

Borneo and Indochina are Major Evolutionary Hotspots for Southeast Asian Biodiversity

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Abstract.—Tropical Southeast (SE) Asia harbors extraordinary species richness and in its entirety comprises four of the Earth’s 34 biodiversity hotspots. Here, we examine the assembly of the SE Asian biota through time and space. We conduct meta-analyses of geological, climatic, and biological (including 61 phylogenetic) data sets to test which areas have been the sources of long-term biological diversity in SE Asia, particularly in the pre-Miocene, Miocene, and Plio-Pleistocene, and whether the respective biota have been dominated by *in situ* diversification, immigration and/or emigration, or equilibrium dynamics. We identify Borneo and Indochina, in particular, as major “evolutionary hotspots” for a diverse range of fauna and flora. Although most of the region’s biodiversity is a result of both the accumulation of immigrants and *in situ* diversification, within-area diversification and subsequent emigration have been the predominant signals characterizing Indochina and Borneo’s biota since at least the early Miocene. In contrast, colonization events are comparatively rare from younger volcanically active emergent islands such as Java, which show increased levels of immigration events. Few dispersal events were observed across the major biogeographic barrier of Wallace’s Line. Accelerated efforts to conserve Borneo’s flora and fauna in particular, currently housing the highest levels of SE Asian plant and mammal species richness, are critically required. [Biogeography; climate change; Ecology; Geology; Palynology; Phylogenetics.]

Since the early research (1859–1871) of Alfred Russel Wallace, Southeast (SE) Asia has held considerable interest for the study of evolutionary biology and the field of biogeography. Megadiverse SE Asia comprises both mainland and numerous archipelagos of oceanic and continental islands (Lohman et al. 2011). The fragmented nature of SE Asia’s geography is mirrored in the distribution of its extant biota and a high degree of regional and local endemism (e.g., Woodruff 2010; Wong 2011). The four biodiversity hotspots that constitute SE Asia (Indo-Burma, Sundaland, Wallacea, and the Philippines; Myers et al. 2000; Woodruff 2010) are under increasing threat from the unsustainable use of native species and their habitats (Koh and Sodhi 2010; Wilcove et al. 2013).

Biotic evolution in SE Asia cannot be understood without considering the region’s complex tectonic and climatic evolution (Fig. 1; Supplementary Figs. S1–S4, Supplementary Information, available from <http://www.sysbio.oxfordjournals.org/>; <http://dx.doi.org/10.5061/dryad.67s40>), dominated since the late Paleozoic by a series of ongoing continental collisions (Metcalf 2011a). These geological events

have influenced many environmental variables, for example, geomorphology, topography, atmospheric circulation, the hydrological cycle and ocean current patterns, the opening and closure of ocean gateways, and as a consequence climate and climate change (see Fig. 2 for Quaternary sea-level scenarios), either directly or indirectly (Hall 2009; Morley 2012). Present-day SE Asia is the result of more than 300 myr of “Colliding Worlds” (van Oosterzee 1997) characterized by continent–continent and continent–arc collisions (see Supplementary Information for reconstructions of tectonic evolution). SE Asian continental blocks (Supplementary Figs. S1–S3) were all derived from the Southern Hemisphere supercontinent Gondwana, and traveled north to progressively collide and coalesce prior to the ongoing collision with the northwards-moving Australian continent (Metcalf 2011a). By the end of the Triassic (ca. 200 Ma), core Sundaland comprising Sumatra, the Thai-Malay Peninsula, and most of the present-day Sunda Shelf, was part of continental Asia (Supplementary Figs. S2 and S3). Vegetation during the early Cretaceous was dominated by the extinct gymnosperm family Cheirolepidiaceae, with thick

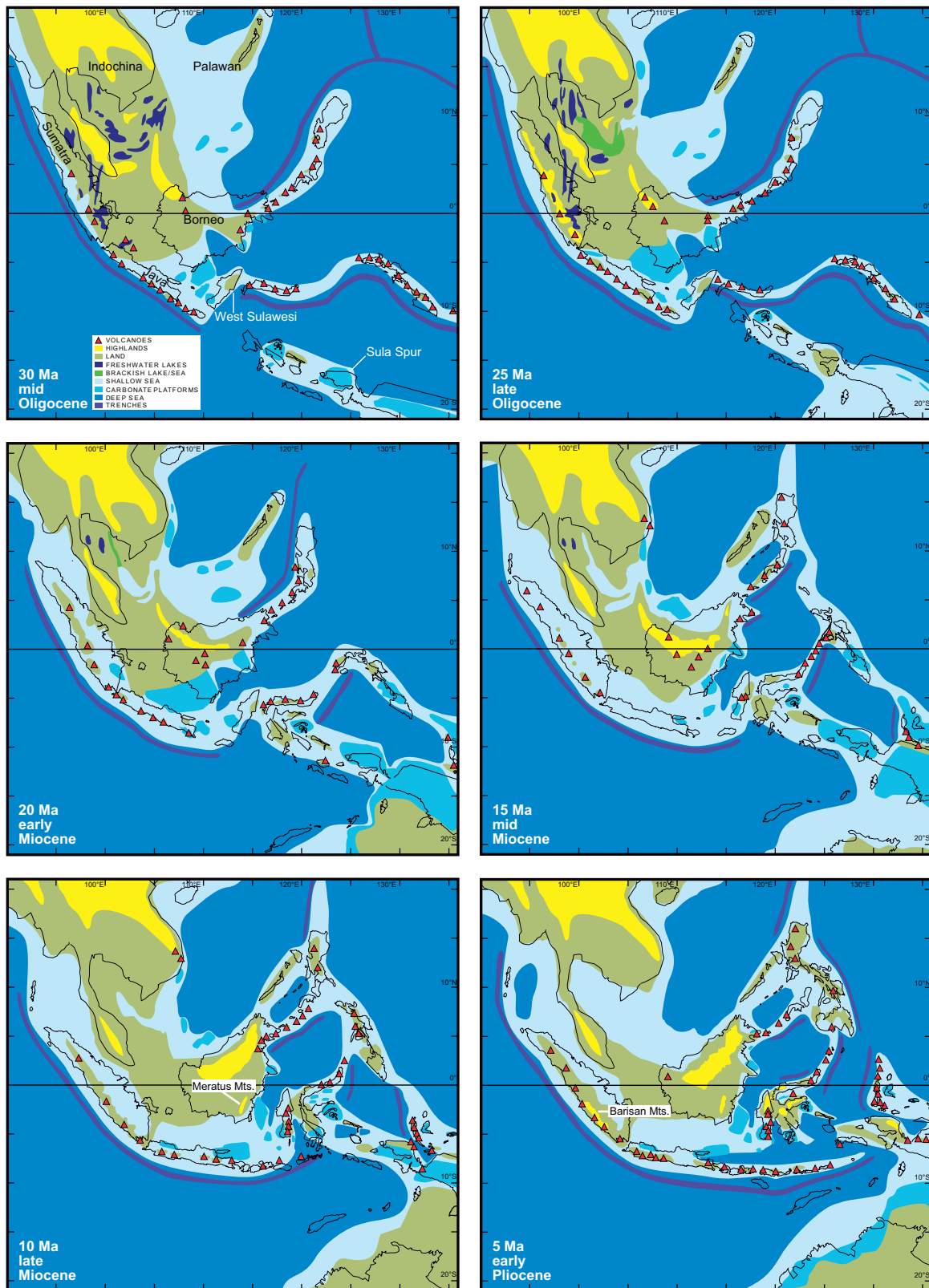


FIGURE 1. Paleogene and Neogene maps of SE Asian paleogeography and key habitat availability. Paleogeography of the region from Sundaland to northern Australia and the west Pacific between 30 and 5 Ma overlay on tectonic reconstructions of Hall (2012a) in which the basis for the reconstructions is described in detail (see Materials and Methods for further information).

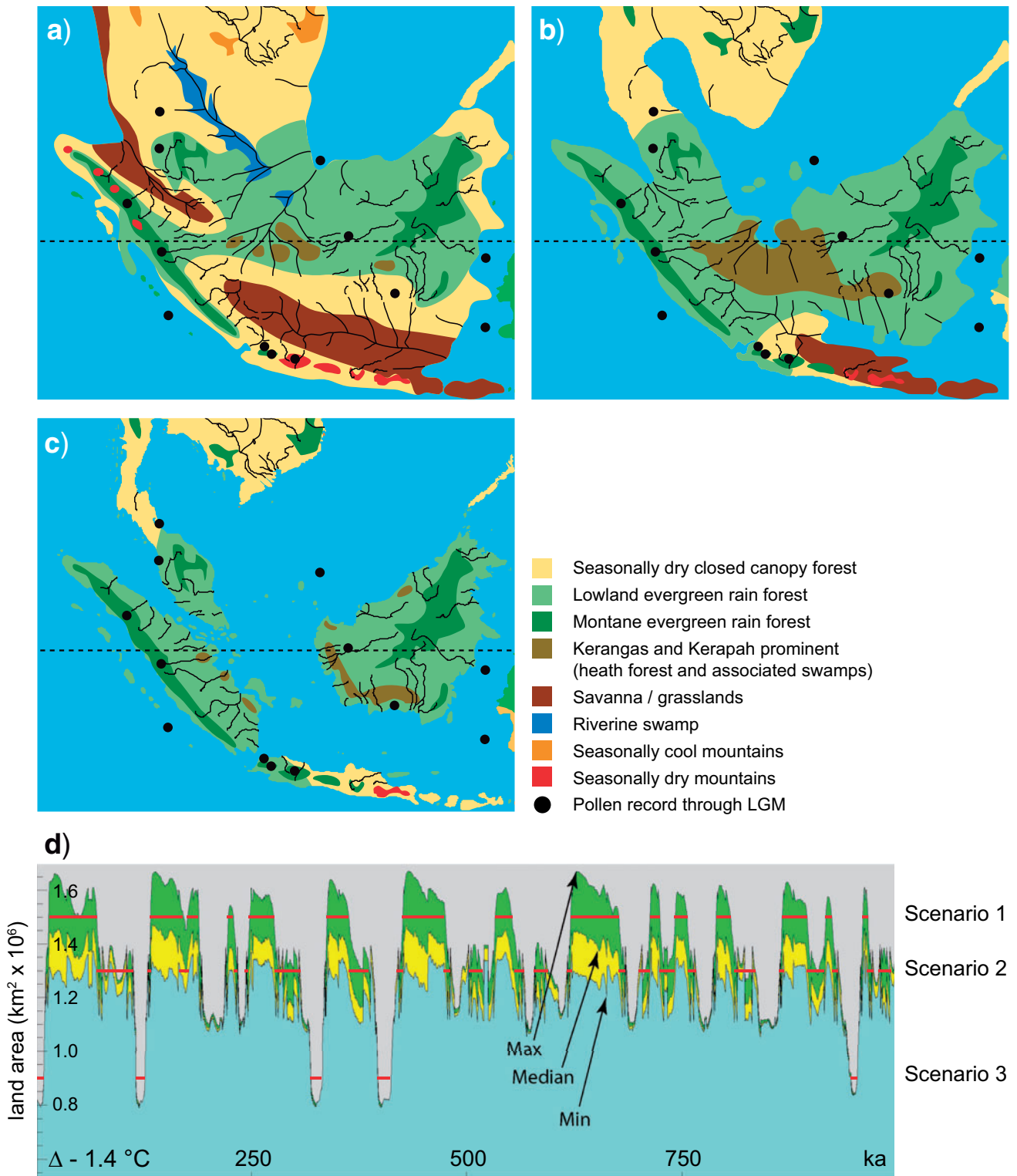


FIGURE 2. Three Quaternary climate sea-level scenarios for SE Asia: a) Scenario 1: 25 ka at lowest sea levels, glacial maximum, Marine Isotope Stage (MIS) 2. b) Scenario 2: 12 ka as sea-flooded Sunda Shelf, intermediate sea level, MIS Stages 1, 3, 4, and 5a–d. c) Scenario 3: present-day, interglacial high sea level, MIS Stages 1, 5e. Rainforest distribution based on fig. 1a in Cannon et al. (2009). LGM pollen localities from Morley (2012). d) Land area of tropical evergreen broadleaf forest over last 1 myr, from Cannon et al. (2009); horizontal red lines show times when scenarios 1–3 would likely have occurred (note that the blue line represents the most conservative model but not the most likely one here). Note that Borneo, in particular, has hosted extensive rainforests throughout all periods shown.

cuticles suggesting a paleoclimate with some degree of water stress (Vakhrameev 1991). Angiosperms increased in number and diversity during the Late Cretaceous (Morley 2000). Occurrence of *Nypa* pollen testifies to the presence of mangroves, whereas common Gnetales and Laurasian conifer pollen suggest upland open woodland vegetation also subject to water stress.

