caledonia, Solomon Islands and Vanuatu). For outgroup selection, we referred to a previous study (Anso et al., 2016), and selected 22 species representing all five tribes of the Eneopterinae subfamily, as well as two more distant species belonging to the subfamily Gryllinae. Detailed information on specimens is presented in Appendix S1.

Most specimens were collected during recent fieldworks and through collaborative works in several countries in SEA. In addition, some specimens used in the current study were obtained from the following institutions: the ‘Muséum d’Histoire Naturelle de Genève’ (MHNG), the ‘Muséum National d’Histoire Naturelle, Paris’ (MNHN), the ‘Museum Zoologicum Bogorise, Bogor’ (MZB), the ‘Nationale Natuurhistorisch Museum, Leiden’ (RMNH), the ‘Natural History Museum, London’ (BMNH), the ‘Naturhistorisches Museum, Vienna’ (NHMW), the ‘Royal Belgian Institute of Natural sciences, Brussels’ (RBINS), and the ‘Zoological Institute, Russian Academy of Sciences, Saint Petersburg’ (ZIN).

### 2.2. DNA extraction, amplification and sequencing

The molecular work was performed at the ‘Service de Systématique Moléculaire’ of the MNHN. Whole genomic DNA was extracted from the median/hind femora of dried or alcohol-preserved specimens using the NucleoSpin® 96 Tissue Kit (Macherey-Nagel, Germany) and an automatic pipetting robot Eppendorf epMotion® 5075 TMX. Five mitochondrial markers and four nuclear markers used in previous phylogenetic studies on crickets (Anso et al., 2016; Chintauan-Marquier et al., 2016; Nattier et al., 2011, 2012; Robillard and Desutter-Grandcolas, 2006) were amplified and sequenced. Mitochondrial markers were partial fragments of two non-protein coding (12S ribosomal RNA (12S), 16S ribosomal RNA (16S)), and three protein-coding, (cytochrome c oxidase subunit I (COI), cytochrome c oxidase subunit II (COII) and cytochrome b (Cytb)) genes. Nuclear markers included partial fragments of elongation factor 1 alpha (EF1a), histone H3 (H3), 18S ribosomal subunit (18S) and 28S ribosomal subunit (28S). The amplified fragment of EF1a consisted of both protein-
coding and non-protein coding regions whereas the amplified fragment of H3 only consisted of protein-coding regions. Whenever possible, we obtained molecular data from the same previous voucher specimens. We used the primers and settings detailed in Anso et al. (2016), Nattier et al. (2011) and Chintauan-Marquier et al. (2016). All sequences obtained in this study were cleaned, checked for sequencing errors and pseudogenes (through BLAST searches, DNA sequences and amino acid translation alignments and inference of gene trees), and deposited in GenBank (see details in Appendix S1). The COI sequences for all sequenced specimens of *Cardiodactylus borneoe* were discarded because of suspicion of pseudogenes. The complete combined dataset consisted of 4,111 aligned base pairs (bp) for 145 terminals: 528 bp for 16S, 419 bp for 12S, 706 bp for COI, 340 bp for COII, 345 bp for Cytb, 653 bp for 18S, 375 bp for 28S, 327 bp for H3 and 405 bp for EF1a.

### 2.3. Phylogenetic analyses

To check for possible contaminations and artifacts, preliminary phylogenetic analyses were carried out for each marker using the IQ-TREE web server (http://iqtree.cibiv.univie.ac.at/; Trifinopoulos et al., 2016) (see the resulting gene trees in Appendix S5). Then the aligned sequences of all nine markers were concatenated in Geneious R8.1.4 (Biomatters Ltd., New Zealand, www.geneious.com).

The concatenated dataset was then analyzed using Bayesian inference (BI) and maximum likelihood (ML). For both BI and ML we used PartitionFinder V2.1.1 (Lanfear et al., 2017) to determine best-fit partitioning schemes and the associated substitution models. One partition was specified for each of the non-protein coding genes (12S, 16S, 18S and 28S) and one partition per codon for the protein-coding genes (COI, COII, Cytb and H3), with the exception of EF1a which included several protein-coding and non-protein coding regions. For the latter we only used one partition to avoid specifying too many small partitions for the protein-coding and non-protein coding regions. PartitionFinder analyses were further carried out using the default ‘greedy’ algorithm option and either the ‘mrbayes’ or ‘raxml’ set of models (for BI and ML analyses, respectively); we also used the ‘linked branch lengths’
option, in order to limit the risk of overparameterization by lowering the number of inferred partitions. The Bayesian information criterion (BIC) was preferentially used to compare partitioning schemes and substitution models following Ripplinger and Sullivan (2008).

Bayesian inference analyses were performed with MrBayes 3.2.6 (Ronquist et al., 2012) whereas ML analyses were performed with RAxML 8.2.8 (Stamatakis, 2014) and IQ-TREE 1.6.2 (Nguyen et al., 2015). All corresponding analyses were performed using the CIPRES Science Gateway 3.3 (Miller et al., 2015).

For ML analyses best-scoring trees were obtained using heuristic searches relying on 100 random-addition replicates. Clade support was assessed using non-parametric bootstrap (for both RAxML and IQ-TREE analyses); for each analysis 1,000 bootstrap replicates were conducted. Nodes supported by bootstrap support values (BS) ≥ 70% were considered strongly supported following Hillis and Bull (1993).

For BI analyses we conducted two independent runs with eight Markov chain Monte Carlo (MCMC): one cold and seven incrementally heated that ran for 50 million generations with trees sampled every 1,000 generations. We used a conservative burn-in of 12.5 million generations per run after checking for stability on the log-likelihood curves and the split-frequencies of the runs in Tracer v.1.7 (Rambaut et al., 2014). Support of nodes for MrBayes analyses was provided by clade posterior probabilities (PP) as directly estimated from the majority-rule consensus topology. A clade with a PP value higher than 0.95 was considered as well supported following Erixon et al. (2003). Whenever a Cardiodactylus species (for which multiple specimens were sequenced) or a specific taxonomic group of interest was recovered paraphyletic, we used Bayes factors (BF) to assess whether there was statistical support for their non-monophyly. To do so, specific analyses (in which taxa of interest are constrained to be monophyletic) were carried out using MrBayes.

2.4. Divergence time estimation

We generated a species-level dataset (with one specimen per sampled Cardiodactylus species; see details in Appendix S1) to properly conduct dating and all subsequent analyses
(i.e. historical biogeography and diversification analyses). Divergence times were estimated using Bayesian relaxed clocks as implemented in BEAST 1.8.4 (Drummond et al., 2012). The partitions/clocks and substitution models were selected under PartitionFinder 2.1.1 following the settings presented above but with the 'beast' set of models (see details in Table 1). We were not able to fully implement a two steps strategy recommended by several authors (e.g., see Foster and Ho, 2017). The first step corresponds to a PartitionFinder analysis with the partition-rich ‘linked branch lengths’ option, to be followed by the use of the ‘ClockstaR’ R package (Duchêne et al., 2014), which requires having no missing gene fragments in the dataset; the latter step is expected to reduce the number of clocks in molecular dating procedures (hence limiting the risk of overparameterization). For comparison purpose, we nonetheless decided to conduct BEAST analyses with both options (number of partitions/clocks inferred with either the ‘linked branch lengths’ or the ‘unlinked branch lengths’ option). BEAST analyses were performed on the CIPRES Science Gateway using BEAGLE to improve and speed up the likelihood calculation (Ayres et al., 2012; Miller et al., 2015). For each clock model/partitioning scheme an uncorrelated lognormal relaxed clock was implemented. The Tree Model was set to a birth-death speciation process (Gernhard, 2008) to better account for extinct and missing lineages. The ucl.d.mean prior of each clock model was set to an uninformative interval (0.0001-1.0) with a uniform prior distribution.

