doi:10.1111/evo.12084

GEOGRAPHIC AND TAXONOMIC DISPARITIES IN SPECIES DIVERSITY: DISPERSAL AND DIVERSIFICATION RATES ACROSS WALLACE'S LINE

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Received September 10, 2012
Accepted January 24, 2013

Broad-scale patterns of species diversity have received much attention in the literature, yet the mechanisms behind their formation may not explain species richness disparities across small spatial scales. Few taxa display high species diversity on either side of Wallace's Line and our understanding of the processes causing this biogeographical pattern remains limited, particularly in plant lineages. To understand the evolution of this biogeographical pattern, a time-calibrated molecular phylogeny of Livistoninae palms (Arecaceae) was used to infer the colonization history of the Sahul tectonic plate region and to test for disparities in diversification rates across taxa and across each side of Wallace's Line. Our analyses allowed us to examine how timing, migration history, and shifts in diversification rates have contributed to shape the biogeographical pattern observed in Livistoninae. We inferred that each of the three genera found in Sahul crossed Wallace's Line only once and relatively recently. In addition, at least two of the three dispersing genera underwent an elevation in their diversification rate leading to high species richness on each side of Wallacea. The correspondence of our results with Southeast Asian geologic and climatic history show how palms emerge as excellent models for understanding the historical formation of fine-scale biogeographic patterns in a phylogenetic framework.

KEY WORDS: **Biogeography, diversification rate, *Licuala*, *Livistona*, Livistoninae, *Saribus*.**

Since Darwin (1859) and Wallace (1878), biologists have hypothesized about the mechanisms driving disparities in species diversity across geographic space. Broad patterns of species diversity have been the focus of most studies such as the disparities between temperate and tropical regions (e.g., Middlebach et al. 2007) and the Neotropics and Paleotropics (e.g., Phillips et al. 1994). There are many potential explanations for differences in these large-scale patterns including geological and climatic history, the size of the geographic area, the extent of biotic interactions, and speciation versus extinction rates. Outside of these large-scale patterns are sharp differences in species diversity within relatively small biogeographic regions and these discrete instances may lead to the understanding of local-scale processes that are fundamental in shaping large-scale diversity patterns (e.g., Ricklefs 1987).

Southeast Asia is divided by one of the most widely recognized biogeographic barriers, Wallace's Line (Wallace 1860). Wallace's Line separates the Asian (Sunda tectonic plate) and Australian (Sahul plate) biotic regions and over a relatively small geographic area many lineages exhibit a sharp break in their distributions where groups are primarily found on only one side and few are found on both sides. This distributional pattern was first observed in lineages that have nearly complete differences in their taxonomic composition from west to east, including birds and mammals (Wallace 1878;

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Mayr 1944; Simpson 1977; Mayr and Diamond 2001). After Wallace's original placement of the line, further study revealed that a single line could not accommodate the species distribution patterns observed across the tree of life (Huxley 1868; Lydekker 1896; Weber 1902). Although the exact location of the transition in taxonomic composition varies, the existence of such a sharp transition has long intrigued biogeographers.

In some taxonomic groups, Wallace's Line causes a strong discontinuity in their distribution, whereas other groups have been reported to cross the biogeographic barrier once (e.g., Mercer et al. 2003) or multiple times (e.g., Evans et al. 2003) during their evolutionary history. This biogeographic barrier has been shown to be weaker for plants (Whitmore 1982; Van Welzen et al. 2011) and some insects (e.g., Beck et al. 2006), where increased dispersal ability is thought to have allowed species to colonize both sides of the line (e.g., *Aglaia*, Muellner et al. 2008; *Rhododendron*, Van Welzen et al. 2005). Despite this evidence, even species known to have high dispersal abilities show discontinuities in their distribution across Wallace's Line (e.g., Atkins et al. 2008).

The complex geological history of the region, which combines the reorganization of terrestrial habitats with the collision of the Sunda and Sahul shelves, high volcanic activity, and repeated fluctuations in sea level (Morley 2000; Hall 2009), has engendered many opportunities for habitat fragmentation, migration, and colonization of new habitats, and ultimately allopatric speciation (e.g., Beck et al. 2006; Esselstyn et al. 2009). Therefore, the geological legacy of the region and the evolutionary history of groups found on each side of Wallace's Line together help us tease apart the processes that have contributed to the generation of the hyperdiversity in Southeast Asia where three of the 25 recognized global biodiversity hotspots are located (Myers et al. 2000).

To further understand how diverse groups can be distributed on each side of Wallace's Line, the timing and the relative contribution of migration events, and diversification rates within each biogeographic region need to be examined. At one extreme, numerous instances of migration across Wallace's Line could be followed by low in situ diversification. At the other extreme, a single to few migration events could be followed by high in situ diversification. Furthermore, rates of diversification can be influenced by intrinsic morphological characteristics associated with particular species (i.e., "key innovations" such as plant elaiosomes; Forest et al. 2007), some extrinsic geological or environmental feature associated with the biogeographic region (e.g., episode of vicariance or the onset of an ecological association; Moore and Donoghue 2009), or some combination of both (e.g., adaptive radiation of morphotypes following colonization of a novel habitat; Baldwin and Sanderson 1998; Losos et al. 1998; Schluter 2000; Wagner et al. 2012). By estimating diversification rates using time-calibrated phylogenies, the likelihoods of diversification models with different rates for each biogeographic region, each taxonomic group, or a combination of both can be compared. Through the synthesis of these results we can gain insight into the processes that shape the patterns of diversity and further understand the constraints that some clades have overcome when crossing biogeographic barriers, such as Wallace's Line, and more generally contributes to our understanding of why some groups are more diverse than others.

Several groups of angiosperms are diverse in both Sunda and Sahul with a reduction in species richness in Wallacea primarily due to its comparatively small land area and this pattern is suggested to be most pronounced in the palm family, Arecaceae (Dransfield 1981, 1987; Baker et al. 1998; Baker and Couvreur 2012). The prevailing biogeographic pattern in Southeast Asian palms is interesting because of the extreme biogeographical disjunction it forms across a relatively small area where from west (Sunda) to east (Sahul) 302 palm species are found in Borneo, 62 in Sulawesi, and 243 in New Guinea. Within the palms, subtribe Livistoninae (Arecaceae, Coryphoideae, Trachycarpeae) is an ideal group to examine disparities in biogeographic patterns across Wallace's Line because it includes genera that are differentially species rich on either side and, although intergeneric relationships have remained tenuous, it has been the focus of a recent phylogenetic study (Bacon et al. 2012). Livistoninae comprise 198 species (Dransfield et al. 2008) in six genera—*Johannesteijsmannia* (four species), *Lanonia* (eight; Henderson and Bacon 2011), *Licuala* (144), *Livistona* (27), *Pholidocarpus* (six), *Saribus* (nine; Bacon and Baker 2011). The ancestral stem lineage of this monophyletic subtribe originated in the New World in the Late Oligocene to Early Miocene (North and Central America and / or the Caribbean ca. 18.5–34 Ma; Bacon et al. 2012) and the extant distribution of Livistoninae is from Bhutan and China into Malesia and crosses Wallace's Line into New Guinea and Australia (Henderson 2009).