Three major Cenozoic collision events had a great influence on the current archipelago setting and probably substantially affected both climate and the assembly of regional biota, possibly in tandem. The impact of the Indian–Asian collision during the Eocene (Supplementary Fig. S4) on SE Asia's geography is debated but likely to have been small (Hall 2009). The terrestrial connection between India and Asia, however, had a huge effect on some SE Asian fauna (e.g., Shih et al. 2009; Klaus et al. 2010; Li et al. 2013) and flora (Morley 2000), which changed dramatically in the earliest middle Eocene (ca. 49 Ma) compared with that of the Paleocene and late Mesozoic. Dispersal of many plant taxa of Indian origin into SE Asia resulted in extinction of many elements of the older Paleocene flora (Supplementary Fig. S4) and by 45 Ma, pollen data indicate a diverse new flora (Morley 2000). Following the late Eocene change to a global “Ice House” climate, early Oligocene pollen floras were of markedly lower diversity but by the end of the Oligocene most pollen types characteristic of the wet, rainforest-dominated early Miocene were in place (Supplementary Information).

The vegetation of SE Asia was similarly influenced by the Asia–Australia collision (ca. 25–23 Ma), although the extensive forests of the Sunda Shelf islands were not substantially invaded by Australian elements (Richardson et al. 2012). However, the collision had a major impact on the climate and vegetation of the region by disrupting the Indonesian throughflow, the major interoceanic current that passes through the Malay Archipelago (*sensu* Alfred Russel Wallace). Moisture that previously moved between the Pacific Warm Pool (area enclosed by the 28.5°C sea-surface temperature isotherm) and the Indian Ocean in the throughflow subsequently fell on Sundaland (Morley 2006). This climate change coincided with the development of the East Asian Monsoon across China (Sun and Wang 2005). The Australian–Sunda collision thus appears to have initiated the East Asian monsoon (Morley 2012). This change to a wetter climate led to the development of the modern-aspect Malesian flora (Morley 2000).

The third collision, of the westernmost Australian promontory the Sula Spur with Sulawesi during the Miocene, led to the first amalgamation of continental fragments derived from Sundaland and Australia, respectively (Hall 2009, 2011). Emergence of land in central and eastern parts of Sulawesi (Hall 2009, 2011) is supported by biological evidence such as timing of the first major colonization wave of Sulawesi by terrestrial animal taxa from both east and west of Wallacea (the group of islands lying between the Asian and Australian continental shelves, including Sulawesi, the Moluccas,

and the Lesser Sunda islands) in the late Miocene and Plio-Pleistocene (Sahul and Sunda Shelf; Stelbrink et al. 2012). Several islands (e.g., Borneo, Sumatra, and Java) west of “Wallace's Line”—a major biogeographic barrier running between Bali and Lombok (Lombok Strait), and between Borneo and Sulawesi (Makassar Strait) following the Indonesian Throughflow—are largely of continental origin, being linked to the Sunda Shelf, and formed a contiguous landmass when sea-level dropped (Sundaland). The Sunda Shelf attained its greatest land area during the middle Eocene (ca. 49–45 Ma) with predominantly southward flowing rivers and widespread, palm-dominated (Harley and Morley 1995) peat swamps across what is now southeastern Borneo, Java, and southern Sulawesi. An easternmost rift of SW Sundaland resulted in the middle Eocene isolation of SW Sulawesi from mainland Borneo, forming the Makassar Strait and separating Sulawesi from Sundaland (ca. 45 Ma; Hall 2009), creating the central section of the major biogeographic break today recognized as “Wallace's Line.” From the later middle Eocene (ca. 42 Ma) onward, southern Sundaland subsided, and by the end of the Oligocene (ca. 25 Ma) much of the region now occupied by Java and southern Borneo (Kalimantan) was submerged, characterized by widespread shallow shelves with many extensive reefs (Fig. 1, 25 Ma). However, central Borneo and its northwestern extension to the Asian mainland remained emergent throughout this time (Fig. 1, 25 and 20 Ma) enabling everwet rainforest expansion northwards about 25 Ma (e.g., Morley 2000; see below).

The onset of wetter conditions in the latest Oligocene/Miocene, and Plio-Pleistocene climate-driven sea-level changes (Fig. 2) is superimposed upon this dynamic geological framework, leading to the repeated inundation of the region's continental shelves during interglacials (Hanebuth et al. 2011). During the early Quaternary, both Sundaland and the Sahul Shelf (Australian continental shelf) underwent fundamental changes in character as the amplitude of sea-level fluctuations increased (Zachos et al. 2001), resulting in these previously submerged shelves being exposed and flooded during glacials and interglacials, respectively (Fig. 2) (Voris 2000; Hanebuth et al. 2011). This phenomenon has been best studied across Sundaland, which over the past approximately 2 myr effectively doubled in size during glacials, and currently exhibits its smallest geographical area for that period with biota generally in a state of refuge (Cannon et al. 2009; Woodruff and Turner 2009). For most of the Quaternary sea levels fluctuated approximately 40–60 m below present-day levels, and climate was neither so dry nor cool as during the Last Glacial Maximum (LGM). The dual impact of geological and global climatic cycles has generally been regarded as important factors contributing to the region's biotic assembly (Hall 2009; Lohman et al. 2011).

Building on earlier work on SE Asian biogeography (e.g., Wallace 1869; Mayr 1944; Simpson 1977; Whitmore 1981, 1987), recently refined geological and tectonic

models from this region provide information on the timing and distribution of various landmasses and islands (Hall 2009, 2011, 2012a) (Fig. 1 and Supplementary Information). These models underpin biological models of historical distribution of ecosystems through time (Fig. 2) informed by paleontological and palynological data and based on paleoclimatic interpretations (e.g., Cannon et al. 2009). Recent studies provide estimates of divergence times, vicariance, and dispersal events and can, in combination with other empirical geological and biological data, identify key areas for the generation and maintenance of biotic diversity (e.g., Stelbrink et al. 2012). However, the complex geological history of SE Asia raises issues in the testing and interpretation of single-taxon studies, particularly across the region's heterogeneous mix of volant versus nonvolant terrestrial and freshwater taxa.

Thus, we here conduct meta-analyses and syntheses of geological, climatic, and biotic (including 61 phylogenetic) data sets from the SE Asian region to examine the assembly of the region's ecosystems and biota through time and space. We examine whether the SE Asian biota has been characterized primarily by *in situ* diversification, immigration and/or emigration, or equilibrium dynamics between our predefined biogeographic areas across three major time periods for which phylogenetic and paleogeographic data were available, the pre-Miocene, Miocene, and Plio-Pleistocene. We use divergence time and ancestral area estimation to test whether the sources of long-term biological diversity in SE Asia accord with predictions based on our geological, climatic, and biotic meta-analyses and syntheses. These predictions, based on major events in SE Asia's known history presented above, include 1) levels of *in situ* diversification events—that is, the accumulation of new lineages within areas—should reflect emergent ages and sizes of our predefined areas; 2) areas with recent histories of sea-level inundation (e.g., Sumatra and Java) should be characterized by higher levels of (recent) immigration than emigration; 3) number of colonization events should be greater between adjacent areas compared with more distant areas; and 4) an increase in diversification rates should be evident during the Plio-Pleistocene resulting from increased connection–disconnection events related to sea-level fluctuations.

MATERIALS AND METHODS

SE Asian Geological Reconstructions

Paleogeographic reconstructions for the Paleozoic and Mesozoic follow those published in Metcalfe (2011b). Maps were generated using a wide range of multidisciplinary data including stratigraphic, sedimentological, biostratigraphic, biogeographic, paleomagnetic, paleoclimatic, structural, isotopic, and geochronological data and plutonic and volcanic

activity (e.g., Wakita and Metcalfe 2005). Tectonic reconstructions for the late Jurassic to present depicting the evolution of continental blocks, ocean basins, and distributions of land and sea are modified versions of Spakman and Hall (2010) and Hall (2012a) and were produced using geodynamic reconstruction modeling software. The methodology and software used are described in Hall (2012a, 2012b). The distribution of land and sea is shown for a larger area than in previous publications, extending further north, as discussed in Hall (2012b, 2013) and includes additional details of Sunda Shelf marine embayments (Morley and Morley 2013) and shows freshwater rift lakes and inland seas for the Sunda Shelf (Shoup et al. 2012).

Development of the SE Asian Flora Inferred from Palynology

For the Cenozoic, patterns of paleoclimate change have been established from palynological records generated by petroleum industry studies (partly unpublished) from across the region (Morley 2012). These records total in excess of 150 data sets, extending from East and West Java Seas, Makassar Straits, offshore Sabah and Sarawak, Nam Con Son and Cuu Long Basins offshore Vietnam, the West Natuna Basin in Indonesia, the Malay and Penyu Basins offshore West Malaysia and Gulf of Thailand Basins, the more important of which are published (e.g., Morley and Morley 2011). All the data sets are placed within a high-resolution sequence biostratigraphic framework (following Morley 2012) allowing paleoclimates to be consistently reconstructed for individual time slices across the entire region. The high-resolution biostratigraphy used to provide the temporal framework for the Sunda Shelf paleogeographic maps was undertaken by characterising transgressive–regressive cycles using a sequence biostratigraphic approach initially outlined in (Morley, 1996). The detailed stratigraphic framework used for preparing the Sunda Shelf maps is presented in Morley et al. (2012). The time slices for the Sunda Shelf were mapped seismically, interpreted in terms of paleoenvironment and presented in Shoup et al. (2012). Those maps were then simplified, rescaled, and incorporated into the regional paleogeographic maps of Hall (2011). For Sumatra, basin outlines and stratigraphy were obtained from Moulds (1989) and Aldrich et al. (1996), with environments interpreted from unpublished data. For the Quaternary, maps have been prepared using published palynological and other climate-indicative data sets combined with climate modeling techniques (e.g., as in Cannon et al. 2009 and biogeographic considerations, as in Morley 2012).

Phylogenetics: Molecular Clocks and Ancestral Area Estimation

A literature search was performed for published molecular phylogenies including taxa (subsequently

assigned to the following categories: plants, insects and spiders, freshwater crustaceans, freshwater molluscs, freshwater fishes, herpetofauna, birds, and mammals) from SE Asia (and adjacent regions). Data sets were not included *a priori* if, firstly, sample sites were restricted to less than three areas predefined for the ancestral area estimation, and secondly, sequences, fossil data for calibration/substitution rates, and outgroup taxa were not available for performing molecular clock analyses. Some potential biases/artifacts might occur while performing meta-analyses such as that conducted here: 1) sampling artifacts, that is, weak taxonomic and geographic coverage due to sampling area access problems and 2) incomparable divergence times among intraspecific and interspecific data sets. However, we screened data sets carefully and omitted a substantial number ($n=68$; see Supplementary Information for a list of excluded publications/data sets) prior to further analyses to reduce potential sampling bias (see Tables 1 and 2 for details). Sixty-one data sets were retained for the final molecular clock analyses and ancestral area estimation, the majority ($n=45$) of which were performed or rerun for the present study using taxon-specific calibration points or substitution rates from several source publications (Table 1).