Based on the available worldwide biogeographical framework of Eneopterinae crickets (Vicente et al., 2017), three secondary calibration points were enforced using normal distributions centered on previously estimated median ages: (1) the node for the most recent common ancestor (MRCA) of Cardiodactylus was assigned an interval of 33.60-55.19 Ma (normalPrior mean="42.6" stdev="6.0"), (2) the node for the MRCA of the Novaeguineae species group was assigned an interval of 23.32-39.73 Ma (normalPrior mean="30.0" stdev="6.0"), and (3) the node for the MRCA of C. guttulus, C. oeroe, C. tankara and C. singapura was assigned an interval of 17.83-31.17 Ma (normalPrior mean="23.4" stdev="6.0").
BEAST analyses consisted of 50 million generations of MCMC with the parameters and trees sampled every 1,000 generations. A burn-in of 25% was applied after checking the log-likelihood curves. Trees obtained from distinct analyses were combined using LogCombiner v1.8.4 (http://beast.bio.ed.ac.uk/). The maximum credibility tree, median ages and their 95% highest posterior density (HPD) were generated with TreeAnnotator v1.8.4 (https://github.com/beast-dev/beast-mcmc/releases/tag/v1.8.4).

2.5. Ancestral area estimation

The package BioGeoBEARS (Matzke, 2014) implemented in R was used to infer the biogeographical history of *Cardiodactylus* crickets across SEA. The dispersal-extinction-cladogenesis (DEC; Ree and Smith, 2008), dispersal-vicariance analysis (DIVA; Ronquist, 1997; herein DIVALIKE) and Bayesian Analysis of Biogeography (BayArea, Landis et al., 2013; herein BAYAREALIKE) models were used to estimate ancestral areas. Because of concerns with its statistical validity (Ree and Sanmartín, 2018) we did not use the +J model of Matzke (2014) in our analyses. The analyses were conducted with the maximum clade credibility (MCC) tree inferred under BEAST. The geographical distribution of each species was estimated based on fieldwork data, extant literature, and information provided by museum specimens (see details in Appendix S1). Twelve operational areas were defined (see details in Appendix S2) based on the distribution ranges of extant *Cardiodactylus* crickets (Robillard et al., 2014): Indochina (A), Thai-Malay Peninsula (B), Sumatra (C), the Philippines (minus Palawan) (D), Palawan (E), Borneo (F), Java (G), Sulawesi (H), Lesser Sunda Islands (I), Moluccas (J), New Guinea (K) and the archipelagoes in the Southwest Pacific (L).

In previous studies (de Bruyn et al., 2014; Hall, 2011; Morley, 2012), it has been shown that three major Cenozoic collision events had a great influence on the current archipelago setting: (1) the India-Asia collision at ca. 45 Ma facilitated the isolation of West Sulawesi from Sundaland, (2) the Australia-Asia collision at ca. 25 Ma generated the Bird’s Head region of New Guinea, and (3) the collision of the Sula Spur promontory with the
Southeast Asian margin in Sulawesi ca. 15 Ma formed the region now known as Wallacea (Hall, 2009a). To account for these major geological events, three distinct time slices were enforced in our time-stratified biogeographical model; the first time slice runs from 45.0 to 25.0 Ma, the second one from 25.0 to 15.0 Ma and the last one from 15.0 Ma to the present (Hall, 2013; Hall and Sevastjanova, 2012; see more details in Appendix S2). For each time slice, we constructed a basal matrix of scaling factors (multipliers) (0, 0.01, 0.1, 0.25, 0.50, 0.75, 1.0) for the dispersal rates between areas according to their geographical position and changes in sea level. Alternative and more simplified sets of multipliers were also tested (0, 0.01, 0.1, 0.25, 1.0; 0, 0.01, 0.1, 0.50, 1.0; and 0, 0.01, 0.1, 0.75, 1.0). Analyses were repeated with two, three or four maximum ancestral areas (parameter max_range_size in BioGeoBEARS). Therefore, a total of 36 processes (four distinct multipliers sets, three speciation models (DEC, DIVALIKE and BAYAREALIKE), three distinct maximum range sizes), were implemented to estimate ancestral areas (the details of these processes are listed in Appendix S2 and S3).

Finally, to ensure that the time framework imposed by the secondary calibration does not constrain the biogeographical results through strong constraint on allowed areas and dispersal multipliers, we implemented nine additional processes without time slices (unstratified analyses) using the basal set of multipliers with three speciation models and three distinct maximum ancestral areas (see Appendix S3).

2.6. Colonization events and in situ diversification

As mentioned above, only one member of the *Efordi* species group is distributed in SEA; in contrast, the *Novaeguineae* species group is more widely distributed, including in SEA, New Guinea and the Southwest Pacific. Therefore, we study colonization events and in situ diversification events of *Cardiodactylus* in SEA by focusing on the *Novaeguineae* species group. Within this clade, major colonization routes were inferred for each time slice. Emigration and immigration events for each area were analyzed by summarizing colonization
events using SPPS Statistics 22 (SPSS Inc.). We also followed de Bruyn et al. (2014) to estimate *in situ* diversification events using SPPS Statistics v.22 (SPSS Inc.).

2.7. Diversification analyses

Bayesian Analysis of Macroevolutionary Mixtures 2.5 (BAMM; Rabosky et al., 2013) was used: (1) to estimate rates of speciation ($\lambda$), extinction ($\mu$), and net diversification ($\gamma$) either for all *Cardiodactylus* species or only for the SEA species belonging to the *Novaeguineae* species group (which constitutes a monophyletic group), (2) to conduct rate-through-time analysis of these rates, and (3) to identify and visualize shifts in species rates across the *Cardiodactylus* phylogeny. BAMM accounts for non-random and incomplete taxon sampling in the phylogenetic trees by allowing all non-sampled species to be associated with a particular tip or more inclusive clade. Species numbers were obtained from the ‘Orthoptera species file online’ website (Cigliano et al., 2017) and published sources.