To understand the relative importance of migration between biogeographic regions and diversification rates in shaping the distribution pattern observed in palm lineages in the Southeast Asian region, we infer the tempo and mode of species diversification in Livistoninae. We use a densely sampled and time-calibrated phylogeny to test the monophyly of genera and the timing of lineage origination and diversification. Likelihood models of historical biogeography allow us to localize the timed lineages in geographical space and infer the number of vicariance and dispersal events that occurred among ancestral ranges to test the contribution of migration in patterns of species diversity. We compare the likelihoods of various models of diversification to determine whether constraints associated with either taxonomic identity, biogeographic area, or both have contributed to shape the patterns of diversification observed in Livistoninae. Taken together, these analyses permit a synthesis of origin, diversification, timing, and biogeography of species diversity patterns

Figure 1. Map of Southeast Asia and Australia with the two major tectonic plates, Sahul and Sunda, as well as the biogeographic region Wallacea and the demarcation of Wallace's Line.

into a geological and paleoclimatic framework to examine the mechanisms that formed the biographic patterns and rich biodiversity found in the Southeast Asian hotspot today.

Materials and Methods

STUDY REGION—SOUTHEAST ASIA

The Sunda continental shelf spans southern Indochina, to the Thai–Malay peninsula, and to Sumatra, representing the ancient continental core of the region (Fig. 1; Hall and Morley 2004). To the east is the Sahul shelf, which forms the Australian continent. Within the suture zone between the Sunda and Sahul regions is Wallacea, which is bounded to the west by Wallace's Line, the biogeographic demarcation between Asian and Australian biota. Wallacea is the collision area between the two plates and constitutes the most geologically complex part of Southeast Asia (Hall 2009). The sharp biotic differentiation on either side of Wallacea has been maintained by a deep, cold-water oceanic trench (Nagao and Selya 1995) and in general, Sunda and Sahul regions are characterized by an ever-wet climate, whereas the intervening area of Wallacea has a dry monsoonal climate (Van Welzen et al. 2005).

TAXON SAMPLING AND DNA SEQUENCING

Dense species-level sampling allowed for accurate assessments of phylogenetic relationships and was based on Bacon et al. (2012) with the addition of 26 species and DNA sequences for an additional nuclear gene (malate synthase [MS]; Table S1). The two outgroups (*Acoelorrhaphe wrightii* H. Wendl and *Serenoa repens* [W. Bartram] Small) were chosen based on previous analysis (Bacon et al. 2012). Between 31% and 100% of species from each Livistoninae genus were sampled and a total of 98 terminals were included in the simultaneous analysis (Kluge 1989; Nixon and Carpenter 1996). Total genomic DNA was extracted from silica gel–dried leaves following Alexander et al. (2007). Sequences for three plastid (*matK*, *ndhF*, and *trnD-T*) and four nuclear loci (CISP4, CISP5, MS, and RPB2) were generated (Fig. S1). Single amplifications of the *matK* locus used primers *matK*-19F and *matK*-1862R, with internal sequencing primers *matK*-300F, *matK*-809F, and *matK*-971R to construct contiguous sequences (Steele and Vilgalys 1994; Asmussen et al. 2006). Amplifications of CISPs 4 and 5 followed Bacon et al. (2008), MS followed Crisp et al. (2010), *ndhF* followed Cuenca and Asmussen-Lange (2007), RPB2 followed Roncal et al. (2005), and *trnD-T* followed Hahn (2002). Amplified products were purified using Qiagen PCR Purification Kits and sequenced by the Cancer Research Center DNA Sequencing Facility at the University of Chicago, IL. All new sequences generated in this study have been deposited in GenBank under accession numbers HQ720156–HQ720240 and HQ720962–HQ721101 (Table S1).

PHYLOGENETIC ANALYSIS

Multilocus phylogenies enabled the testing of monophyly of Livistoninae genera and biogeographic groups. Preliminary nucleotide alignments were obtained independently for each of the seven loci using default parameters in MUSCLE v3.6 (Edgar 2004) and manual adjustments were performed in MacClade v4.03 (Maddison and Maddison 2001) following Simmons (2004). Gap characters, the inclusion of which often affect the inferred tree topology and increases branch support values (Simmons et al. 2001), were scored using modified complex indel coding (Simmons and Ochoterena 2000; Müller 2006). Only parsimony-informative gap characters were scored from unambiguously aligned regions and parsimony tree searches were conducted using 1000 random addition tree–bisection–reconnection (TBR) searches in PAUP* v4.0b10 (Swofford 2001) with a maximum of 10 trees held per replicate. Parsimony jackknife (JK) analyses (Farris et al. 1996) were conducted using PAUP* and 1000 replicates were performed with 100 random addition TBR searches per replicate. jModeltest v0.1.1 (Posada 2008) was used to select the best-fit likelihood model for each data matrix using the Akaike Information Criterion (Akaike 1974) without considering invariant-site models following Yang (2006). Searches for optimal maximum likelihood trees (Felsenstein 1973) and 1000 bootstrap replicates (Felsenstein 1985) in the CIPRES Portal v2.2 used the RAxML-III algorithm (Stamatakis et al. 2005, 2008). The simultaneous analysis was performed using the GTR + Γ model and the data matrix is available from TreeBase (study accession 11108).

BAYESIAN DIVERGENCE TIME ESTIMATION

We estimated divergence times using BEAST v1.5.4 (Drummond et al. 2006; Drummond and Rambaut 2007) by reducing the matrix to include only one individual per species. Because we do not know of any unambiguously identified fossils in Livistoninae, we used a secondary calibration point obtained from a broader study based on primary fossil calibrations (tribe Trachycarpeae; Bacon et al. 2012). A normal distribution for the secondary calibration point at the stem node of Livistoninae was implemented using a mean of 26 Ma and a 2.7 standard deviation of the prior to capture the variation around the mean (18–34 Ma Livistoninae stem age; Bacon et al. 2012). The normal distribution has been shown to be most appropriate for modeling secondary calibrations because it reflects the uncertainty in imported date estimates (Ho 2007; Ho and Phillips 2009).

The data were partitioned by locus to allow for variation in substitution models, which can alleviate or remove the impact of saturation caused by using relatively older fossils for inferences directed at more recently evolved nodes (sensu Ho et al. 2005). The analysis was run using an uncorrelated lognormal molecular clock model, a Yule pure birth speciation model with no starting tree, the GTR + Γ model of nucleotide substitution with four rate categories, and the default operator. The Markov chains were run for 50 million generations and repeated 10 times to test for Markov Chain Monte Carlo chain convergence and to ensure effective sample sizes exceeded 200. After verifying that chains had reached stationarity in Tracer v1.5, 10% was removed as burn-in and BEAST log files were combined in LogCombiner v1.5.4. Tree files were combined to estimate median node height and the 95% highest posterior density (HPD) in TreeAnnotator v1.5.4.

BIOGEOGRAPHICAL RECONSTRUCTIONS

To test whether disparity in species diversity is due to the history of migration, we estimated the number of dispersal and vicariance events along phylogenetic branches and the historical biogeography of Livistoninae. Ancestral range patterns were inferred using five geographic areas: (A) southeastern North America; (B) Africa and Arabia; (C) eastern Asia (India to Thailand, excluding the peninsular region), China (including Hainan), and Japan; (D) west of Wallace's Line (peninsular Thailand and the Philippines to Borneo), (E) east of Wallace's Line (Sulawesi, New Guinea, and Australia to Vanuatu). We separated continental (C) from insular (D) areas of Sunda to account for the high amounts of geological change in D. Biogeographic areas were delimited based on areas of endemism in the tribe while also minimizing the total number of areas and the number of polymorphic distributions (Sanmartín and Ronquist 2004). Geographic areas were also set up to allow for explicit hypothesis testing of dispersal and its effects on diversification rates where area D is west and area E is east of Wallace's Line. In applying character-state reconstruction methods to ancestral distributions, we coded geographic ranges as discrete, multistate characters that allowed for ranges spanning more than one of these five geographic areas (e.g., Hardy and Linder 2005).