Sequences were aligned using MAFFT (default settings; <http://www.ebi.ac.uk/Tools/msa/mafft>; [Katoh and Toh 2008](#)) and corrected by eye if necessary, that is, removing potential gap artifacts produced by MAFFT (see Supplementary Information for alignment files). Alignments were reduced to unique haplotypes using DAMBE v. 5.1.1 ([Xia and Xie 2001](#)). Best-fitting substitution models were estimated using jModelTest v. 0.1.1 ([Posada 2008](#); 24 models, AIC; Table 2). Substitution rates or fossil calibration points were obtained from the publication or secondary sources (Table 2). Phylogenetic dating analyses were conducted with BEAST v. 1.6.2 ([Drummond and Rambaut 2007](#)) using an uncorrelated lognormal relaxed-clock model. MCMC chains were run using a Yule tree prior for 20 million generations, or 40 million generations if ESS was less than 200 for several parameters. Fossil, geological, and indirect calibration points (see Table 2) were assigned normal distributions. Maximum clade credibility (MCC) trees were summarized using TreeAnnotator (BEAST package; burnin = 35,001). All BEAST log files were visualized and checked in Tracer v. 1.5 ([Rambaut and Drummond 2007](#)) to ensure ESS values were more than 200. In a few cases ($n=8$), ESS values did not reach values more than 200 for “prior” and “posterior” whereas the remaining parameters show ESS values considerably higher than 200. In those cases, we performed reanalyses using the less complex HKY model (plus Gamma and PropInv parameters when selected by jModelTest for the best-fitting model), because low ESS values might indicate overparameterized substitution models (see e.g., [Grummer et al. 2014](#)). Importantly, divergence time estimates did not differ substantially between default and modified analyses for the majority of

data sets (cf. Table 2 and Supplementary Tables S1 and S2). Distribution of relaxed-clock (BEAST) divergence times (credibility intervals and mean ages) is shown in Supplementary Figures S5–S13; see Supplementary Information for BEAST input xml files.

Localities of specimens were obtained either from the source publication or from web sources (e.g., GenBank) if needed and were assigned to 1 of 12 areas of endemism, partly modified from areas of endemism proposed by [Turner et al. \(2001\)](#): Indochina = Indo-Burma *sensu* [Myers et al. \(2000\)](#), Thai-Malay Peninsula, Sumatra, Philippines, Palawan, Borneo, Java, “Wallacea excl. Sulawesi”, Sulawesi, “East of Wallacea,” India and Sri Lanka, and Japan, or to additional areas such as “Africa.” A presence-absence matrix was created for the ancestral area estimation conducted using Lagrange (Lagrange configurator: <http://www.reelab.net/lagrange/configurator/index>) ([Ree et al. 2005](#); [Ree and Smith 2008](#)); see Supplementary Information for Lagrange input and output files. Analyses were performed with default (unconstrained) settings (i.e., equal dispersal rates, single time matrices) and were constrained to a maximum range size of 2 areas because for the majority of data sets specimens could be assigned to single predefined areas only (see Supplementary Information). Increasing the number of ancestral ranges allows for widespread ancestors, however, by limiting this number the determination of dispersal directionalities across two areas is simplified.

Lagrange results (i.e., estimated ancestral areas for each node with the highest relative probability) were transferred to BEAST MCC tree printouts for each data set. Changes in geographic range representing colonizations from one area to the other have been included for resolved branches (posterior probabilities >0.5), though a higher threshold would increase the reliability of performed ancestral area estimation (see Supplementary Information for BEAST tree files). BEAST mean ages plus ancestral areas of ancestral and descendent nodes were used to assign these colonization routes to the preselected time frames “pre-Miocene,” Miocene, and “Plio-Pleistocene” (until the present) (Figs. 3 and 4; see Supplementary Figs. S14 and S15 for group-specific colonization routes through time among taxonomic groups). Counting dispersal events within each time bin allows for comparison of timeframe-specific patterns with paleogeographic reconstructions for that period (Fig. 1).

Speciation and dispersal through time were explored by counting and analyzing number of lineages, *in situ* (intra-area) diversification, and emigration events in each area across all taxonomic groups (Figs. 4 and 5, Table 3, and Supplementary Tables S3 and S4). The results were subsequently subjected to pairwise rank-based Mann-Whitney U tests using SPSS Statistics v. 17.0.0 (SPSS Inc.) to test the null hypothesis of equality between areas (asymptotic significance, two-tailed; Supplementary Information).

TABLE 1. List of data sets used for phylogenetic meta-analysis including information on taxa, generalized habitat, and molecular markers used in the original study

Data set ^a	Common name	Family	Genus [generalized habitat] ^b	Genetic marker	Taxonomic coverage ^f	<i>n</i> Taxa (ingroup) ^g	BEAST/Lagrange performed ^h	Source Ref ⁱ
01	Plants	Meliaceae	<i>Aglaia</i> [1]	ITS	82 spec (all genera)	42	This study	42
02	Plants	Araceae	<i>Alcatia</i> [1]	cpDNA + nuDNA	71/113 species	73	*	46
03	Plants	Begoniaceae	<i>Begonia</i> [1]	cpDNA	92 spec (all families)	66	#	61
04	Plants	Gesneriaceae	<i>Cyrtandra</i> [1]	ITS	26/300 species [A]	30	This study	2
05	Plants	Ericaceae	<i>Rhododendron</i> [1]	RPB2-d	46/300 species [B]	46	This study	20
06	Plants	Rafflesiaceae	Several [1]	mtDNA + cpDNA + nuDNA	80% spec (all genera)	27	#	3
07	Mosquitoes	Culicidae	<i>Anopheles</i> [2]	mtDNA	Population-based data set	40	This study	16
08	Butterflies	Nymphalidae	<i>Cethosia</i> [1]	mtDNA + nuDNA	All species	42	#	43
09	Butterflies	Nymphalidae	<i>Charaxes</i> [1]	mtDNA + nuDNA	All species	29	#	44
10	Butterflies	Pieridae	<i>Delias</i> [1]	mtDNA + nuDNA	30/44 species (Wallacea)	131	#	69
11	Net-winged beetles	Lycidae	<i>Metricorhynchus</i> [1]	mtDNA	All species	56	S	5
12	Giant wood spiders	Tetragnathidae	<i>Nephila</i> [1]	COI	Population-based data set	56	This study	59
13	Cockroaches	Blaberidae	<i>Salganea</i> [1]	COII	22/50 species [C]	36	This study	33
14	Net-winged beetles	Lycidae	<i>Scarletus</i> [1]	mtDNA	18/32 species	18	*	35
15	Cockroaches	Blaberidae	Several [1]	COII	21 species (9/10 genera)	22	This study	34
16	Mite harvestmen	Stylocellidae	Several [2]	mtDNA + nuDNA	98/300 putative species (36 species described)	95	This study/ ¹	10
17	Fig wasps	Sycophaginae	Several [1]	mtDNA + nuDNA	55 spec (all genera)	55	#	12
18	Prawns	Palaeomonidae	<i>Macrobrachium</i> [3]	COI	Population-based data set	93	This study/ ²	13
19	Prawns	Palaeomonidae	<i>Macrobrachium</i> [3]	16S rRNA	45/105 species	43	This study	67
20	Crabs	Gecarcinucidae	Several [3]	mtDNA + nuDNA	61 species (55% genera, 60% species)	61	\$	26
21	Crabs	Potamidae	Several [3]	16S	72 species (51% genera, 14% species)	65	This study (AAR)	57
22	Freshwater bivalves	Corbiculidae	<i>Corbicula</i> [3]	COI	7/c. 30 species [D]	55	This study/ ³	64
23	Freshwater snails	Pachychilidae	Several [3]	16S rRNA	21/c. 140 species (all genera)	21	This study	28
24	Freshwater snails	Cyprinidae	<i>Sulcospira</i> [3]	16S rRNA	57/c. 140 species (all genera)	129	This study/ ³	27
25	Cyprinids	Adrianichthyidae	<i>Barbodes</i> [3]	CR	Population-based data set	19	This study	36
26	Ricefishes	Cobitidae	<i>Oryzias</i> [3]	mtDNA	13/24 species [E]	23	This study	60
27	Fanged frogs	Dicroglossidae	<i>Pangio</i> [3]	Cyt b	18/32 species	77	This study	6
28	Frogs	Ranidae	<i>Limnonectes</i> [1]	mtDNA	45/55 species [F]	78	This study	19
29	Frogs	Ranidae	<i>Rana</i> [2]	ND3	14/7 species (several cryptic species)	15	This study	58
30	Water snakes	Homalopsidae	Several [3]	mtDNA	10/? species (several cryptic species)	54	This study	21
31	Spiderhunters	Nectariniidae	<i>Araclimothera</i> [1]	Cyt b	20/34 species	24	This study	1
32	Bush warblers	Cettiidae	<i>Cettia</i> [1]	mtDNA	10/10 species	46	This study	41
33	Kingfishers	Alcedinidae	<i>Ceyx</i> [1]	Cyt b	4/4 species (13/28 subspecies)	12	This study	48
34	Robins	Turdidae	<i>Copsychus</i> [1]	ND2	4/6 species [G]	19	This study	30
35	Flowerpeckers	Dicaeidae	Several [1]	mtDNA	9/19 subspecies	33	This study	56
36	Forktails	Muscicapidae	<i>Dicaeum</i> [1]	ND2	Population-based data set	16	This study	31
37	Flycatchers	Muscicapidae	<i>Enicurus</i> [1]	mtDNA	Population-based data set	15	This study	40
38	Cuckooshrikes	Campephagidae	<i>Ficedula</i> [1]	Cyt b	25/25 species	27	This study/ ⁴	49
39	Cuckooshrikes	Campephagidae	<i>Lalage</i> [1]	ND2	Population-based data set	12	This study	31

(continued)

TABLE 1. Continued

Data set ^a	Common name	Family	Genus [generalized habitat] ^b	Genetic marker	Taxonomic coverage ^c	nTaxa (ingroup) ^d	BEAST/Lagrange performed ^e	Source Ref ^f
40	Spiderhunters	Nectariniidae	<i>Nectarinia</i> [1]	ND2	Population-based data set	30	This study	31
41	Leaf-warblers	Phylloscopidae	<i>Phylloscopus</i> [2]	ND2	Population-based data set	19	This study	24
42	Bulbuls	Pycnonotidae	<i>Pycnonotus</i> [1]	ND2	Population-based data set	46	This study	31
43	Fantails	Rhipiduridae	<i>Rhipidura</i> [1]	ND2	Population-based data set	50	This study	31
44	Megapodes	Megapodiidae	Several [1]	ND2	15/22 species	23	This study	4
45	White-eyes	Zosteropidae	Several [1]	mtDNA	42/c. 80 species ("clade B")	57	This study	39
46	Whistlers	Pachycephalidae	Several [1]	ND2	35/49 species	39	*	25
47	Bulbuls	Pycnonotidae	Several [1]	mtDNA	43/>130 species [H]	46	This study	47
48	Shrews	Soricidae	<i>Crocidura</i> [1]	Cyt b	27/27 species (Malay Archipelago) [I]	47	§	18
49	Wild dogs	Canidae	<i>Cion</i> [2]	CR	Population-based data set	19	This study	22
50	Fruit bats	Pteropodidae	<i>Cynopterus</i> [1]	Cyt b	5/7 species [J]	140	This study	9 + 53
51	Elephants	Elaphantidae	<i>Elephas</i> [2]	mtDNA	Population-based data set	32	§	63
52	Bats	Hipposideridae	<i>Hipposideros</i> [2]	ND2	21/70 species	57	This study	45
53	Macaques	Cercopitheciidae	<i>Macaca</i> [1]	mtDNA + nuDNA	5/20–22 species [K]	23	This study	62
54	Macaques	Cercopitheciidae	<i>Macaca</i> [1]	mtDNA	15/20–22 species [K]	17	This study	68
55	Clouded leopards	Felidae	<i>Neofelis</i> [1]	mtDNA	2/2 species	7	This study	8
56	Tigers	Felidae	<i>Panthera</i> [1]	mtDNA	Population-based data set	25	This study	32
57	Palm civets	Viverridae	<i>Paradoxurus</i> [1]	mtDNA	Population-based data set	86	§	50
58	Rodents	Muridae	Several [2]	mtDNA + nuDNA	36 species (4/22 genera)	36	This study/ ⁴	23
59	Squirrels	Sciuridae	Several [2]	mtDNA	15 species (all genera)	15	This study/ ⁴	37
60	Tree squirrels	Sciuridae	<i>Sundascirus</i> [1]	Cyt b	14/15 species	29	§	15
61	Treeshrews	Tupaiaidae	<i>Tupaia</i> [1]	mtDNA	20/20 species	18	§	54