Priors for BAMM were generated using the R package BAMMtools v.2.5.0 (Rabosky et al., 2014a,b) by providing the BEAST maximum clade credibility tree and the total species numbers across *Cardiodactylus* (see Appendix S4). We used a gradient of prior values ranging from 0.1 to 1.0 to test the sensitivity to the prior, to account for the recent debate on the reliability of BAMM estimates (Moore et al., 2016, but see Rabosky et al., 2017). We ran BAMM by setting four independent MCMC running for 50 million generations and sampled every 50,000 generations; convergence was assessed by computing ESS of log likelihoods. After removing 10% of trees as burn-in, the BAMM output were analyzed with employing BAMMtools package in R and the 95% credible rate shift configurations was estimated using Bayes factors. The best shift configuration with the highest maximum a posteriori probability was estimated in this analysis. Rates-through-time plots were generated for speciation ($\lambda$), extinction ($\mu$) and net diversification ($\gamma$), either for all *Cardiodactylus* species or only for the SEA species. All visualization was performed using R and C code available through the R package BAMMtools.
3. Results

3.1. Data collection and phylogenetic analyses

The best-fit partition schemes and substitution models used in BI and ML analyses of the combined dataset are shown in Table 1. Both BI and ML phylogenetic analyses yielded robust and largely congruent topologies (Figure 2; see also Appendix S6 for original outputs of both BI and ML analyses); it is especially the case for the results of RAxML analyses which are presented in Figure 2 (90% of nodes within Cardiodactylus supported by BV ≥ 70%). In all analyses the subfamily Eneopterinae and the genus Cardiodactylus are recovered as monophyletic with a high support (BS_{RAxML} of 100%, PP of 1.0 and BS_{IQ-TREE} of 100% and 76%, for Eneopterinae and Cardiodactylus, respectively). All Cardiodactylus species are also recovered as monophyletic, with the exception of C. floresiensis. However, additional analyses carried out under BI do not support the paraphyly of C. floresiensis: MCMC runs where C. floresiensis representatives are constrained to be monophyletic yield a harmonic mean estimate of -50151.29 versus -50150.18 for the unconstrained MCMC runs; hence the difference corresponds to a non-statistically significant B_F of 2.22 (B_F < 10; see Kass and Raftery, 1995).

Within Cardiodactylus, the monophyly of the Novaeguineae species group is strongly supported in both analyses (BS_{RAxML/IQ-TREE} of 100%, PP of 1.0). By contrast, the Efordi species group is recovered as paraphyletic in all analyses due to the placement of C. javare and C. enkraussi. Cardiodactylus javare is found as sister to the Novaeguineae species group, forming a well-supported clade (BS_{RAxML} of 97%, BS_{IQ-TREE} of 78%, PP of 1.0). Both RAxML and MrBayes analyses recover Cardiodactylus enkraussi as sister to the clade (C. javare + Novaeguineae species group), but its position is less robust (BS_{RAxML} of 85%, PP of 0.73); with IQ-TREE C. enkraussi is grouped with C. niugini, this clade being the sister group of C. javare + Novaeguineae species group, with a very weak support (BS_{IQ-TREE} of 34% and 24% for the two corresponding nodes). Both RAxML and MrBayes analyses indicate that the remaining species of the Efordi species group constitute a well-supported clade (BS_{RAxML} of 78% and PP of 0.96) whereas IQ-TREE analyses infer two distinct
lineages, due to the placement of *C. enkraussi* (see above). Additional analyses carried out under BI support the paraphyly of the *Efordi* species group: MCMC runs where members of the *Efordi* species group are constrained to be monophyletic yield a harmonic mean estimate of -50162.07 versus -50150.18 for the unconstrained MCMC runs. Hence the difference corresponds to a statistically significant $B_F$ of 21.68 ($B_F > 10$; see Kass and Raftery, 1995).

Within the *Novaeguineae* species group, *C. haddocki* and *C. novaeguineae* form a robust clade (BS$_{RAxML/QI\text{-TREE}}$ of 100%, PP of 1.0), sister to another well-supported clade (BS$_{RAxML}$ of 99%, BS$_{IQ\text{-TREE}}$ of 66%, PP of 1.0) comprising all the remaining species of the group. Within this clade, three species are the first lineages to branch off, sister to the remaining species of the group; these three species correspond to two species distributed in New Guinea (*C. lucus* and *C. maaia*) and one in the Western Pacific (*C. tankara*). The remaining members of the species group form a generally well-supported clade (BS$_{RAxML}$ of 76%, PP of 0.97; but BS$_{IQ\text{-TREE}}$ of only 18%), which splits into two main clades (hereby referred as clade 1 and clade 2 on Figure 2). Clade 1 is generally well supported (BS of 84%, PP of 1.0; but BS$_{IQ\text{-TREE}}$ of only 40%) and consists of lineages that are also well supported (see Figure 2 for details). Clade 2 is only moderately supported, with low BS (BS$_{RAxML}$ of 40%, BS$_{IQ\text{-TREE}}$ of 19%) and a moderate support under BI (PP of 0.91). Within clade 2, two main clades (clade 3 and clade 4) can be distinguished. All species belonging to the clade 4 are distributed in SEA, whereas only two species (*C. manus* and *C. quatei*) are not distributed in SEA in clade 3.

### 3.2. Divergence time estimation

BEAST analyses relying on the 11 partitions/clocks selected through the use of the ‘*linked branch lengths*’ option did not converge, as underlined by low ESS values (below 200) for 53 parameters. On the contrary BEAST analyses relying on the two partitions/clocks selected through the use of the ‘*unlinked branch lengths*’ option converged quickly, with all parameters showing ESS values $\geq 200$. As a result, we only present and discuss the results of the latter analyses in our study. The resulting median ages are presented in Figure 3 and
Age estimates for the genus *Cardiodactylus* suggest an origin in the Middle Eocene ca. 43.2 Ma (95% HPD: 33.47-52.93 Ma). The members of the *Efordi* species group form a monophyletic group, except *C. javarere*, which is recovered as sister to the *Novaeguineae* species group. Members of the *Efordi* species group apparently started their diversification in the Late Eocene about 41.0 Ma (95% HPD: 29.22-48.83 Ma). The lineage leading to *C. javarere* then diverged from the *Novaeguineae* species group ca. 39.1 Ma, while members of the *Novaeguineae* species group started diversifying during the Late Oligocene about 27.0 Ma (95% HPD: 20.39-33.67 Ma). The divergence time for the MRCA of *C. haddock* and *C. novaeguineae*, which are sister to the remaining members of the *Novaeguineae* species group, is inferred at ca. 8.4 Ma (95% HPD: 5.18-11.84 Ma), at the end of the Miocene. Most speciation events within the *Novaeguineae* species group happened during the Miocene (ca. 23.0-5.3 Ma). Only a few lineages appear to have diverged recently (less than 4 Ma).

### 3.3. Ancestral area estimation

DIVALIKE model shows higher statistical support over the DEC and BAYAREA models for all tested dispersal multiplier matrices (see more details in Appendix S3). Furthermore, the matrix of scaling factors involving five distinct rates (0, 0.01, 0.25, 0.5, 0.75, 1.0) implemented with a DIVALIKE model and a maximum range size of two areas was supported as the best-fit model over more simplified sets of multipliers and more allowed areas; the corresponding ancestral areas estimation is presented in Figure 3. Analyses without time slices (unstratified analyses) result in the same biogeographical pattern (see more details in Appendix S3) in SEA *Novaeguineae* species group, but it inferred an origin in New Guinea for the genus *Cardiodactylus* and for the *Efordi* species group. However, according to Hall’s work (2009, 2013), New Guinea only began to emerge about 25 Ma; therefore, a New Guinea origin of *Cardiodactylus* ca. 43 Ma is not compatible with geological evidences. The latter illustrates the importance of using stratified analyses to account for geological changes through time; hence for our study we only focus on the results inferred with the stratified
analysis relying on the inferred best-fit model (DIVALIKE model with five distinct rates and a maximum range size of two areas).