A likelihood framework for examining historical range shifts was implemented using the dispersal–extinction–cladogenesis model (DEC; Ree et al. 2005) in Lagrange build 20120508 (Ree and Smith 2008a). DEC has been shown to be a robust model of inferring historical biogeography because it can incorporate parameters such as divergence time estimates, dispersal capacities, extinction rates, and paleogeographic information between regions in geological time (Ree and Smith 2008b). Lagrange estimates the relative likelihood of each possible ancestral range at each node, given a particular probability of dispersal and extinction. The evolution of geographic range was simulated using a rate matrix method that exponentiates branch-specific transition probabilities and enabled the likelihood of the observed species distributions to be evaluated for a given phylogeny. We used the ultrametric tree generated by BEAST to infer ancestral distributions with default parameters for extinction rates and an equal rate for dispersal capacity among all areas in the analysis. The statistical support for biogeographic reconstructions is defined by its relative probability (fraction of the global likelihood).

LIKELIHOOD ESTIMATION OF DIVERSIFICATION RATES

To test whether shifts in diversification rates may have contributed to the geographic and taxonomic disparities of species diversity, we fit models of diversification to the consensus phylogeny of Livistoninae inferred with BEAST using the R functions provided as supplementary information in Morlon et al. (2011) and others (H. Morlon, pers. comm. 2012). Outgroups were removed and the tree was reduced to include only one individual per species (Rabosky 2006), resulting in a tree with 74 terminals.

We fit models of diversification to the Livistoninae phylogeny with speciation and extinction rates being constant (λ_0, μ_0) or being allowed to vary linearly [$\lambda(t) = \lambda_0 + \lambda t$, $\mu(t) = \mu_0 + \mu t$] or exponentially [$\lambda(t) = \lambda_0\, e^{\alpha t}$, $\mu(t) = \mu_0\, e^{\beta t}$] through time. Given the location of the reconstructed migration events on the phylogeny and given that *Licuala*, *Livistona*, and *Saribus* are the three most diverse genera in the Livistoninae, we then fit diversification models where the speciation and extinction rates could vary among lineages, and be constant or vary through time. In particular, we compared the likelihoods of models with shifts in diversification rates that were associated with the taxonomic identity of the lineages (i.e., different rates for *Licuala*, *Livistona*, and *Saribus*), their extant biogeographic distribution (i.e., within Sahul or outside of Sahul), or a combination of both. Therefore, the models with the most shifts included different speciation and extinction rates for the six following lineages: *Licuala* within Sahul, *Licuala* outside of Sahul, *Livistona* within Sahul, *Livistona* outside of Sahul, *Saribus* within Sahul, and other lineages (model "A" in Table 1). In total, we assessed 17 hypotheses characterized by zero to five shifts in diversification rate located at the nodes

Table 1. List of diversification models (uppercase letters, A–Q) fitted to the Livistoninae phylogeny. The log-likelihood (LogLik) and corrected Akaike information criterion (AICc) are reported for the models fitted on the incomplete phylogeny. *k* is the number of subtrees on which diversification rates were estimated for each model. The lowercase letters (a–v) show lineages on which the diversification rates were estimated. For instance, model "P" is characterized by one rate for lineages within Sahul (denoted by r) and one rate for lineages outside of Sahul (denoted by "j"). Models are ranked based on their AICc scores. Akaike weights are calculated from the AICc scores. *Pho.* = *Pholidocarpus*; *Johan.* = *Johannesteijsmannia.*

Model	*k*	Sahul *Licuala*	Other Other	Sahul *Livistona*	Other *Livistona*	Sahul *Saribus*	Other *Saribus*	Others (*Pho.*, *Lanonia*, *Johan.*)	LogLik	AICc	Akaike weights	Ranks	Ranks from simulated phylogenies
A	6	a	b	c	d	e	f	f	−194.47	402.70	0.116	3	3
B	**5**	**a**	**b**	**c**	**g**	**e**	**g**	**g**	**−195.15**	**401.44**	**0.218**	**1**	**1**
C	5	a	h	c	d	e	h	h	−197.06	405.69	0.026	10	8
D	5	a	b	c	d	i	i	i	−196.36	403.86	0.065	6	4
E	4	a	j	c	j	e	j	j	−197.46	403.90	0.064	7	10
F	4	a	b	c	k	k	k	k	−197.16	402.87	0.107	4	2
G	4	l	l	m	m	n	n	o	−201.45	411.61	0.001	14	9
H	3	a	b	p	p	p	p	p	−201.89	410.14	0.003	12	5
I	3	q	q	c	d	q	q	q	−201.69	410.14	0.003	11	13
J	4	r	b	r	d	r	f	f	−197.05	402.98	0.101	5	7
K	3	r	b	r	g	r	g	g	−197.72	401.72	0.189	2	6
L	3	r	h	r	d	r	h	h	−198.83	404.38	0.050	9	12
M	2	s	s	s	s	e	s	s	−206.06	416.72	<0.001	17	14
N	2	a	t	t	t	t	t	t	−203.84	411.92	0.002	15	11
O	2	u	u	c	u	u	u	u	−203.54	411.27	0.002	13	17
P	2	r	j	r	j	r	j	j	−200.03	404.19	0.055	8	15
Q	1	v	v	v	v	v	v	v	−206.07	414.20	<0.001	16	16

corresponding to the three genera and their extant biogeographic distribution.

We assessed the fit of the models based on their corrected Akaike information criterion (AICc) value (see Morlon et al. 2011). We used this criterion (1) to select the most likely mode of diversification (pure-birth or birth-death; constant or time varying) for each subtree on which the speciation and extinction rates were estimated (lower-case letters "a" through "v" in Table 1); (2) to determine whether models that included shifts in diversification rates during the radiation of the Livistoninae were more likely (uppercase letters "A" though "Q" in Table 1). To ensure that the maximum likelihood optimizations were converging on stable solutions, we tested several combinations of starting parameters for each of the diversification rate estimations.

We assigned missing taxa to the phylogeny using the best estimate of the total number of species in each group based on morphology, published and unpublished work, recent field expeditions, and the World Checklist of Palms (http://apps.kew.org/wcsp/home.do). The proportion of sampled species for each subtree on which diversification rate estimations were performed was calculated based on these assignments. The fraction of missing species is accounted for in the likelihood formulation providing unbaised estimates of the diversification rates if the missing species represent a random sample of the species pool. Given that the unsampled species in our phylogeny do not represent a random sample of the species pool, we tested whether this violation of the assumptions affected our conclusions. To this end, we generated 500 phylogenies that included the missing species by grafting random phylogenies for each group of missing species onto the tree used in our previous analysis, based on the species assignments. As constant pure-birth diversification models were always favored when estimated on the incomplete phylogeny (see Results), we fit constant pure-birth models on the subtrees corresponding to each of the 17 hypotheses of shifts in diversification rates on the simulated phylogenies. These hypotheses were then ranked based on the sum of the ranks obtained for each one of the 500 simulated phylogenies according to their AICc scores. All the diversification analyses were performed in R 2.15.0 (R Core Team 2012) using the ape (Paradis et al. 2004), multicore (Urbanek 2011), doMC (Revolution Analytics 2012), and phylobase (Bolker et al. 2011) packages.