^aData sets showing "Out-of-Borneo" signatures are marked gray. ^bGeneralized habitat type: 1 = rainforest, 2 = other habitat(s), 3 = freshwater. ^cCalibration (F) = fossil calibration, calibration (G) = geological calibration, calibration (F+G) = fossil and geological calibration, calibration (I) = indirect calibration points from other study. ^dNumber of haplotypes/lineages/species according to source publication. ^eRoot height inferred from BEAST analyses; numbers in square brackets denote root ages directly obtained from source publication. ^fTaxonomic coverage according to source authors; e.g., 71/113 species = 71 of 113 currently described species used in analysis. ^gNumber of haplotypes (see source for information on lineages/species). ^hAAR/Lagrange information: *Source publication uses Lagrange, DIVA, and MrBayes for AAR, respectively—data used for statistics and colonization routes in Figure 4 and Supplementary Figures S14 and S15; # source publication performed AAR, but some defined areas summarize several islands (e.g., "Sundaland"); §AAR not performed in source publication; \$ AAR not performed in source publication but colonization routes inferred from topology; ¹not all terminal colonizations shown in Figure 4 and Supplementary Figures S14 and S15, that is, single lineages from Indochina, Thai-Malay Peninsula, Sumatra, and Borneo with uncertain ancestral area; ²Lagrange not required, but topology suggests colonization from East of Wallacea to Sumatra in the Plio-Pleistocene (shown in Fig. 4 and Supplementary Fig. S14), the remainder shows unresolved colonization routes between Indochina, Thai-Malay Peninsula, Sumatra, and Borneo; ³Lagrange not feasible due to several unresolved basal relationships; and ⁴Lagrange not feasible due to several ambiguous distribution areas in certain taxa. ⁵Source reference: see Supplementary Information for source references.

TABLE 2. List of data sets used for phylogenetic meta-analysis (plus ancestral area reconstructions) including information on taxa, substitution rates/fossil calibration applied by (source) authors, and results inferred from BEAST analyses (root height)

Data set	Family	Genus	Substitution model used for analyses ^a	jModelTest selection AIC, BIC ^a	Rates (%/Ma)/dates used for BEAST ^b	Root height (Ma): mean (95% HPD) ^c	Source ref ^d	Rates/dates source ref ^d
01	Meliaceae	<i>Aglaia</i>	G+G	G+G, G+G	Calibration (F)	108.3 (70.8, 156.7)	42	See source
02	Araceae	<i>Allocasia</i>			Calibration (F)	[47.5 (47.0, 48.0)]	46	See source
03	Begoniaceae	<i>Begonia</i>			Calibration (F)	[22.3 (N.A., N.A.)]	61	See source
04	Gesneriaceae	<i>Cyrtandra</i>	H+G*	G+G, H+G	0.1	1679 (107.6, 245.2)	2	See source
05	Ericaceae	<i>Rhododendron</i>	G+G	G+G, G+G	Calibration (F)	59.9 (58.0, 61.9)	20	38
06	Rafflesiaceae	Several			Calibration (I)	[96.1 (83.6, 110.7)]	3	See source
07	Culicidae	<i>Anopteles</i>	G+G/H+I+G	G+G/H+I+G, G+G/H+I	2.3	1.5 (0.9, 2.2)	16	7
08	Nymphalidae	<i>Cethosia</i>			Calibration (F)	[67.0 (57.0, 82.0)]	43	See source
09	Nymphalidae	<i>Charaxes</i>			Calibration (F)	[41.5 (38.5, 44.0)]	44	See source
10	Pieridae	<i>Delias</i>			Calibration (I)	[N.A.]	69	See source
11	Lycidae	<i>Metricriothynchus</i>			2.3	[N.A.]	5	See source
12	Tetragonathidae	<i>Nephila</i>	H+G	H+G, H+G	2.3	1.6 (0.9, 2.4)	59	7
13	Blaberidae	<i>Salganea</i>	\$		3.8	12.6 (9.4, 16.1)	33	34
14	Lycidae	<i>Scarelus</i>			2.3	[N.A.]	35	See source
15	Blaberidae	Several	H+I+G	H+I+G, H+I+G	3.8	17.2 (10.1, 24.9)	34	See source
16	Stylocellidae	Several	\$		Calibration (F)	425.0 (423.0, 427.0)	10	See source
17	Sycophaginae	Several			Calibration (F+G)	[48.2]	12	See source
18	Palaemonidae	<i>Macrobrachium</i>	H+G	H+G, H+G	1.485	3.5 (2.2, 4.8)	13	66
19	Palaemonidae	<i>Macrobrachium</i>	H+G	H+G, H+G	0.745	44.3 (24.3, 65.9)	67	14
20	Gecarcinucidae	Several			Calibration (F)	54.5 (35.0, 76.6)	26	See source
21	Potamidae	Several			Calibration (F+G)	[N.A.]	57	See source
22	Corbiculidae	<i>Corbicula</i>	\$		1.48	1.9 (1.1, 2.9)	64	66
23	Pachychilidae	Several	\$		1.0	78.7 (53.3, 106.8)	28	See source
24	Pachychilidae	<i>Sulcospira</i>	G+G [#]	H+G, H+G	1.0	13.2 (8.9, 18.0)	27	28
25	Cyprinidae	<i>Barbodes</i>	H+G	H+G, H+G	3.6	9.3 (2.3, 20.7)	36	See source
26	Adriamichthyidae	<i>Oryzias</i>	\$		2.5	7.7 (5.3, 10.4)	60	17
27	Cobitidae	<i>Pangio</i>	G+I+G	G+I+G, H+I+G	0.68	48.0 (32.0, 66.4)	6	See source
28	Dicroglossidae	<i>Limnonectes</i>	\$		1.48	22.8 (17.0, 29.5)	19	11
29	Ranidae	<i>Rana</i>	G+G	G+G, G+G	2.4	13.7 (9.3, 18.5)	58	52
30	Ranidae	<i>Rana</i>	H+I+G*	G+I+G, G+I+G	2.4	11.4 (7.7, 15.3)	21	52
31	Homalopsidae	Several			Calibration (F)	41.9 (29.6, 55.1)	1	See source
32	Nectariniidae	<i>Amchomothera</i>	H+I+G/H+I+G*	G+I+G/G+I+G, G+I+G/H+I+G	2.1	15.7 (10.8, 20.6)	41	65
33	Cettiidae	<i>Cettia</i>	H+G	H+G, H+G	2.1	11.5 (5.5, 18.0)	48	65
34	Alcedinidae	<i>Ceyx</i>	G+G	G+G, H+G	2.1	7.2 (5.0, 9.5)	30	65
35	Turdidae	<i>Copsychus</i>	H+I+G/H+I*	G+I+G, H+G	2.1	1.8 (1.0, 2.7)	56	65
36	Dicaeidae	<i>Dicaeum</i>	G+G	G+G, G+G	2.1	7.9 (4.5, 11.4)	31	65
37	Muscicapidae	<i>Enticurus</i>	S+I+G/H+G	S+I+G/H+G, S+G/H+G	2.1	71 (4.4, 9.7)	40	65
38	Muscicapidae	<i>Ficedula</i>	G+G	G+G, H+G	2.1	7.7 (5.4, 10.6)	49	65
39	Campephagidae	<i>Lalage</i>	G+G	G+G, H+G	2.1	7.7 (2.9, 12.1)	31	65
40	Nectariniidae	<i>Nectarinia</i>	G+G	G+G, G+G	2.1	6.7 (4.9, 8.5)	31	65

(continued)

TABLE 2. Continued

Data set	Family	Genus	Substitution model used for analyses ^a	jModelTest selection AIC, BIC ^a	Rates (%/Ma)/dates used for BEAST ^b	Root height (Ma):	Source ref ^d	Rates/dates source ref ^d
41	Phylloscopidae	<i>Phylloscopus</i>	H+I+G	H+I+G, H+G	2.1	7.4 (3.8, 11.1)	24	65
42	Pycnonotidae	<i>Pycnonotus</i>	H+I+G*	G+I+G, H+G	2.1	8.4 (4.4, 12.8)	31	65
43	Rhipiduridae	<i>Rhipidura</i>	H+I+G*	G+I+G, G+I+G	2.1	9.6 (2.3, 24.8)	31	65
44	Megapodiidae	Several	\$	G+I+G/H+I+G	1.79	22.6 (14.8, 30.6)	4	51
45	Zosteropidae	Several	G+I+G/H+I+G	G+I+G/H+I+G, G+I+G/H+I+G	2.1	22.7 (19.3, 26.1)	39	65
46	Pachycephalidae	Several	G+I+G/H+I+G	G+I+G/H+I+G, G+I+G/H+I+G	2.1	[7.2 (4.1, 10.9)]	25	65
47	Pycnonotidae	<i>Crocidura</i>	H+G	H+G, H+G	Calibration (F)	20.1 (16.5, 23.7)	47	65
48	Soricidae	<i>Cuon</i>	H+I+G*	H+G, H+G	5.48	[8.0 (7.2, 8.9)]	18	See source
49	Pteropidae	<i>Cynopterus</i>	H+I+G*	G+I+G, G+I+G	4.7	1.4 (0.6, 2.5)	22	29
50	Elaphantidae	<i>Elaphus</i>	G+G	G+G, G+G	4.7	1.3 (0.8, 1.7)	9+53	55
51	Hipposideridae	<i>Hipposideros</i>	G+G/H+G/H	G+G, G+G	4.7	7.4 (7.3, 8.0)	63	See source
52	Cercopithecidae	<i>Macaca</i>	H+G/H+G	G+G/H+G/H, JC/H+G/K80	4.7	8.2 (5.3, 11.1)	45	55
53	Cercopithecidae	<i>Macaca</i>	H+G/H+G	H+G/H+G, H+G/H+G	Calibration (F)	7.3 (4.6, 10.3)	62	See source
54	Felidae	<i>Neofelis</i>	H+I+G*	H+G/H+G, H/H+G	Calibration (F)	9.9 (7.1, 12.8)	68	See source
55	Felidae	<i>Panthera</i>	H+I+G*	H+G/H+G, H/H+G	1.53	7.1 (5.4, 9.0)	8	See source
56	Viverridae	<i>Paradoxurus</i>	G+I+G	G+I+G, H+G	Calibration (F)	1.6 (0.8, 2.8)	32	See source
57	Muridae	Several	\$	G+I+G, G+I+G	[N.A.]	[N.A.]	50	See source
58	Sciuridae	Several	\$	G+I+G, G+I+G	Calibration (F)	140.4 (99.5, 185.8)	23	See source
59	Sciuridae	Several	\$	G+I+G, G+I+G	Calibration (F)	39.0 (34.5, 45.2)	37	See source
60	Sciuridae	<i>Sundascirus</i>	\$	G+I+G, G+I+G	Calibration (I)	[10.0]	15	See source
61	Tupaiaidae	<i>Tupaia</i>	\$	G+I+G, G+I+G	Calibration (F)	[83.5 (68.0, 93.0)]	54	See source

^aSubstitution models: G = GTR, H = HKY, S = SYM; for example, G+I = GTR+I, H+G = HKY+G, S+I+G = SYM+I+G; \$ = data set reused from [Stelbrink et al. \(2012\)](#); * = less complex model used and also Gamma and Propinv parameters from AIC (jModelTest) due to low ESS values for parameters "prior" and "posterior" (see text for details); # model selected by AIC resulted in low basal branch supports and thus in a non-monophyly of the ingroup—therefore, GTR+G was used; part1/part2/part3 refers to different partitions. ^bCalibration (F) = fossil calibration, calibration (G) = geological calibration, calibration (F+G) = fossil and geological calibration, and calibration (I) = indirect calibration points from other study. ^cRoot height inferred from BEAST analyses; numbers in square brackets denote root ages directly obtained from source publication. ^dSource reference: see Supplementary Information for source references.