Ancestral areas estimation suggests an origin of Cardiodactylus in the Southwest Pacific during the Middle Eocene, followed by a complex and dynamic biogeographical history. Lineages belonging to the *Efordi* species group diverged earlier (ca. 40 Ma) than the *Novaeguineae* species group (ca. 27 Ma) and colonized New Guinea several times, twice independently, after 37.1 Myrs (*C. niugini*) and 39.1 Myrs (*C. javarera*), and twice independently after 22.5 Myrs (*C. busu* and *C. nobilis*).

The members of the *Novaeguineae* species group colonized New Guinea four times from the Southwest Pacific: twice at the end of the Oligocene (once after 24.0 Myrs (*C. lucus*)) and once ca. 22.1 Ma (main clade in SEA), and twice more recently, ca. 8.4 Ma for the clade made of (*C. haddocki + C. novaeguineae*). From New Guinea, Cardiodactylus independently colonized SEA three times: the first one linked New Guinea to SEA through the Philippines ca. 19.5 Ma; the second one through Sulawesi ca. 16.4 Ma; a third colonization of SEA from New Guinea occurred more recently, during the Middle Miocene, through Java and the Lesser Sunda Islands ca. 13 Ma.

Through the first passageway, *Cardiodactylus* colonized Palawan after 19 Myrs through the Philippines, then the Thai-Malay Peninsula and Borneo. *Cardiodactylus* colonized Indochina twice recently, once from the Thai-Malay Peninsula, ca. 4 Ma (*C. thailandia*) and once from the Philippines ca. 5 Ma (*C. guttulus*). Meanwhile a lineage from the Thai-Malay Peninsula dispersed to Borneo after 3.4 Myrs.

From the Philippines, *Cardiodactylus* also colonized the Moluccas (*C. halmahera*) after 17 Myrs, and recently dispersed to Sulawesi (*C. empagatao*). After colonizing Borneo ca. 15 Ma, the genus colonized Sumatra ca. 12 Ma and reached Java through Sumatra ca. 8 Ma.

3.4. Colonization routes, emigration / immigration events and in situ diversification
Colonization routes of the *Novaeguineae* species group are presented in Figure 4a. Before
the Miocene, as deduced from our biogeographical analyses, no colonization event
happened. During the Miocene, 10 distinct colonization routes are inferred; interestingly New
Guinea is recovered as a major biogeographical crossroad (four different routes are inferred,
to Java, Sulawesi, the Lesser Sunda Island and the Philippines), followed by the Philippines
(three routes), the Southwest Pacific (two routes), and Borneo and Sumatra (one route each).
Along these routes, colonization events from the Southwest Pacific to New Guinea happened
twice. During the Plio-Pleistocene eight colonization routes are identified: three depart from
the Philippines; two depart from New Guinea, and two from the Thai-Malay; and one goes
from the Southwest Pacific to New Guinea.

Estimated emigration and immigration events through time are presented in Figure 4b.
When summing the total numbers of events for each area, six areas only had immigration
events inferred (Indochina, Java, the Lesser Sunda Islands, Palawan, Sulawesi and the
Moluccas). The total number of inferred emigration events is higher than that of immigration
events for New Guinea, the Philippines, the Southwest Pacific and the Thai-Malay Peninsula,
while the opposite (more immigration than emigration events) is inferred only for Borneo.
Moreover, the total number of emigration and immigration events is at equilibrium only for
Sumatra.

*In situ* diversification events through time are presented in Figure 4c. When summing
the total numbers of events for each area, three areas (New Guinea, Sulawesi and the
Philippines) are associated with the highest number of *in situ* diversification events (four
events), followed by the Lesser Sunda Islands and the Thai-Malay Peninsula (three events),
Sumatra and the Southwest Pacific (two events) and Borneo (one event).

3.5. Diversification analyses
A poissonRatePrior of 0.5 was recovered as the best-fit prior by BAMMtools (see more
details in Appendix S10). Convergence of the MCMC chains in the BAMM analyses was
observed after discarding the burn-in period (ESS > 900 for both the number of shifts and log
likelihoods). The 95% credible set of rate shift configurations sampled with BAMM provides more support (probability of 0.36) for a scenario without shifts in diversification rates within Cardiodactylus (Figure 5); less supported scenarios (probabilities of 0.16, 0.17 and 0.17) inferred a single shift in diversification rates near the base of the Novaeguinae species group (the placement of the shift differs, as illustrated in Figure 5). BAMM analyses strongly support a diversity-dependent speciation process across Cardiodactylus with the following rates: (1) net diversification rate of 0.06 species/Myr (95% quantile=0.023-0.071), (2) speciation rate of 0.12 species/Myr (95% quantile=0.075-0.202), and (3) extinction rate of 0.06 species/Myr (95% quantile=0.003-0.170). Rate-through-time plots for the three corresponding rates are presented in Figure 6, for the whole genus and within the Novaeguineae species group. The resulting plots indicate that Cardiodactylus speciation and net diversification rates have decreased through time, with the exception of an increase in speciation and net diversification rates occurring from 20.0 to 15.0 Ma. By contrast, the inferred extinction rates are quite constant and relatively low. A similar trend was recovered in the Novaeguineae species group. For the whole genus, speciation and net diversification rates rised slowly with several fluctuations between the Late Oligocene (ca. 26 Ma) and the Middle Miocene (ca. 15 Ma) (Figure 6a). These tendencies are similar for the Novaeguineae species group, with a sharper peak during the Early Miocene (ca. 18-23 Ma) (Figure 6b).

4. Discussion

4.1. Phylogenetic relationships

Both BI and ML analyses recovered a similar placement of the genus Cardiodactylus within the subfamily Eneopterinae in the tribe Lebinthini (Figure 2), as in previous studies (Anso et al., 2016; Nattier et al., 2011; Robillard and Desutter-Grandcolas, 2004, 2006; Vicente et al., 2017). Within Cardiodactylus, we were able to assess the status of the two species groups defined by Otte (2007) on morphological grounds.
Our results clearly support the monophyly of the species group *Novaeguineae* and the paraphyly of the *Efordi* species group (-50150.18 versus -50162.0, $B_F$ of 21.78; $B_F$>$10$). The paraphyly of the latter can be accounted for by the placement of two species: *C. javarere* and *C. enkraussi*. When using $B_F$ we found out that the placement of *C. enkraussi* outside of the *Efordi* species group is not statistically supported (harmonic mean estimate of -50150.18 versus -50151.98, $B_F$ of 3.6; $B_F$<$10$); it is also the case for *C. javarere* (harmonic mean estimate of -50150.18 versus -50149.44; $B_F$ of 1.48, $B_F$<$10$). Further molecular analyses with a denser sampling will be necessary to reach a stable conclusion on the status of the *Efordi* species group. Within the *Novaeguineae* species group, our results strongly support a clade grouping *C. novaeguineae* and *C. haddocki* as the sister group of all remaining species of the group. When comparing results of BI and ML analyses, similar relationships are inferred within the species group, except for the positions of *C. manus* and *C. quatei*, perhaps as a consequence of missing taxa from New Guinea and the Southwest Pacific. Nevertheless, the species distributed in SEA are clearly nested within a clade including species from New Guinea and the Southwest Pacific.