Results

GENE TREE INCONGRUENCE AND SYSTEMATICS OF LIVISTONINAE

Parsimony and maximum likelihood analyses similarly resolved relationships across loci although incongruence was detected for intergeneric relationships in three of the seven gene trees (Fig. S1). The CISP4, *matK*, and RPB2 gene trees show differences in the position of *Pholidocarpus* and *Livistona*. In the CISP4 gene tree *Pholidocarpus* is resolved as sister to *Lanonia* and *Pholidocarpus* + *Lanonia* are nested within a polytomy also encompassing *Johannesteijsmannia*, *Saribus*, and *Licuala*. In the *matK* gene tree, *Pholidocarpus* is resolved outside of the subtribe and in contrast to both the CISP4 and *matK* gene trees, the RPB2 gene tree resolved *Pholidocarpus* in a clade with *Licuala* and *Saribus*. In the simultaneous analysis, *Lanonia* is resolved as sister to *Johannesteijsmannia*, which together are sister to *Saribus*, *Licuala*, and *Pholidocarpus* (Figs. S2 and S3). Furthermore, the partitioned Bayesian analysis (BEAST) resolved the same topology with similar branch-support values as the likelihood and parsimony simultaneous analyses (*Lanonia* and *Johannesteijsmannia* are sister with 1.0 PP). Despite these incongruences, our sampling of one or two individuals per species and seven loci is insufficient to determine the coalescent species tree for Livisontinae (sensu Fig. 10.7 in Knowles 2010). In agreement with previous studies (Asmussen and Chase 2001; Asmussen et al. 2006; Baker et al. 2009; Bacon et al. 2012), Livistoninae was highly supported as monophyletic (Figs. S1–S3). Each of the Livistoninae genera was resolved as monophyletic and highly supported (Figs. S2 and S3) and our results also corroborate the recent recognition of *Lanonia*, a new genus of palms (Henderson and Bacon 2011).

DIVERGENCE TIMES IN LIVISTONINAE

Two metrics were used to evaluate the appropriateness of assuming a model of uncorrelated rates of molecular evolution when estimating divergence times. First, the covariance statistic was examined in Tracer v1.5, which provides an approximation of phylogenetic autocorrelation of molecular rates. The distribution for this analysis centers on zero ($P = -0.0414$, 95% HPD of -0.1713 to 8.4707E^{-2}], indicating that there is no support for molecular rates to be inherited from parent to child nodes across the entire phylogeny. Second, the coefficient of variation was also examined in Tracer, which measures the proportion of the variation in molecular rates surrounding the mean. The distribution of possible coefficients of variation is centered far from zero (0.5495 with 95% HPD of 0.4 to 0.7068), suggesting that rates vary more than 55% about the mean and is indicative of the extreme rate heterogeneity that was specifically accounted for in the model. Our results indicate that the crown group of Livistoninae originated at ca. 24 Ma (Fig. 2; Table S2; 95% HPD of 16.1–28.5 Ma, PP = 1.0). The three genera with distributions across Wallace's Line had monophyletic crown groups that originated between ca. 12 and 15.5 Ma and are the three oldest crown ages in the phylogeny. Despite this, the highest species diversity is in *Licuala*, which did not have the oldest inferred age of the clades that crossed Wallace's Line.

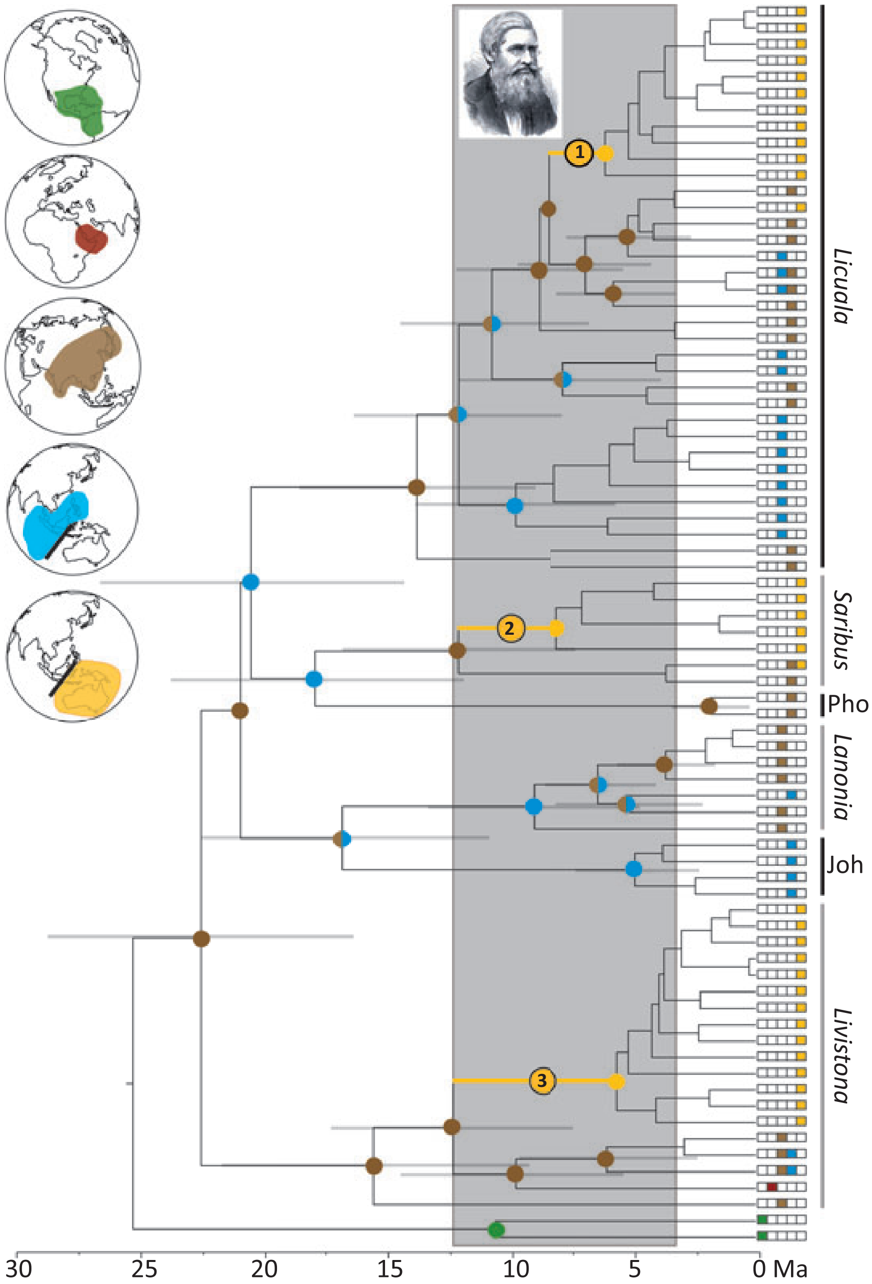

Figure 2. The maximum clade credibility tree from the Bayesian-divergence-time analysis with the biogeographical reconstruction produced from ancestral range analysis, where uncertainty in reconstructions is described in Table S3. The HPD range for each major clade supported with greater than 0.5 posterior probability is indicated with node bars. The five biogeographic regions are color coded and mapped to their geographic position where circles at nodes with two colors represent polymorphic distributions. The black line in the two lower maps represents Wallace's Line. Yellow branches for the three instances of successful dispersal across Wallace's Line and occur between ca. 3.2–12 Ma, which is highlighted in gray. *Pholidocarpus* and *Johannesteijsmannia* are abbreviated as Pho and Joh, respectively and the portrait of A. R. Wallace is adapted from *Popular Science Monthly* 11 (1877).