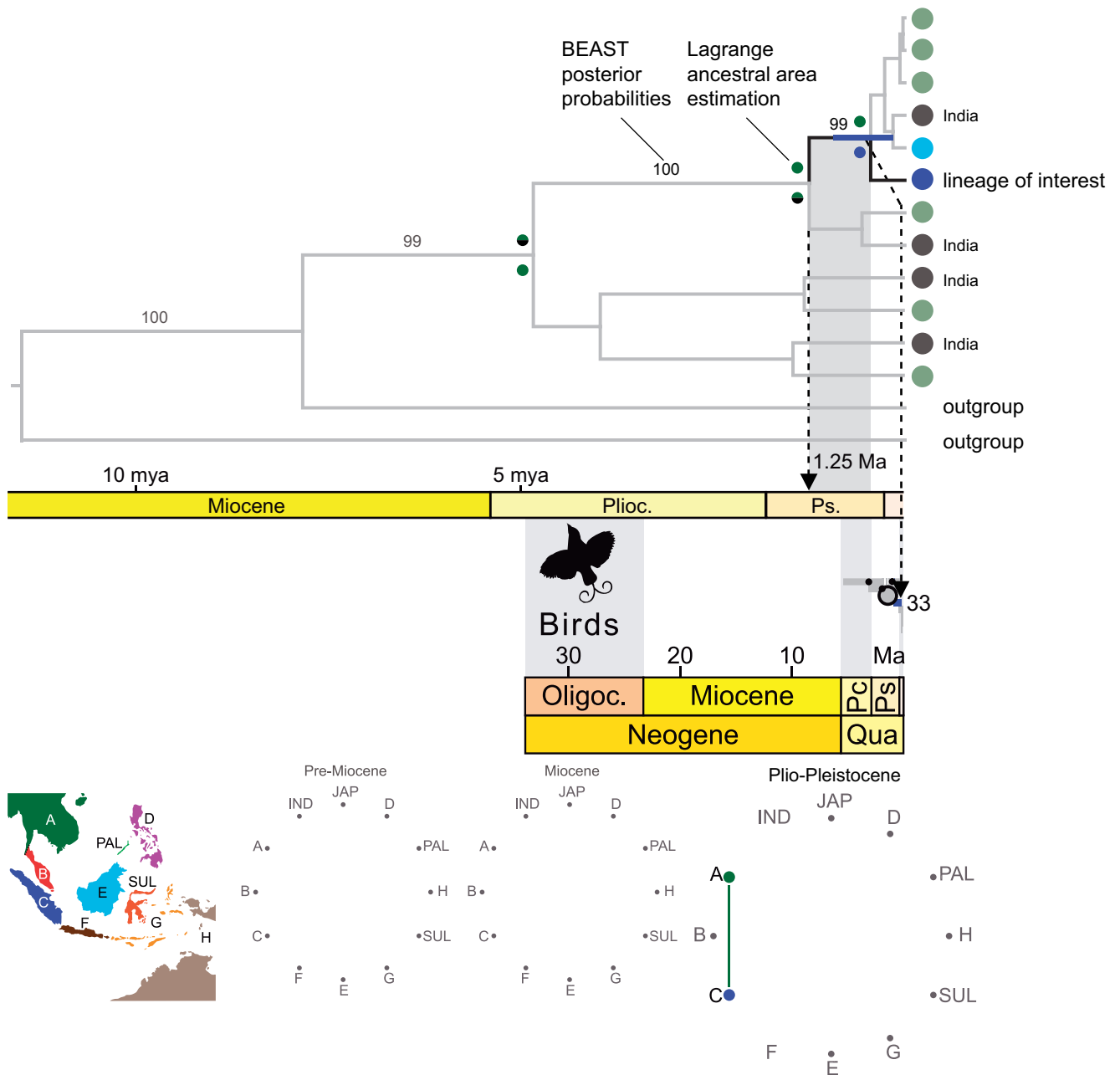


FIGURE 3. Exemplary illustration (data set 33, bush warblers) how colonization routes through time were inferred from both MCC trees (BEAST) and ancestral area estimation (Lagrange; colored circles). The blue time bar (0.16–0.9 Ma) represents the divergence time of the MRCA in Sumatra and is plotted in Supplementary Figures S11 and S13 (middle panel). The lineage of interest represents a specimen from area C (Sumatra). This lineage can be traced back to a node with an ancestral area in A (Indochina) 1.25 Ma (black arrow) and hence a colonization route from area A to area C in the “Plio-Pleistocene” timeframe is visualized in the bottom panel (see Fig. 4 and Supplementary Figs. S14 and S15).

Mammal and Plant Species Richness across SE Asia

Comprehensive distribution data exist for SE Asian plants and mammals, allowing comparison of extant species richness of these groups across our predefined areas to that recovered from our phylogenetic and ancestral area analyses. To construct a map of mammal species richness, we collected information on the current distribution of all mammal species occurring in the study area through the Global Mammal Assessment

(Rondinini et al. 2011). Considering an area ranging from Myanmar to New Guinea, we covered a total of 1086 mammal species, belonging to 17 orders (Catullo et al. 2008): Rodentia (number of species = 388), Chiroptera (328), Primates (76), Diprotodontia (58), Soricomorpha (56), Carnivora (54), Artiodactyla (52), Scandentia (17), Dasyuromorphia (16), Peramelemorphia (12), Erinaceomorpha (7), Lagomorpha (6), Perissodactyla (3), Pholidota (3), Dermoptera (2), and Proboscidea (1). For each species, we obtained the most updated available

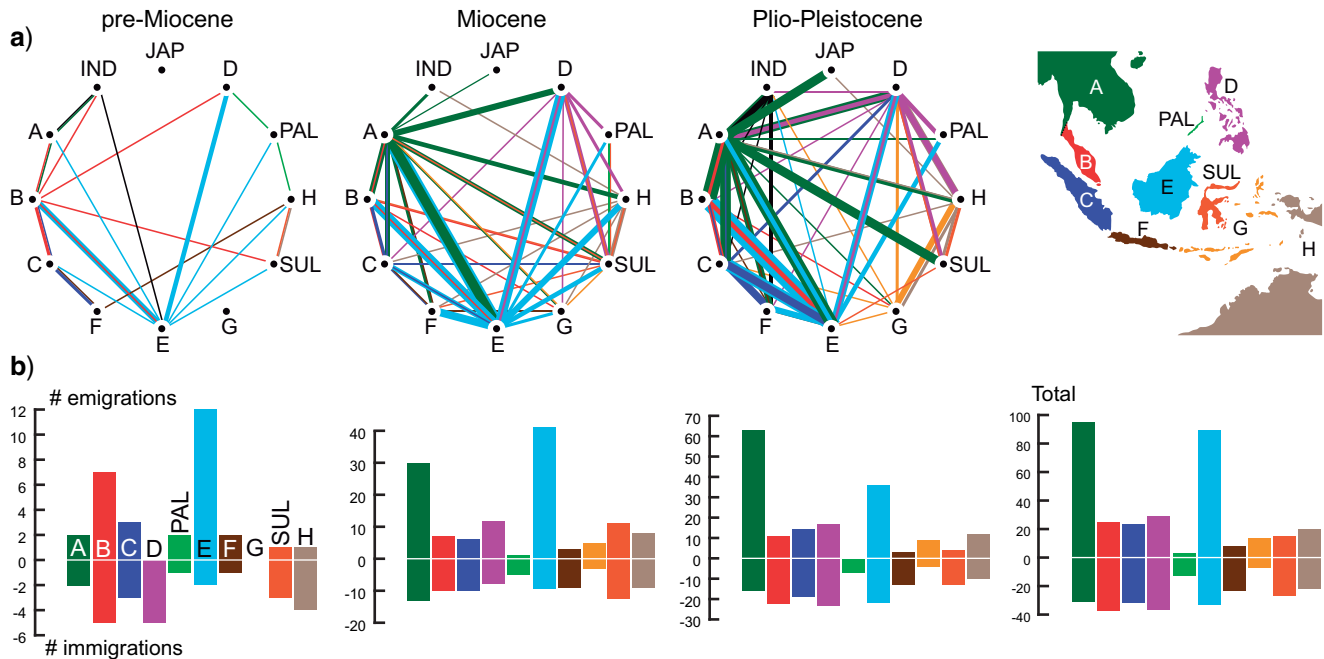


FIGURE 4. Colonization routes of extant SE Asian taxa. a) Colonization routes inferred from ancestral area estimation (DEC model, Lagrange) for lineages among studied taxa in the pre-Miocene, Miocene, and Plio-Pleistocene (see Materials and Methods and Fig. 3 for details). Line-color corresponds to inferred area of origin (see inset map), whereas line thickness corresponds to number of colonizations; multiple colonizations found for a specific source and destination (e.g., Indochina–Sumatra) from a single data set are counted once only. See Supplementary Figs. S14 and S15 for group-specific colonization routes. b) Number of emigration (positive bars) and immigration (negative bars) events observed for pre-defined areas in the pre-Miocene, Miocene, and Plio-Pleistocene.

global distribution range. We weighted each species according to the inverse of its area of distribution (i.e., species presence is divided by the square kilometers of their distribution ranges) and calculated a map of species richness (10 arcminutes spatial resolution) (Fig. 6). Endemic species and species mostly abundant in SE Asia, “locally restricted taxa” with a high number of specimens in a comparatively small area, will result in a higher weighted value and are thus considered more important in the analyses.

Data for vascular plants was used from [Kreft and Jetz \(2007\)](#) to create a map (Fig. 6) of species richness, with permission (*Copyright (2012) National Academy of Sciences, U.S.A.*). Considering 1032 geographic units worldwide and a set of bioclimatic and environmental variables, the source authors generated a set of predictions for species richness (1 degree resolution) [Kreft and Jetz \(2007\)](#). Among all models of species richness available from [Kreft and Jetz \(2007\)](#), we considered the kriging estimate here as it was demonstrated that the inclusion of neighborhood effects substantially improves the quality of predictions.

RESULTS

Setting the Scene: Palynological and Geological Syntheses Suggest Major Wet Refugia in Indochina and Borneo

The early Miocene collision of Australia with the eastern margin of Sundaland dramatically changed

the region’s paleogeography ([Hall 2009](#)). This collision resulted in the formation of widespread uplands in central Borneo from the early Miocene onward, and the development of major rivers such as the Mahakam and Baram and their respective deltas. The Meratus Mountains (SE Borneo) were uplifted during the middle and late Miocene (Fig. 1; 15 and 10 Ma) ([Witts et al. 2012](#)) and Mount Kinabalu during the late Miocene ([Hall 2011](#)). Widespread evergreen rainforests would have covered much of Sundaland during the early and middle Miocene. There was some climate variability with drier climates being widespread during periods of low sea level at subequatorial latitudes, and with rain forests reaching their maximum northward extent during the middle Miocene. However, whereas palynological data from the late Miocene and Pliocene suggest periodicity of climate in the region of the Sunda Shelf to the west, high-resolution palynological data (Supplementary Information) back to at least 9 Ma from East Borneo suggest continued everwet climates characterizing periods of both high and low (glacial) sea level in the equatorial region ([Morley and Morley 2011](#)). This climatic stability has been invoked as an explanation for high floristic diversity witnessed in areas such as Lambir Hills in Sarawak (Borneo), which harbors rain forests rivaling those of the Neotropics. The northern Sunda Shelf was subject to extensive marine inundation, with the development of widespread inland shallow seas reaching their greatest extent by the middle Miocene thermal (and sea level) maximum (Fig. 1, 15 Ma).