### 4.2. Origin of Cardiodactylus in the Southwest Pacific

Our study estimated the divergence time and ancestral areas of *Cardiodactylus* by implementing secondary calibrations based on the study of Vicente et al. (2017), which inferred that *Cardiodactylus* diverged from its sister clade within the tribe Lebinthini in SEA. As a result, similar age estimates for the MRCA of *Cardiodactylus* were recovered: 43.2 Ma in our study vs. 42.57 Ma in the study of Vicente et al. (2017). Secondary calibrations may be a source of bias in dating procedures (Graur and Martin, 2004; Schenk, 2016); however, it is worth highlighting that another study (relying on a larger phylogenetic context) using a different set of secondary calibrations gave a similar age range for *Cardiodactylus* (Anso et al., 2016).
All DIVALIKE stratified analyses infer an origin for *Cardiodactylus* in the Southwest Pacific; it is also the case for all DEC stratified analyses and some of the BAYAREA stratified analyses. This result seems to conflict with the widely accepted assertion that less diverse island communities are easier to invade (Bellemain and Ricklefs, 2008). However, the global biogeographical history of the tribe Lebinthini, as inferred by Vicente et al. (2017), suggests that *Cardiodactylus* diverged from its sister clade in SEA before colonizing the islands of the Southwest Pacific during the Middle Eocene. During that time, the species richness in SEA was likely much higher than that of the Southwest Pacific. The genus probably first occurred in islands now under water, since many islands in this region had not emerged yet (e.g., the Solomon and Fiji Islands) or were just coral reef formations (i.e. New Caledonia; Neall and Trewick, 2008). In fact, the origin of *Cardiodactylus* in the Southwest Pacific and its recent recolonization of SEA support the “reverse colonization” hypothesis (from small Pacific islands back to continent) as presented in Bellemain and Ricklefs (2008). This hypothesis was recently supported by several studies of other insect clades, such as in *Polyura* butterflies (Toussaint and Balke, 2016) and *Camponotus* ants (Clouse et al., 2015), while it was not recovered for other clades (Economo et al., 2015). Our results consequently bring some new insights into the discussion of Pacific island biogeography and of the role of Pacific clades in contribution to the diversity of surrounding archipelagoes (e.g., Claridge et al., 2017). In the case of *Cardiodactylus*, additional studies with a denser sampling of the species distributed in the archipelagoes of the Southwest Pacific will be necessary to precise their origin in the Southwest Pacific. As a reminder, our conclusions are based on ca. 50% of the species of *Cardiodactylus* only. Consequently, some conclusions are likely to change as our knowledge on this genus will continue improving and be further implemented in future biogeographical studies.

4.3. New Guinea as a corridor between the Southwest Pacific and SEA

During the period ranging from its origin in the Middle Eocene to the collision between Australia and Asia (ca. 25 Ma), there is no evidence that *Cardiodactylus* colonized any area
other than New Guinea (Figure 3). Our results inferred colonization events from the Southwest Pacific to New Guinea after the emergence of the Bird’s Head region of New Guinea (ca. 25 Ma). New Guinea thus appeared to have been a significant corridor between the Southwest Pacific and SEA, even if this aspect of the biogeography of Cardiodactylus is likely not yet addressed with a sufficient taxonomic sampling.

Two independent colonization events of SEA from New Guinea are inferred before the emergence of the Wallacea (ca. 15 Ma), and a third colonization event occurred afterward immediately (ca. 13 Ma). This result is consistent with the dispersal route documented in flightless beetles, which crossed Lydekker’s line from New Guinea and reached the Moluccas ca. 5 Ma (Tanzler et al., 2016). Cardiodactylus initially departed from New Guinea and colonized SEA by crossing the Wallace line, which is a good example of faunal boundaries permeation between Wallace’s line and Lydekker’s line (Lohman et al., 2011). It was also found in other insect groups: Müller et al. (2013) inferred that colonization events happened several times between Wallacea and New Guinea in Pieridae butterflies; similarly, Kalkman et al. (2018) found that the Odonate family Argiolestidae colonized Sulawesi from the north of Australia.

4.4. Colonization routes from east to west in SEA and priority of adjacent area in colonization routes

Cardiodactylus colonized SEA three times independently from east to west across New Guinea, through four different passageways: the Philippines, Sulawesi, the Lesser Sunda Islands and Java.

The colonization of SEA through the Philippines occurred during the early Miocene (ca. 19 Ma), when the Philippines (minus Palawan), a true oceanic island archipelago, began to emerge, initially scattered along the margin of the Philippine Sea Plate (Yumul et al., 2004). From the Philippines, the genus rapidly dispersed to the rest of the region. It also colonized Sulawesi twice, first ca. 16.4 Ma, then recently as a range expansion of C. empagatao.
The colonization of SEA through Sulawesi ca. 16.4 Ma was followed by subsequent in situ diversification within this island. This is consistent with the “predominantly tectonic dispersal origin” of 20 taxa in Sulawesi, as shown by the review of Stelbrink et al. (2012) based on 27 animal datasets: in this study, the authors inferred that speciation on Sulawesi did not occur before the Miocene, which is consistent with geological evidence indicating an increase of landmasses along with more heterogeneous landscapes (Hall, 2009b).

During the Late Miocene, colonization events occurred less frequently and were only confined to adjacent areas: the Thai-Malay Peninsula / Indochina, Java / Sumatra, the Philippines / Indochina (Figure 3 and Figure 4a). However, the frequent transgressing events along the Wallace’s line (or the modified Huxley’s line) documented in the beetle genus Rhantus and the avian family Campephagidae (Lohman et al., 2011), were not found in Cardiodactylus. These results are consistent with the conclusions on flightless weevils (Tänzler et al., 2016), which showed that the Sunda Arc (region including Borneo, Java and Sumatra) could be a potential dispersal corridor between mainland SEA and Melanesia through its continuous chain of islands.

The study of de Bruyn et al. (2014) inferred that colonization events happened more frequently between adjacent areas than between distant ones. This conclusion is verified in our study, but it could however be tempered by the fact that the probabilities of transition amongst our areas were set proportionally to the distance between them.