BIOGEOGRAPHICAL RECONSTRUCTIONS

Estimation of historical ranges and biogeographical events (e.g., dispersal, vicariance) allowed for the localization of ancestral lineages in geographical space. Coding of the distributions required scoring the following five species as polymorphic: one (*Saribus rotundifolius*) that is found from Borneo to New Guinea (areas D and E) and four others (*Licuala paludosa*, *L. spinosa*, *Livistona saribus*, and *L. jenkinsiana*) that are found in both eastern Asia and Peninsular Thailand and the Philippines to Borneo and Java (areas C and D). The nodes of interest with likelihood scores that were not significantly different between reconstructions (within $-2 \ln L$; Ree and Smith 2008b) are shown in Table S3. The "widespread ancestor problem" (Ree et al. 2005) was not detected in the Livistoninae biogeographic reconstructions and only six internal nodes were reconstructed as ranging in more than one area (Fig. 2).

The backbone of the Livistoninae tree is inferred to have ancestral distributions in eastern Asia (area C; Fig. 2). All other Livistoninae genera are inferred to have either an eastern Asian or Sunda origin (area D). From the consensus scenario of range inheritance in Livistoninae 15 instances of dispersal, 13 local extinctions, and two vicariance events were reconstructed. Five instances of dispersal were reconstructed from the Sunda region across Wallace's Line into the Sahul region, all of which were inferred in *Licuala*, *Livistona*, and *Saribus*. Despite this, only three dispersal events resulted in further diversification (nodes 1–3 respectively; Fig. 2). The number of biogeographic events per genus that crossed Wallace's Line also lends support to the hypothesis that the history of migration may factor into species richness patterns. No events were inferred to have occurred in the crown lineages of *Pholidocarpus* and *Johannesteijsmannia*, whereas *Lanonia* had three, *Saribus* four, *Livistona* six, and *Licuala* had 12 events inferred.

DIVERSIFICATION RATE SHIFTS IN LIVISTONINAE

For each diversification rate estimation (lowercase letters "a" through "v"; Table 1), pure-birth models with constant rate through time were consistently favored based on their AICc values. Models that included shifts in diversification rates were generally favored over the model with a single diversification rate for the entire Livistoninae phylogeny (model "Q" ranked 16 out of 17 models for both the incomplete phylogeny and the simulated phylogenies; Table 1), indicating that rates of diversification are heterogeneous among Livistoninae lineages. The model with the best AICc score included five diversification rates: *Licuala* within Sahul, *Licuala* outside Sahul, *Livistona* within Sahul, *Saribus* within Sahul, other species (*Livistona* outside Sahul, *Saribus* outside Sahul, *Johannesteijsmannia*, *Pholidocarpus*, and *Lanonia*; Table 1; Fig. 3). More generally, models that included different diversification rates for a combination of taxonomic identity and biogeographic origin had better AICc scores than models with different diversification rates based solely on taxonomic identity (model "G" ranked 14 and 9 for the incomplete phylogeny and the simulated phylogenies, respectively) or biogeographic origin (model "P" ranked 8 and 15; Table 1).

Using either the incomplete phylogeny or the simulated phylogenies, the model of diversification that fit the data best inferred five diversification rates with three shifts that corresponded to the crossing of Wallace's line, as well as one shift for *Licuala* found outside of Sahul (model "B"; Table 1). This model was also favored in more than 98% of the 500 simulated phylogenies. Overall, the models for which the ranks were most different when estimated on the incomplete phylogeny compared to the simulated phylogenies were the simpler models with fewer shifts.

The pure-birth speciation rates for model "B" estimated on either the incomplete phylogeny or the simulated phylogenies are higher after crossing Wallace's Line than the rate for the ancestral lineages of *Licuala* and *Livistona* (1.4 and 1.7 times higher based on the estimates obtained from the simulated phylogenies, respectively; Fig. 3). The magnitude of the shift in speciation is less pronounced in *Saribus* and the direction of the shift is different whether it is estimated from the incomplete phylogeny (speciation rate increases from 0.146 to 0.152) or from the simulated phylogenies (speciation decreases from 0.183 to 0.161).

Discussion

The potential explanations for broad-scale patterns in species richness may apply generally to disparities across smaller spatial scales. Despite this, explicit hypothesis testing to understand sharp differences in species diversity at a local-scale may lead to novel insights that can be applied to other regions and biogeographic patterns. In this study we focused on Southeast Asia and specifically the biogeographic pattern in species richness between the Sunda and Sahul regions. Based on the evidence from *Licuala*, *Livistona*, and *Saribus*, the distributions result from a few, relatively recent migration events across Wallace's Line followed by in situ diversification within the Sahul region. Furthermore, the biogeographic pattern is accentuated by the rapid diversification of *Licuala* and *Livistona*, and to some extant *Saribus* in the Sunda region. Although there are limitations to the method used (e.g., secondary age estimates, difficulties with diversification rate inference), our estimates, taken together, detect mechanisms of species diversification that correspond to the geological and climatic history of the region.

TAXONOMIC HYPOTHESES

The monophyly of Livistoninae has been previously recognized, although intergeneric relationships within Livistoninae were poorly understood due to weak branch support (Asmussen and Chase 2001; Asmussen et al. 2006; Baker et al. 2009; Bacon et al. 2012). Our data indicate that *Livistona* is the earliest divergent genus in the tribe (Fig. S2) and corroborates previous results (Bacon et al. 2012). The CISP 5 gene tree resolved a nonmonophyletic *Livistona*, with *L. carinensis* separated from the rest of the genus by one poorly supported branch. In this study, the other six gene trees, each genome partition, the combined analysis, and the partitioned Bayesian analysis resolved a monophyletic *Livistona* (Fig. S2). Nonmonophyly of *Livistona* had been reported before (Crisp et al. 2010) and *L. carinensis* had