TABLE 3. Number of colonizations found between two areas (redundant "Out-of" colonizations in a single data set are counted once only)

Area-pair: source-destination	pre-Miocene	Miocene	Plio-Pleistocene	Total	Area-pair: source-destination	pre-Miocene	Miocene	Plio-Pleistocene	Total
A-B	1	4	10	15	E-A	1	9	2	12
A-C		3	7	10	E-B	4	6	11	21
A-D		4	6	10	E-C	1	3	8	12
A-PAL			1	1	E-D	3	6	5	14
A-E		6	8	14	E-PAL	1	3	2	6
A-F		2	4	6	E-F		5	4	9
A-G		1	1	2	E-G		2		2
A-SUL		3	6	9	E-SUL	1	3	2	6
A-H		3	3	6	E-H	1	4		5
B-A	1	1	3	5	F-A		1	1	2
B-C	2	1	3	6	F-B			1	1
B-D	1			1	F-C	1	1		2
B-PAL				0	F-D				0
B-E	1	1	3	5	F-PAL				0
B-F				0	F-E				0
B-G		1	1	2	F-G		1		1
B-SUL	1	1		2	F-SUL				0
B-H				0	F-H	1			1
C-A		1	1	2	G-A		1		1
C-B	1	2	1	4	G-B				0
C-D			2	2	G-C			1	1
C-PAL				0	G-D			2	2
C-E		1	5	6	G-PAL				0
C-F	1	1	5	7	G-E			1	1
C-G				0	G-F				0
C-SUL		1		1	G-SUL		1		1
C-H				0	G-H			4	4
D-A			3	3	SUL-A		1		1
D-B			1	1	SUL-B		1		1
D-C		1		1	SUL-C				0
D-PAL		2	3	5	SUL-D		1	1	2
D-E		1	2	3	SUL-PAL		1		1
D-F			1	1	SUL-E				0
D-G		1		1	SUL-F		1		1
D-SUL		3	3	6	SUL-G				0
D-H		2	4	6	SUL-H	1	1	2	4
PAL-A				0	H-A			1	1
PAL-B				0	H-B				0
PAL-C				0	H-C		1	1	2
PAL-D	1			1	H-D			5	5
PAL-E				0	H-PAL				0
PAL-F				0	H-E				0
PAL-G				0	H-F		1		1
PAL-SUL		1		1	H-G		1	2	3
PAL-H	1			1	H-SUL	1	3	2	6

Notes: Area codes in square brackets denote areas defined *a priori*: A = Indochina, B = Thai-Malay Peninsula, C = Sumatra, D = Philippines, PAL = Palawan, E = Borneo, F = Java, G = Wallacea excluding Sulawesi, SUL = Sulawesi, H = East of Wallacea. Top 20 are highlighted in gray. Note that the total number of emigrations/immigrations presented in Supplementary Table S4 and tested statistically for significance is higher as they also include emigrations/immigrations to/from India/Sri Lanka and Japan (see Fig. 4).

Phylogenetic Meta-Analyses: Origins of SE Asian Biota

Our meta-analyses of published molecular data sets using a standardized relaxed Bayesian dating approach (Supplementary Information) identified a history of phylogenetic lineage diversification in SE Asian biota since the Jurassic (Supplementary Figs. S5–S13 and Table S1 for detailed results). Only two of our study groups date back to the Mesozoic (plants, insects, and spiders). Although SE Asia's continental core—Indochina and Sundaland—was essentially established by the end of

the Mesozoic, its current largely insular topography and megadiverse biota were decisively shaped by Cenozoic events. For the majority of phylogenetic data sets examined, diversification events were Cenozoic in age (Supplementary Figs. S5–S13 and Table S1 for detailed results). Geographic and biotic changes are examined here in light of the interplay of tectonics and climatic oscillations, most notably evident during three distinctive stages in the Paleogene (~65.5–23 Ma), Neogene (~23–2.6 Ma), and the Quaternary (~2.6 Ma–present; see timeline in Supplementary Fig. S13).

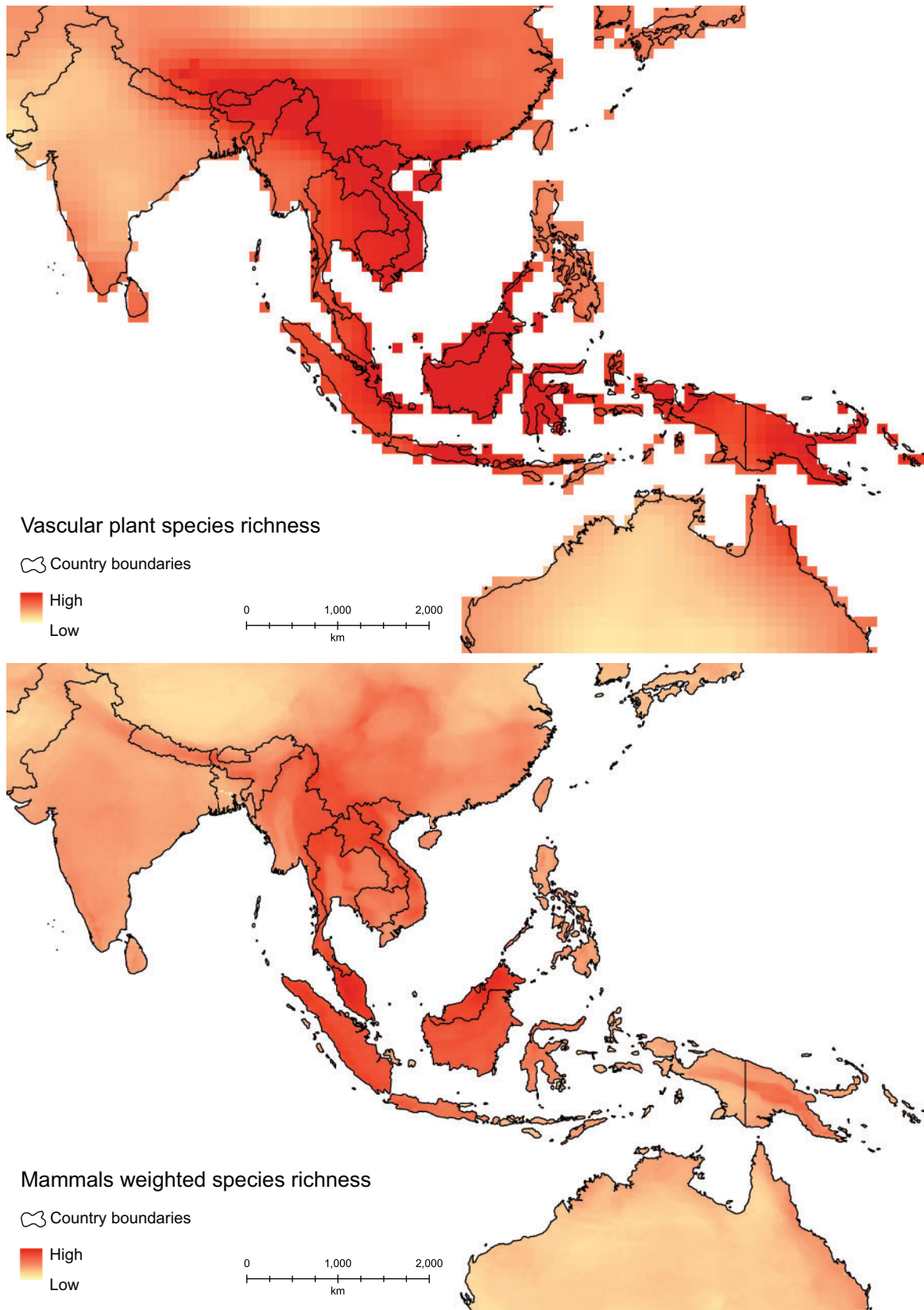


FIGURE 6. Extant SE Asian mammal and plant species richness calculated as the sum of species-specific distribution models. Borneo hosts the highest extant number of mammalian species ($n=230$), and also the highest weighted species richness for both vascular plants and mammals (together with Thai-Malay Peninsula for top 10% of mammals) for SE Asia (see Materials and Methods for details). Plant species richness data from [Kreft and Jetz \(2007\)](#), *Copyright (2012) National Academy of Sciences, U.S.A.*

Phylogenetic and Ancestral Area Estimation: Borneo and Indochina—Major “Evolutionary Hotspots”

Diversity can be evaluated here as the number and variety of lineages found in a specific predefined area (Table 1). This diversity may have arisen through the accumulation of immigrants, by *in situ* diversification, or some combination of the two. Indochina, the Philippines, and Borneo held the highest total number of lineages across all taxonomic groups ($n > 300$; Fig. 5a), which were statistically significantly higher than the other predefined areas: “East of Wallacea” ($n = 295$), the Thai-Malay Peninsula ($n = 233$), Sulawesi ($n = 199$), Sumatra ($n = 168$), Java ($n = 93$), “Wallacea excl. Sulawesi” ($n = 74$), and Palawan ($n = 46$) (Mann-Whitney U test: $P < 0.05$; Supplementary Table S4); other significant differences in pairwise comparisons are due to low numbers. These differences remained when population-based data sets were excluded (Supplementary Fig. 5a and Table S4).

Significantly higher numbers of *in situ* diversification events were observed in several areas: Indochina compared with all areas except “East of Wallacea” (see Fig. 5b; $P < 0.05$; Supplementary Table S4); Borneo compared with Sumatra, Palawan, Java, and “Wallacea excl. Sulawesi” ($P < 0.05$; however, this can primarily be attributed to particular taxonomic groups, namely plants, fishes, herpetofauna, and birds); and Sulawesi compared with Palawan and “Wallacea excl. Sulawesi” for most taxon groups ($P < 0.05$). However, inclusion of population-based data sets (see Table 1) increased both the number of total lineages and diversification events. The removal of population-based data sets reduced significant differences to some extent, particularly for Indochina (Fig. 5; Supplementary Table S4).

Indices for total number of lineages and *in situ* diversification events for each predefined area (excl. population-based data sets) were calculated in an attempt to control for potential biases resulting from increased lineage sampling for a particular area. These indices were tested for significant differences between areas (Mann-Whitney U tests, Supplementary Table S4). A significantly higher proportion of *in situ* diversification events were still observed for Indochina (vs. Thai-Malay Peninsula, Sumatra, Palawan, Java, and “Wallacea excl. Sulawesi”; $P < 0.05$) and Borneo (vs. Java; $P < 0.05$), when considering total number of lineages sampled per area (excl. population-based data sets).

Because statistically significant higher total lineage numbers and number of *in situ* diversification events for Indochina and Borneo could simply have been a function of area size, an area size-dependent index for all taxonomic groups among all areas was calculated for these parameters (Table 4). Interestingly, the comparatively large current size of both Indochina and Borneo was not reflected by higher indices reflecting size-dependent diversity (total number of lineages and number of *in situ* diversification events). A comparatively lower diversity-size index was found for

the biogeographic area “East of Wallacea,” likely related to under-sampling of Sahul Shelf representatives. In contrast, Sulawesi and the Philippines—both biogeographic areas with comparatively high numbers of lineages and *in situ* diversification events—showed comparatively high indices for their relatively small geographic sizes. Similarly, Palawan, the smallest area examined here showed the highest indices for these two parameters (Table 4). One important caveat on these findings is that current area size is not necessarily representative of the extended timeframe under investigation here.