4.5. Weak influence of recent sea level changes on Cardiodactylus diversification dynamics

The drastic changes of sea level during the Plio-Pleistocene have been considered of greater influence on species diversification in SEA, through the fragmentation of areas when the sea level rose and the increasing landmass area when the sea level decreased (Guo et al., 2015; Lohman et al., 2011). Interestingly, according to the results of BAMM analyses, net diversification rates of Cardiodactylus rose rapidly during the Miocene, and then decreased before the Plio-Pleistocene (Figure 6). Moreover, inferred colonization events during the Plio-
Pleistocene in SEA are far less common than expected. These recent events only happened from the Philippines to the Moluccas, Palawan and Sulawesi, and from the Thai-Malay Peninsula to Borneo and Indochina, but they did not generate any detectable diversification (Figures 3 and 4a). It may indicate that the recent changes of sea level and their consequences in terms of fragmentation of habitats were not sufficient to establish stable barriers between the populations, or that the flight abilities of the species prevent speciation to occur.

These results are consistent with the Thai-Malay Peninsula position as a biogeographic crossroad between Indochina and the Sundaic faunal regions (Borneo, Java and Sumatra; Lohman et al., 2011). One interesting point in our results is the absence of inferred immigration of *Cardiodactylus* in Java and Sumatra (Figure 4b in Plio-Pleistocene), which differs from the conclusion of de Bruyn et al. (2014), where these two areas are characterized by higher levels of immigration than emigration. This is related with the low diversity of the genus in these islands, which can in turn be linked with missing knowledge of the species distributed in large areas of Sumatra and Java, which could not be sampled.

4.6. Dynamics of diversification through the history of Cardiodactylus

Our diversification analysis indicates that there was no distinct rate shift within *Cardiodactylus* and that the speciation rate of the genus changed slowly through time (Figures 5 and 6). However, when we focus on the diversity in each area of SEA, each lineage of *Cardiodactylus* shows a contrasted history.

According to the meta-analysis implemented by de Bruyn et al. (2014), the diversity of SEA biota may have arisen through the accumulation of immigrants, by *in situ* diversification, or by a combination of the two. In our results (Figures 4b and 4c), the highest level of immigration occurred in Borneo, Indochina, Java, Moluccas and Sulawesi, and to a lesser extend in the remaining areas.
The areas are however characterized by significantly different levels of *in situ* diversification. There was no event of *in situ* diversification in Indochina, Palawan, Java and the Moluccas, and only one in Borneo. Sulawesi and the Philippines show the highest level of *in situ* diversification, followed by the Thai-Malay Peninsula and the Lesser Sunda Islands. The early colonization of Sulawesi, the Philippine and the Thai-Malay Peninsula from New Guinea and the fragmentation of these areas from the Miocene to the present day may explain that the levels of *in situ* diversification are higher compared with other areas. This result is consistent with the conclusions of de Bruyn et al. (2014), who showed that the level of *in situ* diversification in ancient areas (originating area) was higher than in others. However, the higher level of *in situ* diversification found in the Lesser Sunda Islands contrasts with this conclusion: this group of islands is relatively small and recent, since they emerged during the Middle Miocene. They partly come from microcontinental fragments sliced from Java or/and Australia, while some parts of these islands truly emerged from the ocean. During their history, connections and disconnections between the Lesser Sunda Islands were very common (Hall, 2009a) and this may have resulted in higher speciation rate. Linking the complex geological history in the Lesser Sunda Islands easily explains the species diversity found in this area, despite its recent age and small size. These results suggest that higher levels of species diversification can be driven by frequent connection and disconnection between two areas, at least in some parts of the genus distribution. However, we cannot exclude that this level of *in situ* diversification could partly be linked to a positive sampling bias, since extensive field work has been done recently in this archipelago, while other regions of SEA remain less sampled (Robillard et al., 2014). Similarly, the low level of *in situ* diversification estimated in large islands colonized almost as early as Sulawesi, such as Java and Borneo, could be explained by biases in taxonomic sampling in these areas.

To summarize, the species diversity of *Cardiodactylus* in SEA seemingly results from:

1. the accumulation of colonizers in Indochina, Palawan, Java and Moluccas, and
2. the accumulation of colonizers and *in situ* diversification in the Thai-Malay Peninsula, Sumatra, the Philippines, Borneo, Sulawesi and the Lesser Sunda Islands.
5. Conclusion

In summary, the historical biogeography of *Cardiodactylus* appears to be linked to the early geological history of SEA. After originating from the Southwest Pacific (diverging from its sister group among the Lebinthini tribe), *Cardiodactylus* lineages crossed the Lydekker’s line multiple times, but more rarely transgressed the Wallace’s line. SEA was colonized three times independently by members of the *Novaeguineae* species group and once by the *Efordi* species group. In addition, the New Guinea acted as a major colonization source of *Cardiodactylus* in SEA from east to west, while the Thai-Malay Peninsula served as an important corridor between Indochina and Borneo. In addition, Sulawesi served as a diversification hub for *Cardiodactylus* through a combination of high immigration and *in situ* diversification events.

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**Figure titles**

**Figure 1.** Distribution map of *Cardiodactylus* in Southeast Asia. In this study, we sampled 28 out of 35 *Cardiodactylus* species distributed in Southeast Asia. The sampled species are written in black (collecting localities in black circles), and species missing in the sampling are shown in grey. Map modified after Robillard et al. (2014).

**Figure 2.** Phylogeny of the genus *Cardiodactylus* inferred from Maximum likelihood (ML) and Bayesian inference (BI). Values on nodes indicate branch support; the first two values correspond to non-parametric bootstrap values (BV from RAxML analyses first, then BV from IQ-TREE analyses) whereas the third value corresponds to BI posterior probabilities (PP). Asterisks are used to indicate maximum support (100% for BV and 1.0 for PP). Signs ‘*’ indicate topological incongruences between analyses, the topology inferred with RAxML being represented. The bold red circles with letters indicate the secondary calibration points used in the dating analyses; the circled numbers highlight clades discussed in the text.

**Figure 3.** Reconstruction of historical biogeography for *Cardiodactylus* using a stratified dispersal-vicariance analysis (DIVALIKE) model. The left panel and map represent the 12 areas implemented in the biogeographical model. Present-day distributions of each species are given at the tips by colored circles corresponding to colored areas on map; a colored square represents the inferred area(s) with the highest relative probability in the DIVALIKE analysis; corner positions represent geographic ranges immediately after a cladogenesis event. The red numbers near each node correspond to the median age inferred in Beast analysis and the gray lines indicate its 95% height posterior distribution (HPD). Bayesian posterior probabilities below 0.50 are not shown.
Figure 4. Colonization routes, numbers of emigration and immigration events and *in situ* diversification events inferred from ancestral area estimation for lineages of the *Novaeguineae* species group during the pre-Miocene, Miocene and Plio-Pleistocene. a) Colonization routes; line colors correspond to inferred area of origin (same color code as in simplified map): multiple lines of the same color correspond to multiple colonization events. b) Number of emigration (positive bars) and immigration (negative bars) events inferred from colonization events (Figure 4a) for each area in the pre-Miocene, Miocene and Plio-Pleistocene; column colors correspond to inferred areas as above. c) *In situ* diversification events inferred from ancestral area estimation for each area in the pre-Miocene, Miocene and Plio-Pleistocene.