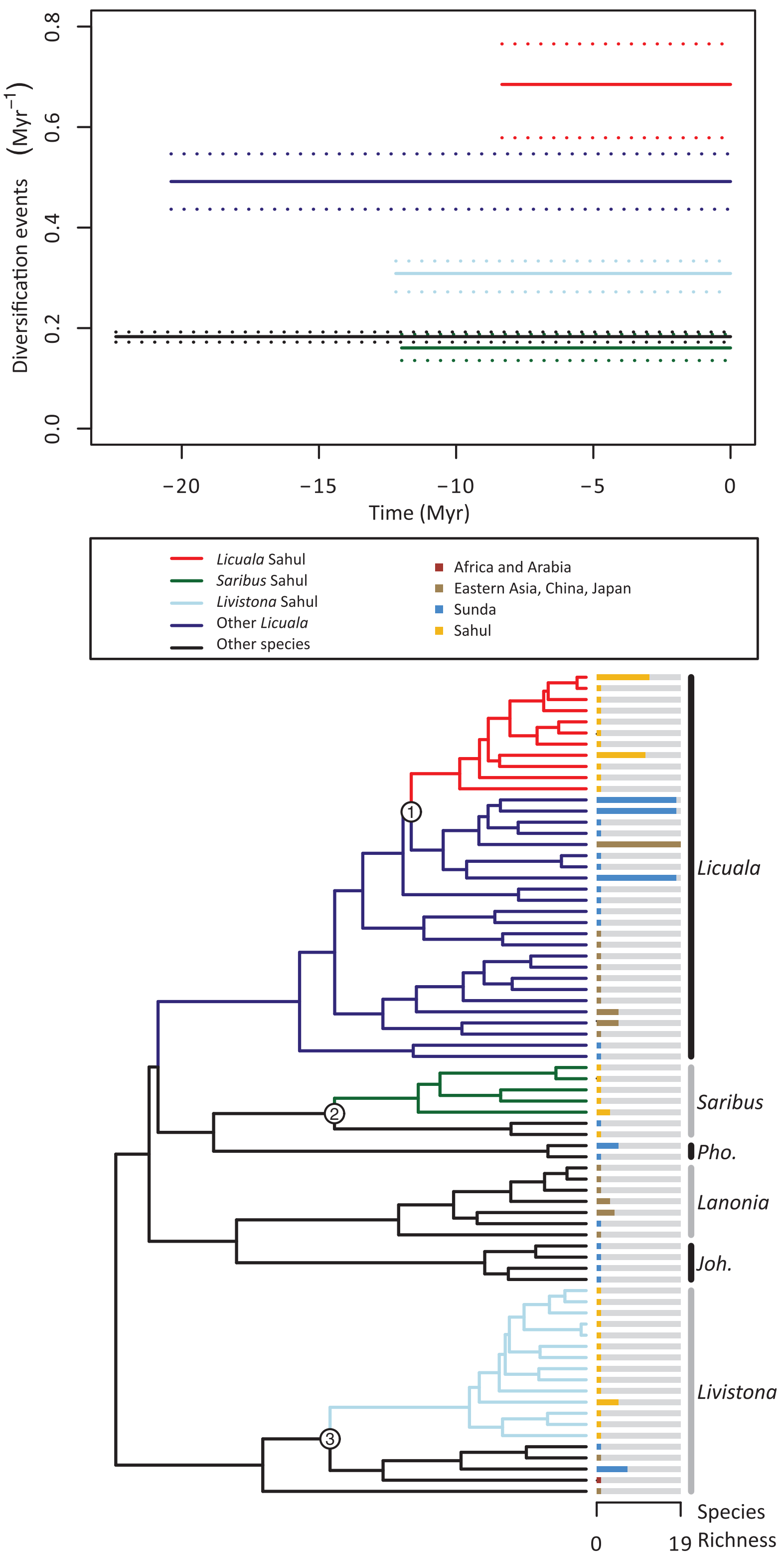

Figure 3. Analysis of diversification rates in Livistoninae. Top: mean (solid line) and 95% confidence interval (dashed line) for the diversification rates from the best model estimated from the set of 500 simulated phylogenies (pure-birth models for each of the following lineages: ***Licuala*** within Sahul, ***Licuala*** outside of Sahul, ***Livistona*** within Sahul, ***Saribus*** within Sahul, other species). Bottom: phylogeny of the Livistoninae with the reconstructed successful instances of dispersal across Wallace's Line (circled 1– 3), bar plot showing the phylogenetic distribution and assignment of the unsampled species (species richness), the extant biogeographic origin of the species (using the same colors as in Fig. 2), and the different lineages being characterized by different diversification rates according to the best-fit model.

been previously recognized as the separate genus *Wissmannia* until 1983 (Dransfield and Uhl 1983). Based on morphology and molecular results, *Livistona* is monophyletic and its distribution is likely relictual because of past climate changes and shifts in boreotropical forest distribution throughout the Miocene (Dransfield 1987; Bacon et al. 2012).

Outside of *Livistona* and sister to the rest of the Livistoninae, we resolved a sister relationship between *Johannesteijsmannia* and *Lanonia* (Fig. S2). Interspecific relationships of *Johannesteijsmannia* were poorly resolved in our analysis, with two nonexclusive species, potentially reflecting misidentifications in the field or with botanical garden material. The clade of *Saribus* + *Pholidocarpus* was resolved as sister to *Licuala* (Figs. S2 and S3). *Saribus* has recently been resurrected as a genus based on molecular and morphological data (Bacon et al. 2012) and is further supported in this study with the additional sampling of three other species (Fig. S2). *Licuala* is highly supported as monophyletic, although interspecific relationships are poorly resolved (Fig. S3). The following three major groups within *Licuala* were reconstructed: *L. longicalycata* + *L. mattanensis*, an Indochina grade, and an east-of-Wallace's-Line clade (clades A–C; Fig. S3).

TEMPORAL AND SPATIAL PATTERNS OF DIVERSIFICATION

Although secondary calibration can be a potential source of estimation error (e.g., Graur and Martin 2004), our estimate was derived from a broader study based on robust fossil data and the uncertainty therein was incorporated in the credible interval at the stem node of Livistoninae (Bacon et al. 2012). Our results show that the dates estimated for Livistoninae correlate with the fossil history of the group. For example, the Australian Oligocene (26.5–28 Ma) trunk fossil *Palmoxylon queenslandicum* is suggested to resemble *Livistona* and *Licuala* (Conran and Rozefelds 2003). The divergence times estimated for Livistoninae diversification overlap with the estimated age of the *Palmoxylon* fossil substrate and the topological position of *Livistona* as the earliest divergent genus also substantiates our divergence time results. Furthermore, missing taxa could bias in the biogeographical reconstructions if they were concentrated in one region but all of the geographic regions used in the analysis were densely sampled within each of the clades inferred.

The mean age estimated for the crown node of the tribe was approximately 25 Ma (95% HPD: 19.64–30.39 Ma) and was reconstructed in eastern Asia (area C; Fig. 2). The origin of the tribe corresponds to one of the most important periods of plate-boundary reorganization in the Cenozoic (formation of Southeast Asia at 20–30 Ma; Hall 1998). Our biogeographical reconstruction analysis suggests that the ancestors of modern Livistoninae dispersed into islands of the Sunda region five million years after lineage origination (∼16–21 Ma; Miocene; Fig. 2). Dispersal from eastern Asia to insular areas in Southeast Asia coincides with the timing of major tectonic activity and the collision between the Sunda and Sahul plates that caused continental fragments to be split off and be rearranged throughout the region (Hall 2002). After the Early Miocene rejuxtaposition of land and changes in sea level facilitated the dispersal of the terrestrial flora from Sunda (area D; Fig. 2) into Sahul areas (area E; Fig. 2). During this time period, the former oceanic barrier between the two continental shelves in Wallacea had been reduced and included several small islands that could serve as stepping stones for dispersal across Wallace's Line (Hall 2009).

DIVERSIFICATION IN LIVISTONINAE

To test our hypothesis that dispersal across Wallace's Line increased diversification rates and consequently contributed to the disparity in species diversity across a narrow geographic area, a rate increase would need to be detected in the vicinity of at least one of the three instances of dispersal to the Sahul region (Fig. 2). Based on our diversification rate analysis, an increase in diversification rates was detected in at least two of the three genera that dispersed across Wallace's Line (Fig. 3). This increase in diversification rate therefore drove elevated numbers of species found on the eastern side of Wallace's Line. In addition, our results show no evidence for dispersal between major geographic areas in *Lanonia*, *Johannesteijsmannia*, and *Pholidocarpus*, whereas *Licuala*, *Livistona*, and *Saribus* experienced range expansions into the Sahul regions of New Guinea and Australia to Vanuatu (area E; Fig. 2).