Indochina and Borneo have been major colonization sources reflected by a significantly higher number of emigration events through all time periods examined here compared with our other predefined areas (see Fig. 4; Mann-Whitney U test: $P < 0.01$ for Indochina and $P < 0.05$ for Borneo; Supplementary Table S4). Thirty-two of 49 data sets analyzed for colonization routes show “Out-of-Borneo” signatures (total number of emigrations: $n = 89$; total number of emigrations excl. India/Sri Lanka and Japan: $n = 87$; compare with Fig. 4 and Supplementary Figs. S14 and S15), whereas 36 data sets show colonizations out of Indochina (total number of emigrations: $n = 95$; total number of emigrations excl. India/Sri Lanka and Japan: $n = 73$; Table 3 and Supplementary Table S3). An increased total number of emigrations were observed in the Miocene, and even more pronounced in the Plio-Pleistocene (pre-Miocene: $n = 30$, Miocene: $n = 122$, Plio-Pleistocene: $n = 169$), the latter significantly different to that of the pre-Miocene (Mann-Whitney U test: $P < 0.01$; Supplementary Table S4). In contrast, immigration events are comparably much less frequent for these two areas (Indochina: $P < 0.01$, Borneo: $P < 0.05$), with other areas showing a relatively balanced or even negative emigration–immigration index, for example, Palawan and Java (Fig. 4, lower panel; not significant except for Java $P < 0.05$; Supplementary Table S4). Interestingly, and as expected, very few emigration events were observed from younger volcanically active emergent areas such as Java ($n = 7$) (Fig. 4, Supplementary Figs. S14 and S15). Despite their geographical proximity, colonizations of Sulawesi from Borneo have been infrequent ($n = 6$; Fig. 4, Supplementary Figs. S14 and S15). The total number of immigration events found across all areas is significantly different between the three timeframes, increasing toward the present (pre-Miocene: $n = 26$; Miocene: $n = 86$; Plio-Pleistocene: $n = 149$; pre-Miocene vs. Miocene: $P < 0.01$; pre-Miocene vs. Plio-Pleistocene: $P < 0.001$; Miocene vs. Plio-Pleistocene: $P < 0.05$; Supplementary Table S4).

A pairwise comparison of the number of data sets observed for a particular source–destination route again highlighted Borneo and Indochina as predominantly “sources” rather than “destinations” across SE Asia through time, for example, Borneo–Thai-Malay Peninsula: 21 ↔ 5, Borneo–Philippines: 14 ↔ 3, and Indochina–Thai-Malay Peninsula: 15 ↔ 5 (source ↔ destination number of data sets; Table 3).

TABLE 4. Total numbers of lineages, *in situ* diversification events, and number of mammal species related to area size

Biogeographic area	Area [km ²] ^a	N lineages ^b	Lineages/1000 km ²	N <i>in situ</i> diversifications ^b	Diversifications/1000 km ²	N Mammals species ^c	Mammals species/1000 km ²	N emigrations	Emigration/1000 km ²
A	1,938,743	376	0.19	290	0.15	453	0.23	95	0.05
B	131,598	179	1.36	100	0.76	67	0.51	25	0.19
C	473,481	122	0.26	56	0.12	97	0.20	23	0.05
D	285,350	274	0.96	147	0.52	150	0.53	29	0.10
PAL	14,650	41	2.80	21	1.43	58*	3.96	3	0.20
E	743,330	309	0.42	211	0.28	190	0.26	89	0.12
F	138,794	80	0.58	38	0.27	59	0.43	8	0.06
G	142,090	69	0.49	26	0.18	22	0.15	14	0.10
SUL	174,600	195	1.12	137	0.78	51	0.29	15	0.09
H	6,072,464	227	0.04	189	0.03	101	0.02	20	<0.01

Notes: Area codes denote biogeographic areas defined *a priori*: A = Indochina, B = Thai-Malay Peninsula, C = Sumatra, D = Philippines, PAL = Palawan, E = Borneo, F = Java, G = Wallacea excluding Sulawesi, SUL = Sulawesi, H = East of Wallacea. ^aPresent-day area as in Figure 6. ^bTotal numbers of lineages and *in situ* diversification events excluding population-based data sets. ^cSource: *Esselstyn J.A., Widmann P., Heaney L.R. 2004. The mammals of Palawan Island, Philippines. Proc. Biol. Soc. Washingt. 117:271–302; otherwise: Global Mammal Assessment program: Rondinini C., Di Marco M., Chiozza F., Santulli G., Baisero D., Visconti P., Hoffmann M., Schipper J., Stuart S.N., Tognelli M.F., Amori G., Falcucci A., Maiorano L., Boitani L. 2011. Global habitat suitability models of terrestrial mammals. Phil. Trans. R. Soc. Lond. B 366:2633–2641.

Further, the rate of colonizations between currently adjacent islands/landmasses is generally higher compared with between currently remote areas (Table 3; see also Fig. 4 and Supplementary Figs. S14 and S15). However, even “East of Wallacea” appears to have been colonized to a considerable extent from Indochina and Borneo, even though geographic distances separating these areas have remained comparatively large throughout the timeframe under investigation (Fig. 4). The majority of colonization events were assigned to the Plio-Pleistocene, and most frequently between areas formerly adjoined through “Sundaland” (Fig. 4 and Table 3). To control for total number of lineages sampled per area (sampling effect), we calculated an index for emigrations and total lineages (excl. population-based data sets) (Supplementary Table S4). These indices were tested for significance between areas (Mann-Whitney *U* tests). Interestingly, significant differences were only found between Sulawesi versus Indochina, Sumatra, and Borneo (lower indices for Sulawesi) and Borneo versus Java (lower indices for Java; Supplementary Table S4). This result indicates that the significantly higher levels of emigration events identified for Indochina and Borneo are clearly related to the higher diversity (represented by number of lineages) found in these areas. Elevated levels of emigration events found in Indochina and Borneo might actually relate to the size of the respective source area. However, size-dependent indices were not comparatively elevated for either of these biogeographic areas (Supplementary Table S4), although current area size was used for these analyses and area size has changed considerably through time for several areas (Fig. 1).

Performing multiple pairwise statistical tests can include amendments such as the (sequential) Bonferroni correction, that is, effectively dividing the *P*-value cutoff by the number of tests performed or by identifying rank-based Bonferroni-corrected *P*-value cutoffs. For the

majority of pairwise comparisons made (e.g., number of lineages, *in situ* diversifications, and emigrations) the number of tests was $n = 45$. Applying a Bonferroni-correction resulted in a decreased *P*-value cutoff of 0.0011 and therefore a greatly reduced number of significant differences observed (see Supplementary Table S4). However, several drawbacks have been identified for such corrections (see e.g., [Perneger 1998](#); [Moran 2003](#); [Armstrong 2014](#)); thus, here we base our interpretations on non-corrected significance testing—effectively prioritizing each individual area-pair test (see e.g., [Armstrong 2014](#)).

Mammal and Plant Distributional Data Sets: Elevated Diversity on Borneo

A meta-analysis of mammalian and plant distributional data sets for which high-resolution data across SE Asia was available (Fig. 6), again identified Borneo in particular as an area of special biodiversity significance for SE Asia (Fig. 6). For our predefined areas, Borneo hosts the highest levels of weighted (see Materials and Methods) terrestrial mammalian ($n = 230$) and vascular plant species richness in SE Asia, whereas the top 10% of weighted mammalian species richness is hosted in the northeast of the island and in the Thai-Malay Peninsula ($n = 228$; Fig. 6). This pattern was consistent for Borneo for total number of plant lineages identified here (Fig. 5a and Supplementary Table S4) but was not the case for mammals. For mammalian lineages, Borneo ranked fourth after Indochina, the Philippines, and the Thai-Malay Peninsula. Interestingly, the Philippines showed a marked contrast between present-day mammal species richness (comparatively low) and total number of mammalian lineages (comparatively high) (cf. Figs. 5a and 6). Size-dependent indices of general diversity across all taxonomic groups were

additionally applied to present-day mammal species richness (Fig. 6). However, when *current* island size is taken into account, mammal diversity (total number of species) is comparatively low for Indochina and Borneo, whereas it is comparatively high for Palawan, the Thai-Malay Peninsula, the Philippines, and Java (Supplementary Table S4).

Palynological and Paleontological Syntheses: Middle to Late Quaternary Sunda Shelf Sea-Level Dynamics

There are three predominant sea-level regimes for the middle to late Quaternary Sunda Shelf (Fig. 2) (Morley 2012). The most commonly recurring scenario ($\pm 55\%$ of last million years, Fig. 2b) is of periods with sea levels 40–50 m below current levels, around half the current shelf emergent, and evergreen rainforests extending from Borneo to Sumatra. The second most common scenario ($\pm 37\%$ of last million years, Fig. 2a) is of periods with very low sea levels such as the LGM. Vegetation characteristic of seasonal climates was very widespread, though may not have formed a continuous north-to-south corridor for every glacial maximum, and the exposed sandy soils of the shelf may have acted as a substantial barrier to dispersal (Slik et al. 2011). Seasonality of climate may have varied between glacial maxima, suggested by the occurrence of certain mammalian fossils in Java. Faunas from the penultimate and older glacials included many large mammals requiring open woodland (van den Bergh et al. 2001), whereas there were no such immigrants during the LGM for non-forest species. This suggests that opportunities for migration across the Sunda Shelf may have been inhibited during the LGM, whereas more open vegetation types perhaps with a corridor of semievergreen forests but without true savanna may have been present during earlier glacials (Cannon et al. 2009). Examination of floristic elements in Java suggests that there are semievergreen elements that are common to Java and Indochina, but there are no clear Indochinese deciduous forest elements in Java. This suggests that there may have been a dispersal pathway for semievergreen elements during the LGM but not for elements requiring more seasonality of climate. From the faunal perspective, the mammals from the Javanese last glacial do not include big non-forest browsers except elephants. Again, this suggests limited dispersal opportunities for open-vegetation browsers. However, the presence of large open-vegetation browsers from earlier glacial intervals in Java suggests that more opportunities for browsers may have occurred earlier in the Quaternary, but due to the floristic differences with Indochina it is thought unlikely that there was a continuous “savanna corridor.” The third climatic scenario is represented by the present day (Fig. 2c) with high sea levels and evergreen rainforests extending from the Kra Isthmus to West Java, including Borneo, but importantly occurring for just 8% of the last million

years, emphasizing the “refugial” nature of present-day SE Asian rainforests and fauna (Cannon et al. 2009).

These glacial events are thought to have facilitated repeated biotic range expansions between Sumatra, the Thai-Malay Peninsula, Borneo, and Java during low sea levels, followed by vicariance as sea levels subsequently rose (Cannon et al. 2009; Gower et al. 2012; de Bruyn et al. 2013). Although fossil data could contribute to our understanding of these dynamics, the terrestrial paleontological record from Quaternary SE Asia is still very poorly understood. Although Quaternary sites are relatively abundant throughout the region (Louys and Meijaard 2010), these are mostly represented by cave sites, with often poorly constrained ages. In addition, many taxa have not yet been studied by specialists and much controversy remains regarding taxonomic delineation. Borneo and Sumatra have yielded few terrestrial fossil remains apart from the famous late Pleistocene Niah and Madai Cave sites. There have been a few isolated Proboscidean finds from Samarinda, Brunei, and Sarawak, but the exact stratigraphic origin is invariably poorly known (Hooijer 1952; Earl of Cranbrook 2010). On the other side of “Wallace’s Line” in the realm of Wallacea, increasing efforts in fossil vertebrate studies were carried out during the second half of the 20th century culminating in the discovery of an endemic late Pleistocene hominin, *Homo floresiensis*, on the oceanic island of Flores (Brown et al. 2004).

The majority of data sets examined here show “Out-of-Borneo” and “Out-of-Indochina” signatures for the Plio-Pleistocene period, while colonization routes from both Sumatra and the Thai-Malay Peninsula were substantially fewer (Fig. 4 and Table 3). Borneo and Indochina have thus been *the* major refugia for Sundaland over at least the last 5 Ma, and likely earlier (see Neogene discussion above).