Figure 5. Rate shift configurations with the four highest posterior probabilities from the 95% credible set within *Cardiodactylus*. The tree topology referred to Figure 3. The colored histogram indicates the speciation ($\lambda$), the color gradient corresponds the speciation rate.

Figure 6. Rates-through-time analysis of speciation ($\lambda$), extinction ($\mu$) and net diversification ($\gamma$) in *Cardiodactylus* (a) and within *Novaeguineae* species group (b).
Table 992. Best-fit models of sequence evolution and partitioning schemes selected with PartitionFinder ('unlinked branch lengths' option) for phylogenetic reconstructions using Bayesian Inference (MrBayes/BEAST) and Maximum Likelihood (RAxML/IQ-TREE).

Codon position is denoted by pos1, pos2 and pos3. Subsets are denoted by p1 and p2.

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Supporting Information

Appendix S1. Taxon sampling.

Appendix S2. Time-stratified biogeographical standard implemented in BioGeoBEARS analyses.

Appendix S3. Summary of ancestral area estimation with different models and dispersal rate multipliers with time slices (Table S3a) and without time slices (Table S3b). The gray line highlights the model with the highest statistical support.

Appendix S4. Sampling of species groups in BAMM analysis.

Appendix S5. Gene trees inferred for each marker: 16S (a), 12S (b), COI (c), COII (d), Cytb (e), 18S (f), 28S (g), EF1a (h), H3 (i).

Appendix S6. Original output results of Bayesian inference (BI) and maximum likelihood (ML) analyses for the concatenated dataset.

Appendix S7. Original outputs for dating analyses.

Appendix S8. Results of ancestral area estimation in BioGeoBEARS based on the most complex set of dispersal rate multipliers with three time slices, two maximum ancestral areas and DIVALIKE speciation model.

Appendix S9. Results of ancestral area estimation in BioGeoBEARS based on the most complex set of dispersal rate multipliers without time slices, two maximum ancestral areas and DIVALIKE speciation model.

Appendix S10. Summary of diversification rate under BAMM analysis with gradient of prior values ranging from 0.1 to 1.0. The gray line highlights the model with the highest statistical support.
Fig. 5.
Fig. 6.

(a) Rates-through-time analysis of speciation ($\lambda$), extinction ($\mu$) and net diversification ($\gamma$) within genus *Cardiodactylus*

(b) Rates-through-time analysis of speciation ($\lambda$), extinction ($\mu$) and net diversification ($\gamma$) in *Novaeguineae* species group
Appendix S1. Taxon sampling.

List of all Cardiodyptus and outgroups used in this study with current geographical distribution and GenBank accession numbers of each marker. The abbreviations of taxonomic status indicate as following: subfamily Gryllinae (GRY), subfamily Eneopterinae (ENE), subfamily Gryllinae (Gry), tribe Lebinthani (Leb), tribe Eneopterini (Ene), tribe Eurepinii (Eur), tribe Nisitriini (Nis), tribe Xenogryllini (Xen). NA means missing data. The samples used in the dating analyses to represent each species are show with an asterisk (*).
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Appendix S2. Time-stratified biogeographical standards implemented in BioGeoBEARS analyses.

1. Definition of geographical areas


Here Indochina corresponds to the Southeast Asia mainland, including the northern Ryukyu Islands (not showed on the simplified map), southeastern China (including Taiwan), Vietnam and northern Thailand. The boundary between Indochina and the Thai-Malay Peninsula corresponds to the Isthmus of Kra which intersects the north and south of Thailand. Southwest pacific is not shown on the map, but it includes the archipelagoes located east from New Guinea.

2. Dispersal rates:

Matrix of scaling factors (between 0 and 1.0) for dispersal rates between areas were constructed according to the geographical position of the areas during a given time slice, interpreting greater distances and/or the extent of geographical barriers (inland river, shallow sea, deep sea) as being inversely proportional to expected rates (Condamine et al., 2013; Toussaint and Balke, 2016). Dispersal rates were set as follows: no barrier between two connected areas: 1.0; minor barrier between two
areas, e.g., inland river, shallow sea water: 0.75; large barrier between two areas, e.g., deep sea, strait, high mountain: 0.25; long-distance dispersal between two areas: 0.01; absence of one area at a given time: 0. In addition, whenever two areas were separated by one area, dispersal rates were modified as follows: 0.5 when not involving a minor barrier; 0.25 when the area in between includes a minor barrier; and 0.1 when the area in between encompass a major barrier.

3. Time slices and dispersal multiplier matrices:
Collision events and the resumption of subduction that happened during the Cenozoic had a great impact on SEA terrestrial biogeographic patterns and on the current archipelago setting (Hall, 2013). Time-stratified biogeographical models were defined according to three distinct time slices following three major paleogeological events in SEA:

3.1. Time slice 1 (45-25 Ma): Eocene to Mid Oligocene
The India-Asia collision was related to the 45 Ma plate reorganization during the Eocene, resulting in Australia’s northward moving. The Makassar Straits became a wide marine barrier and separated west Sulawesi from core SEA. The Reed Bank-Palawan-Mindoro Block separated from the South China margin by the opening of the South China Sea during the Oligocene (Hall, 2002). However, at that period Palawan was still a part of Southeast China Mainland. In the Eocene, the southern part of the Philippines, along with the Halmahera Arc, formed part of an arc system which extended into the Southwest pacific at an equatorial/southern hemisphere position. The northern Philippines, principally Luzon, was connected via the Sulu–Cagayan Arc to northern Borneo and Sabah before the Miocene (Hall, 2002). Despite
marked geological activities (collision and subduction events), oceanic islands in the Wallcean region and New Guinea did not emerge from the sea (Hall, 2013). During this period, some islands or parts of current island in the Southwest pacific began to emerge, which is for example the case of New Caledonia that emerged ca. 37 Ma (Grandcolas et al., 2008) or the Fiji islands, which were formed by subduction with the oldest rocks being from a volcanic island-arc of late Eocene (37-34 Ma; Neall and Trewick, 2008).

Dispersal rates between well-connected areas (no barrier) were set to 1.0; this corresponds to dispersal events between Indochina [A] and the Thai-Malay Peninsula [B], Indochina [A] and Palawan [E], Sumatra [C] and Java [G], and Borneo [F] and Java [G]. Dispersal areas between slightly less connected areas (minor barrier) were assigned a rate of 0.75 (for example between the Thai-Malay Peninsula [B] and Palawan [E]; see below for the remaining pairings). Dispersal rates between Palawan [E] and Borneo [F] and the Philippines (minus Palawan) [D] and Borneo [F] were set to 0.5 considering the presence of small continuous fragments of islands between these areas. As explained above whenever two areas were separated by one barrier, lower dispersal rates were used (0.25 and 0.1; see below for all corresponding pairings). Finally, dispersals from the Southwest Pacific to Southeast Asia were considered as long-distance dispersal events (rate of 0.01; see below for all corresponding pairings).