The Livistoninae lineages that crossed Wallace's Line all generally share similar dispersal-related morphological characteristics: fruits that are small in size (<1.5 cm; Henderson 2009) are brightly colored (red in *Licuala*, blue to purple in *Livistona*, orange to red in *Saribus*) and are inferred to be bird dispersed and have high dispersal capability (Dowe 2009). In contrast, those Livistoninae lineages that remained in the Sunda region have low dispersal ability (e.g., *Johannesteijsmannia, Pholidocarpus*) with large, green to brown fruits that are likely mammal dispersed (3.5–12 cm; Zona and Henderson 1989).

Shifts in diversification rate are attributed to both intrinsic (i.e., morphological innovations) and extrinsic correlates (i.e., biotic and abiotic factors) by changing the direction and / or the speed of diversification (e.g., Forest et al. 2007; Moore and Donoghue 2007; Rabosky 2009; Rabosky and Glor 2010; Wagner et al. 2012). The results of our study indicate that both interact to generate the unusual diversity pattern exhibited in Livistoninae. For instance, the best-fit diversification model supports the hypothesis that recent diversification in *Licuala* is characterized by a higher speciation rate compared to its ancestral lineage, which further increased after dispersing into the Sahul region. The highly dynamic nature of terrestrial habitats in Southeast Asia over the last 10 Ma, and in particular the uplift of the New Guinean highlands in the last 5 Ma, has most likely generated multiple opportunities for speciation (Hall 2009), and the higher dispersal abilities of *Licuala*, *Livistona*, and *Saribus* further contributed to the colonization of these novel habitats. However, understanding why New Guinea *Licuala* exhibit elevated diversification would require a detailed analysis including both fine-scale distributional data and morphological data to test for a correlation between diversification and dispersal abilities.

WALLACE'S LINE AND PALM DISTRIBUTIONS

Dransfield (1981) first reported the unusual patterns of species distributions in Southeast Asian Livistoninae with high species richnesses in Sunda and Sahul and lower richness in Wallacea. Dransfield hypothesized that this pattern of species diversity, which he referred to as bicentric, was caused by a combination of post-Miocene migrations from the west and possibly the east (but see Dransfield 1987), and Pleistocene climatic changes that increased extinction rates in Wallacea. Three instances of dispersal were reconstructed from the Sunda region across Wallace's Line into the Sahul region (area E; Fig. 2) indicating that *Licuala, Livistona,* and *Saribus* ancestors most likely colonized Southeast Asia from the west (Fig. 2) and refutes the idea that the group colonized the region on two fronts. No dispersals out of the Sahul region were inferred in Livistoninae, which may reflect the inability for long-distance dispersal further east to the smaller island chains such as Fiji, French Polynesia, and Hawaii.

Recent stable isotope data have shown that islands in Southeast Asia experienced a severe dry period in the Pleistocene that likely caused major forest contractions (∼125 Ka; Bird et al. 2005; Wurster et al. 2010). These dry conditions may have been unfavorable for palm lineages (Bjorholm et al. 2006), leading to their extinction and potentially affecting the biogeographic pattern seen in the Livistoninae. Despite this, we did not detect any significant declines in the diversification rate that could be attributed to extinctions caused by climatic affects. Other ecological factors may also have contributed to the lower diversity in Wallacea, such as species–area relationships and / or competition from ecologically similar species. Species–area relationships in geologically complex systems such as Southeast Asia are difficult to parse, but low species richness in Wallacea could also simply be due to its smaller geographic area (e.g., MacArthur and Wilson 1967) and the fragmented nature of the insular habitats (e.g., the Celebes), which compose Wallacea. Southeast Asia, specifically Malesia, harbors the highest percent of global palm diversity with 50 genera and 992 species in comparison to 65 and 16 genera and 730 and 65 species in South America and Africa, respectively (Baker and Couvreur 2012). From this striking diversity, Livistoninae lineages may have encountered ecologically similar species (e.g., *Areca*, *Calyptroclayx*, *Iguanura*, *Nenga*, *Pinanga*, *Sommieria*) that impeded establishment due to resource limitation or led to competitive exclusion.

Conclusions

On a general scale, our divergence time and historical biogeography results show a close correlation with geological events and climatic oscillations that have shaped current distributions. The fossil history and estimated divergence times for early divergent Livistoninae show the influence of tectonic activity at the Sunda and Sahul plate boundary and the dispersal of *Licuala* to New Guinea corresponds to the timing of island formation and mountain uplift. Plant lineages such as palms, legumes, and Annonaceae have been suggested to be excellent systems to understand the evolution of tropical forests because their physiological requirements largely restrict them to these biomes (Morley 2000) and have been fossilized in the earliest records of rainforests (e.g., Wing et al. 2009). Recent studies in *Pseudovaria* (Annonaceae) closely mirror the biogeographic movements (Su and Saunders 2010) of Livistoninae and are likely concordant with the evolutionary change of Southeast Asian rainforests as a whole.

Although Wallace's Line may be more strongly correlated with extant mammal diversity, we have shown here that it and net diversification rates played an important role in shaping palm distributions. We suggest that the dynamic history of Southeast Asia has generated innumerable opportunities for allopatric speciation and that comparisons with other Southeast Asian lineages should provide general understanding of these spectacular biogeographical patterns. Furthermore, to understand broader scale species diversity disparities, groups like palms may be an important element to reveal general patterns.

ACKNOWLEDGMENTS

We gratefully acknowledge financial support by the National Science Foundation (Doctoral Dissertation Improvement Grant DEB-1010731), the National Tropical Botanical Garden (McBryde Graduate Fellowship), the Montgomery Botanical Center (Research Associateship), and the American Philosophical Society Lewis and Clark Fund to CDB, The Colorado Alliance for Graduate Education and the Professoriate and the McNairs Scholar Programs to AMM, and the National Science Foundation (OISE-0512110), the John D. and Catherine T. MacArthur Foundation, the International Palm Society, a Fulbright Program Research Award, and the University of Aarhus Research Foundation to AJH. The diversification analyses were performed with the computational resources of the High-Performance Computing Center at the University of Florida. We thank W. Baker, C. Heatabun, J. Marcus, and J.-C. Pintaud for DNA samples; L. Tembrock for laboratory assistance; W. Baker, J. Dransfield, and D. Rabosky for helpful discussions; H. Morlon for providing code and guidance; and J. Paul, A. Barfod, and Luke Harmon for comments that greatly improved the manuscript.

LITERATURE CITED

Akaike, H. 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control 19:716–723.

Alexander, P. J., R. Govindarajalu, C. D. Bacon, and C. D. Bailey. 2007. Recovery of plant DNA using a reciprocating saw and silica-based columns. Mol. Ecol. Notes 7:5–9.

Asmussen, C. B., and M. W. Chase. 2001. Coding and noncoding plastid DNA in palm systematics. Am. J. Bot. 88:1103–1117.

Asmussen, C. B., J. Dransfield, V. Deickmann, A. S. Barfod, J. C. Pintaud, and W. J. Baker. 2006. A new subfamily classification of the palm family (Arecaceae): evidence from plastid DNA. Bot. J. Linn. Soc. 151:15–38.

Atkins, H., J. Preston, and Q. C. B. Cronk. 2008. A molecular test of Huxley's Line: *Cyrtandra* (Gesneriaceae) in Borneo and the Phillipines. Biol. J. Linn. Soc. 72:143–159.

Bacon, C. D., and W. J. Baker. 2011. Saribus resurrected. PALMS 55:109–116.