DISCUSSION

Given the taxonomic coverage of SE Asia, our phylogenetic meta-analyses of diverse faunal and floral groups identified initiation of diversification during the Jurassic in plants, and insects and spiders, whereas all other groups examined diversified later during the Cenozoic (Supplementary Figs. S5–S13 and Table S1), consistent with the fossil record. Fossils indicate that a diverse mammalian fauna existed during the Eocene and Oligocene, including various primates, flying lemurs, mustelids, ruminants, and rodents in Myanmar and Thailand (e.g., Marivaux et al. 2004, 2006; Peigné et al. 2006; Beard et al. 2009). There are, however, few Paleogene mammal fossils from island SE Asia, and some of these are of uncertain provenance (e.g., an Eocene anthracothere found on Timor Island and a putative member of the artiodactyl family Haplobunodontidae found in western Borneo; see Ducrocq 1996).

Interestingly, a few data sets show pre-Oligocene diversification events from the Philippines (excluding

Palawan) and Java. However, given the small number of taxa with such patterns, dating issues, extinction, and range evolution seem more likely at present than a major conflict with the geological evidence. Colonization routes and ancestral areas inferred from meta-analyses of phylogenetic data show that Indochina and Borneo were already major evolutionary hotspots and sources of diversification in the pre-Miocene (Fig. 4, Supplementary Figs. S14 and S15, and Tables 2 and 4). These results most likely reflect the paleogeographic history of Borneo and Indochina. Borneo is the largest landmass of the former Sundaland, and was less affected by sea-level changes compared with other islands such as Sumatra and Java, which were largely submerged during the Miocene or even later (Fig. 1). The presence of extended emergent areas including extensive rainforest (Fig. 2) through all time periods examined here may explain the elevated levels of *in situ* diversification and emigration observed for Indochina and Borneo (Fig. 5, see below).

Caveat on Phylogenetic Meta-Analyses

Only a few colonizations from the islands within “Wallacea excl. Sulawesi,” Palawan, and the area east of Wallacea (i.e., mainly New Guinea and Australia) were inferred conducting ancestral area estimation (Fig. 4 and Supplementary Figs. S14 and S15), consistent with a recently published meta-analysis focusing on Sulawesi and Wallacea, which identified that the majority of colonization events were derived from Sundaland, not within or east of Wallacea (Stelbrink et al. 2012). It seems very unlikely that comparatively small and young islands such as the Lesser Sunda Islands and Palawan might have played a major role as refugia and/or colonization sources throughout the timeframe under investigation here, when comparing them with larger, older landmasses such as Borneo. However, one might assume that the lack of particular dispersal routes is a result of weak taxonomic coverage, because some islands are more difficult to access and/or research permits are difficult to procure and therefore taxa from these areas are missing in several phylogenetic studies. One area that is likely to be under-represented in phylogenetic studies is New Guinea, and current evidence suggests this landmass has played a significant role in speciation for the wider region (e.g., Balke 2009; Jönsson et al. 2011; Müller et al. 2013). Similarly, two recent herpetological studies suggest that Palawan may have been more important in the biogeographic history of SE Asia than generally recognized, acting as a raft for mainland SE Asian lineages when separating from the mainland about 30 Ma, and thus facilitated dispersal across the Philippines, Borneo, Sulawesi, and the Thai-Malay Peninsula during the Miocene (so-called “Palawan Ark Hypothesis”; e.g., Blackburn et al. 2010; Siler et al. 2012). However, for most Philippine species groups, Palawan apparently did not function as a dispersal gateway between Borneo and the rest of the Philippines (see

e.g., Brown et al. 2013; cf. also Fig. 4). Some species likely dispersed from Borneo to the Philippines (except Palawan) through the Sulu Archipelago (Oliveros and Moyle 2010), whereas others dispersed from Indochina, probably through Taiwan (Esselstyn and Oliveros 2010). Finally, 15 of 61 data sets analyzed here are based on intraspecific data, whereas the remainder focus on clades containing multiple species (Table 1). This could result in relatively young divergence times for these intraspecific data sets compared with those data sets studying taxa of a higher taxonomic level (interspecific and intergeneric).

Caveat on Plant and Mammal Distributional Modeling

SE Asia is a global hotspot for mammal species richness (Catullo et al. 2008; Rondinini et al. 2011). Roughly one-quarter of global mammal taxa occur in this area, with many new families and species, which have only been discovered recently (Jenkins et al. 2005; Musser et al. 2005). The region is also a global center of plant richness, especially in northern Borneo and New Guinea. Overall, our study area includes four biodiversity hotspots (Sundaland, Wallacea, Philippines, and Indo-Burma) as defined by Myers et al. (2000), more than 56,000 plant species are present in the area, of which 52% are endemic to the four biodiversity hotspots mentioned (Myers et al. 2000).

We caution against an overinterpretation of the species richness map (Fig. 6), as both are probably overestimating actual species distribution. In fact, increasingly, lowland forest areas in SE Asia are characterized by the so-called “empty forest syndrome,” with large animals (mainly primates, carnivores, and ungulates) that are extinct in vast areas of their former distribution range because of commercial hunting, even if suitable habitat is still present (Redford 1992; Milner-Gulland et al. 2003; Corlett 2007). Similar issues characterize also the model of plant species richness (Fig. 6). SE Asia is characterized by the highest rate of deforestation globally (Achard et al. 2002; Wilcove et al. 2013), and primary vegetation losses equate to 92.2% of the original extent for Sundaland, 85% for Wallacea, 97% for the Philippines, and 95.1% for Indo-Burma (Myers et al. 2000) in recent decades. If all forest types are included, some 50% of Borneo remains forested (Miettinen et al. 2011) but annual losses continue (1.3%/year, Miettinen et al. 2011; 3%/year for peat swamp forests only; Wilcove et al. 2013). Given that the plant species richness map has been calculated from a database using statistical models, data points, and bioclimatic variables without considering recent annual deforestation and other variables that are likely important determinants of species distributions (e.g., species interactions, microclimatic conditions, etc.), the output map may overestimate the current vascular plants species richness. Importantly though, if absolute values were too high, the proportion and thus species diversity rankings for each area should remain consistent.

Moreover, the two maps of species richness (Fig. 6) actually provide different information. Although the model of plant species richness gives a “biogeographic” estimate of the potential species richness, mammal species richness is more similar to the actual species richness due to issues related to the historical alteration of the species distribution ranges (e.g., habitat destruction, hunting, and other human-related activities may have altered the original species distribution). Thus, species richness for mammals may also reflect historical/human-related factors, as well as biogeography.

Indochina and Borneo: Major Evolutionary Hotspots

Geological and climatic processes associated with the early Miocene collision (see above) may have effectively divided the biota into two major Miocene areas north and south of the Thai-Malay Peninsula: namely, Indochina and (an extended) Borneo (Fig. 1, 15 Ma). Consistent with an expectation of *in situ* diversification in refugia and thus the accumulation of lineages during the global middle Miocene Climate and sea-level maximum, our analyses of phylogenetic diversification events show an increase in the rate of diversification consistent with this time period (Fig. 5 and Supplementary Fig. S13 and Table S4). This is most evident for Indochina and Borneo, suggesting a role for global Miocene sea-level fluctuations and associated refugia development on biotic evolution.

SE Asia’s biodiversity has evidently been shaped by both geological and climatic drivers resulting in an extremely complicated history of past land (re)connections, including micro-terranic movements, with a young age of many diversification events evident in the phylogenetic meta-analyses, a high proportion of which occur in the latest Pliocene and Pleistocene (Supplementary Fig. S13; see also [Stelbrink et al. \(2012\)](#) for details on Sulawesi). During the Pliocene, Borneo essentially maintained its earlier configuration. The Barisan Mountains of Sumatra continued to develop to their present altitudes (Fig. 1, 5 Ma); the Sumatran coastal plain expanded and at times of low sea level may have been contiguous with the Thai-Malay Peninsula. The island of Java essentially formed during this period and floristic differences from Sumatra as emphasized by [van Welzen et al. \(2011\)](#) probably relate to its persistently drier climate and young geological age. A substantial increase in the colonization of other Greater Sunda Islands and the Philippines from Borneo and Indochina in the Miocene and even more pronounced in the Plio-Pleistocene (Fig. 4 and Table 3), although representing a much shorter timeframe compared with the Miocene. An increase in colonization events between adjacent areas of Sundaland (see Fig. 4 and Table 3) is potentially contemporaneous with the successive (re)emergence of land in these areas and cyclical climate-induced connectivity (Fig. 2). Consistent with these young emergent ages, ancestral area estimation generally

show less frequent colonization events out of Java and Sumatra (compared with Borneo and Indochina), but higher levels of immigration events into these areas (Fig. 4 and Table 3). Hence, climate-forced sea-level changes facilitating interarea connection–disconnection events have played a substantial role in providing new dispersal “corridors” for such lineage dispersal across SE Asia.

Indochina, and Borneo especially, the two largest SE Asian areas examined here with the longest emergent histories, have been major diversification hotspots through time and key sources for lineage dispersal across the region (Fig. 4 and Table 3). Such larger areas may also have experienced comparatively fewer extinction events due to presence of additional putative refugia. Our analyses suggest that length of emergent history has been a more important factor than current area size for both total number of lineages and levels of emigration events for Indochina and Borneo (Supplementary Table S4); however, future analytical approaches should consider changes in area size since emergence. For example, analytical advances to test for both ancestral area estimation and geography–diversification correlations have recently become available (e.g., R package BioGeoBEARS, [Matzke 2013](#); GeoSSE, [Goldberg et al. 2011](#)). Moreover, our analyses show that the prolonged emergent history of Indochina and Borneo initially facilitated the accumulation of lineages in both biogeographic areas (Fig. 5 and Supplementary Fig. S13 and Tables S1 and S5), resulting in increased levels of emigration across SE Asia when remaining islands (re)emerged over the course of Mio- and Plio-Pleistocene sea-level fluctuations (Figs. 2 and 4, Table 3, and Supplementary Table S3).

In summary, we find evidence for all four hypotheses set out in the Introduction, namely: levels of *in situ* diversification events reflected emergent ages (but not current sizes) of our predefined areas; areas with recent histories of sea-level inundation (e.g., Sumatra and Java) were characterized by higher levels of (recent) immigration than emigration; number of colonization events were greater between adjacent areas compared with more distant areas; and finally, an increase in diversification rates was evident during the Plio-Pleistocene, likely resulting from increased connection–disconnection events related to sea-level fluctuations.

Although the importance of Indochina to the evolutionary history of SE Asian biodiversity has long been recognized ([Myers et al. 2000](#); [Lohman et al. 2011](#) and references therein), Borneo, embedded in one of the world’s most exceptionally diverse biodiversity hotspots (Sundaland; see [Myers et al. 2000](#)) is clearly also of extraordinary importance to the SE Asian biota, as shown here across several taxonomic groups through all time periods investigated. Much of Borneo’s remarkable diversity, including remnant populations of conservation icons such as Sumatran rhinoceros (*Dicerorhinus sumatrensis*) and Bornean orangutan (*Pongo pygmaeus*), is under extreme and sustained pressure from anthropogenic habitat conversion ([Miettinen et al. 2011](#))

and unsustainable use (Koh and Sodhi 2010; Wilcove et al. 2013).

These results conclusively drive home the importance of maintaining extensive high priority conservation areas in Borneo as envisaged under the current “Heart of Borneo” agreement between Indonesia, Malaysia, and Brunei. However, the agreement fails to adequately protect extensive areas of lowland rainforest, which harbor the highest levels of diversity. Losing further large areas of forested land to development in this region will result in the irreplaceable loss of the primary refuge area for the entire Sunda Shelf region.

SUPPLEMENTARY MATERIAL

Supplementary material can be found in the Dryad data repository at <http://dx.doi.org/10.5061/dryad.67s40>.

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