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3.2. Time slice 2 (25-15 Ma): Mid Oligocene to Mid Miocene

Between the Eocene and Early Miocene, the southern and southeast margin of Sundaland were constituted of volcanic arcs (Hall, 2002). The volcanic arcs located on the southern and southeast margin of Sundaland were active and these events created a minor inner barrier within Sundaland. The Palawan Continental Terrane was isolated from the mainland because of the opening of Southeast China Sea and it drifted towards Borneo (Walia et al., 2012). New Guinea began to emerge, probably as small islands along the northern edge, but most of the areas, which is nowadays a mountain range, were covered by shallow sea (Hall, 2009, 2013). Oceanic islands emerged from the sea and rift deformation formed some parts of the Philippines and Sulawesi. In addition, deformation and uplift began in Borneo, Java and Sulawesi.

Therefore, there are several minor barriers within Sundaland (dispersal rate of 0.75). Long-distance dispersal was assigned to dispersal events between SEA and New Guinea, as well as between SEA and Southwest pacific. However, the emergence of continuous small fragments / islands between Sulawesi and New Guinea probably increased the chances for dispersal events (dispersal rate of 0.75).
3.3. Time slice 3 (15-0 Ma): Mid Miocene to present-day

The Australian margin drifted from the continent, forming the Bird’s Head region of New Guinea, (Sula Spur promontory). By the Mid Miocene, about 15 Ma, the Sula Spur promontory collided with the margin of SEA in Sulawesi, forming the region now known as Wallacea, including the Philippines, the Moluccas, a completed Sulawesi and the Lesser Sunda Islands (Hall, 2009; Spakman and Hall 2010). The geological pattern in SEA did not change so much since these geological events. Thus, dispersal rates within Sundaland were assigned the same values as before (time slice 25-15 Ma). Considering the persistence of strings of small islands involved in the origin of the Wallacean region, dispersal rates between the Philippines and Palawan, the Philippines and Borneo, the Philippines and the Moluccas, and the Moluccas and New Guinea were set to 0.75.
4. Alternative dispersal multipliers

We implemented alternative sets of dispersal multiplier to test the robustness of our biogeographical analyses and limit the impact of the arbitrariness of the probability attributed to each event. Three more simplified sets of multipliers were tested using the following changes: except the probabilities of 0, 0.01, 0.1 and 1 that remained unchanged, the events with probabilities of 0.25, 0.50 and 0.75 were given homogenous values (either 0.15, 0.50 or 0.75) in the alternative sets of multipliers. The three resulting simplified sets of multipliers are presented below.

Simplified set of dispersal multipliers 1 (0, 0.01, 0.1, 0.25, 1.0) – probabilities of 0.25, 0.5 and 0.75 in the base matrix are given a probability of 0.25.

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Simplified set of dispersal multipliers 2 (0, 0.01, 0.1, 0.5, 1.0) – probabilities of 0.25, 0.5 and 0.75 in the base matrix are given a probability of 0.5.
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Simplified set of dispersal multipliers 3 (0, 0.01, 0.1, 0.75, 1.0) – probabilities of 0.25, 0.5 and 0.75 in the base matrix are given a probability of 0.75.

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**time slice 3: 15 Ma to present**

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**References**


Hall, R., 2013. The palaeogeography of Sundaland and Wallacea since the Late Jurassic. J Limnol 72, 1–17.


**Appendix S3.** Summary of ancestral area estimation with different models and dispersal rate multipliers with time slices (*Table S3a*) and without time slices (*Table S3b*). The gray line highlights the model with the highest statistical support.

### Table S3a.

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<th>LnL</th>
<th>Parameter estimates</th>
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**Table S3b (without time slices)**

**Appendix S4. Sampling of species groups for the BAMM analyses.**

Because *C. javarere* and *C. kolombangara* show intermediate characters between *Novaeguineae* and *Efordi* species groups (Dong and Robillard, 2016), these two species form a third species group, hereby referred as the *Javarere* species group. Therefore, for the purpose of the BAMM analyses we considered that there are 60 species in *Novaeguineae* species group, 20 in *Efordi* species group and two in *Javarere* species group. In total, there are 35 species of the *Novaeguineae* species...
group and one of the *Efordi* species group in SEA. The number of species in each
species group and the sampling fraction in BAMM analyses were given in Table S4.

**Table S4.** Species sampling fraction in BAMM analyses.

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<th>Numbers in SEA</th>
<th>Sampling fraction</th>
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Note: Numbers (*/*) in the column named “Total numbers” correspond to the total numbers in each species group (left of sign /) and the species numbers in this study (right of sign /), respectively. Numbers (*/*) in the column named “Numbers in SEA” correspond the total numbers in each species group distributed in SEA (left of sign /) and the species numbers in this study in SEA (right of sign /), respectively. “Sampling fraction” corresponds the proportion of the number of species sampled in this study vs total numbers of each species group.
Appendix S5. Gene trees inferred for each marker: 16S (a), 12S (b), COI (c), COII (d), Cytb (e), 18S (f), 28S (g), EF1a (h), H3 (i).

16S (a):
16S (a): continued
12S (b):

(continued)
12S (b): continued
COI (c):
COI (c): continued
COII (d): continued
COII (d): continued
Cytb (e):

(continued)
Cytb (e): continued
18S (f): continued
28S (g): continued
EF1a (h): continued
(continued)
H3 (i): continued

(continued)
H3 (i): continued
Appendix S6. Original output results of Bayesian inference (BI) and maximum likelihood (ML) analyses for the concatenated dataset.

BI maximum consensus tree (concatenated dataset): 

(continued)
BI maximum consensus tree (concatenated dataset): continued

(continued)
BI maximum consensus tree (concatenated dataset): continued
**Best ML tree, RAxML (concatenated dataset):**

(continued)
Best ML tree, RAxML (concatenated dataset): continued
Best ML tree, RAxML (concatenated dataset): continued
Best ML tree, IQ-TREE:
Best ML tree, IQ-TREE (concatenated dataset): continued
Best ML tree, IQ-TREE (concatenated dataset): continued
Appendix S7. Original outputs for dating analyses.

Dated phylogeny resulting from BEAST analyses relying on the *unlinked* branch lengths option of PartitionFinder:
Dated phylogeny resulting from BEAST analyses relying on the *linked branch lengths* option of PartitionFinder:
Appendix S8. Results of ancestral area estimation in BioGeoBEARS based on the most complex set of dispersal rate multipliers with three time slices, two maximum ancestral areas and DIVALIKE speciation model.
Appendix S9. Results of ancestral area estimation in BioGeoBEARS based on the most complex set of dispersal rate multipliers without time slices, two maximum ancestral areas and DIVALIKE speciation model.

BioGeoBEARS DIVALIKE analysis
ancstates: global optim, 2 areas max. d=0.0147; e=0.0066; j=0; LnL=-105.83

[Diagram showing ancestral area estimation results]
BioGeoBEARS DIVALIKE analysis
ancstates: global optim, 2 areas max. d=0.0147; e=0.0066; j=0; LnL=-105.83

[Diagram showing a phylogenetic tree with various species and time measurements in millions of years ago.]
Appendix S10. Summary of diversification rate under BAMM analysis with gradient of prior values ranging from 0.1 to 1.0. The gray line highlights the model with the highest statistical support.

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