Bacon, C. D., F. A. Feltus, A. H. Paterson, and C. D. Bailey. 2008. Novel nuclear intron-spanning primers for Arecaceae evolutionary biology. Mol. Ecol. Res. 8:211–214.

Bacon, C. D., W. J. Baker, and M. P. Simmons. 2012. Miocene dispersal drives island radiations in Trachycarpeae (Arecaceae/Palmae). Syst. Biol. 61:426–442.

Baker, W. J., and T. L. P. Couvreur. 2012. Biogeography and distribution patterns of Southeast Asian palms. Pp. 164–190 *in* D. Gower, K. Johnson, J. E. Richardson, B. Rosen, L. Rüber, and S. Williams, eds. Biotic evolution and environmental change in Southeast Asia. Cambridge Univ. Press, Cambridge, U.K.

Baker, W. J., M. J. E. Coode, J. Dransfield, S. Dransfield, M. M. Harley, P. Hoffmann, and R. J. Johns. 1998. Patterns of distribution of Malesian vascular plants. Pp. 243–258 *in* R. Hall and J. D. Holloway, eds. Biogeography and geological evolution of SE Asia. Backhuys Publishers, Leiden, NL.

Baker, W. J., V. Savolainen, C. B. Asmussen-Lange, M. W. Chase, J. Dransfield, F. Forest, M. M. Harley, N. W. Uhl, and M. Wilkinson. 2009. Complete generic-level phylogenetic anlayses of palms (Arecaceae) with comparison of supertree and supermatrix approaches. Syst. Biol. 58:240–256.

Baldwin, B. G., and M. J. Sanderson. 1998. Age and rate of diversification of the Hawaiian silversword alliance (Compositae). Proc. Natl. Acad. Sci. USA 95:9402–9406.

Beck, J., I. J. Kitching, and K. E. Linsenmar. 2006. Wallace's line revisited: has vicariance or dispersal shaped the distribution of Malesian hawkmoths (Lepidoptera: Sphingidae). Biol. J. Linn. Soc. 89:455–469.

Bird, M. I., D. Taylor, and C. Hunt. 2005. Palaeoenvironments on insular Southeast Asia during the Last Glacial Period: a savanna corridor in Sundaland? Quat. Sci. Rev. 24:2228–2242.

Bjorholm, S., J. C. Svenning, W. J. Baker, F. Skov, and H. Balslev. 2006. Historical legacies in the geographical diversity patterns of New World palms (Arecaceae) subfamilies. Bot. J. Linnean Soc. 151:113–125.

Bolker, B. M., M. Butler, P. Cowan, D. de Vienne, D. Eddelbuettel, M. Holder, T. Jombart, S. Kembel, F. Michonneau, D. Orme, et al. 2011. phylobase: Base package for phylogenetic structures and comparative data. R package version 0.6.3. Available via http://CRAN.R-project.org/package=phylobase.

Conran, J. G., and A. C. Rosefelds. 2003. Palmoxylon queenlandicum: a premineralized Oligocene palm trunk from near Srongsure, southeastern Queensland. Acheringa 27:125–134.

Crisp, M. D., Y. Isagi, Y. Kato, L. G. Cook, and D. M. J. S. Bowman. 2010. Livistona palms in Australia: ancient relics or opportunistic immigrants? Mol. Phylogenet. Evol. 54:512–523.

Cuenca, A., and C. B. Asmussen-Lange. 2007. Phylogeny of the palm tribe Chamaedoreeae (Arecaceae) based on plastid DNA sequences. Mol. Phylogenet. Evol. 32:250–263.

Darwin, C. R. 1859. The origin of species by means of natural selection, or the preservation of favored races in the struggle for life. John Murray, London, U.K.

Dowe, J. L. 2009. A taxonomic account of *Livistona* R. Br. (Arecaceae). Gard. Bull. Singapore 60:185–344.

Dransfield, J. 1981. Palms and Wallace's line. Pp. 43–56 *in* T. C. Whitmore, ed. Wallace's Line and plate tectonics. Clarendon Press, Oxford, U.K.

———. 1987. Bicentric distributions in Malesia as exemplified by palms. Pp. 60–72 *in* T. C. Whitmore, ed. Biogeographical evolution of the Malay Archipelago. Clarendon Press, Oxford, U.K.

Dransfield, J., and Uhl, N. 1983. *Wissmannia* reduced to *Livistona*. Kew Bulletin 38:199–200.

Dransfield, J., N. Uhl, C. B. Asmussen, W. J. Baker, M. M. Harley, and C. E. Lewis. 2008. Genera Palmarum: the evolution and classification of palms. Kew Publishing, Richmond, U.K.

Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol. Biol. 7:e214.

Drummond, A. J., S. Y. W. Ho, M. J. Phillips, and A. Rambaut. 2006. Relaxed phylogenetic and dating with confidence. PLoS Biol. 4:699–710.

Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. 32:1792–1797.

Esselstyn, J. A, R. M. Timm, and R. M. Brown. 2009. Do geological or climatic processes drive speciation in dynamic archipelagos? The tempo and mode of diversification in Southeast Asian shrews. Evolution 63: 2595–2610.

Evans, B. J., R. M. Brown, J. A. McGuire, J. Supriatna, N. Andayani, A. Diesmos, D. Iskandar, D. J. Melnick, and D. C. Cannatella. 2003. Phylogenetic of fanged frogs: testing biogeographical hypotheses at the interface of the Asian and Australian faunal zones. Syst. Biol. 52:794–819.

Farris, J. S., V. A. Albert, M. Källersjö, D. Lipscomb, and A. G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12:99–124.

Felsenstein, J. 1973. Maximum likelihood and minimum-steps methods for estimating evolutionary trees from data on continuous characters. Syst. Zool. 27:27–33.

———. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

Forest, F., M. W. Chase, C. Persson, P. Crane, and J. A. Hawkins. 2007. The role of biotic and abiotic factors in evolution of ant dispersal in the milkwort family (Polygalaceae). Evolution 61:1675–1694.

Graur, D., and W. Martin. 2004. Reading the entrails of chickens: molecular timescales of evolution and the illusion of precision. Trends Genet. 20:80–86.

Hahn, W. J. 2002. A phylogenetic analysis of the Arecoid line of palms based on plastid DNA sequence data. Mol. Phylogenet. Evol. 23:189–204.

Hall, R. 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. Pp. 99–131 *in* R. Hall and J.D. Holloway, eds. Biogeography and geological evolution of SE Asia. Backhuys Publishers, Leiden, NL.

———. 2002. Cenozoic geological and plate tectonic evolution of Southeast Asia and the Southwest Pacific: computer-based reconstructions, model and animations. J. Asian Earth Sci. 20:353–434.

———. 2009. Southeast Asia's changing palaeogeography. Blumea 54:148–161.

Hall, R., and C. K. Morley. 2004. Sundaland basins. AGU Geophys. Monogr. 149:55–85.

Hardy, C. R., and H. P. Linder. 2005. Interspecific variability and timing in ancestral ecology reconstruction: a test case from the Cape flora. Syst. Biol. 54:299–316.

Henderson, A. J. 2009. Palms of Southern Asia. Princeton Univ. Press, Princeton, NJ.

Henderson, A. J., and C. D. Bacon. 2011. Lanonia (Palmae), a new genus from Asia, with a revision of species. Syst. Bot. 36:922–932.

Ho, S. Y. W. 2007. Calibrating molecular estimates of substitution rates and divergence times in birds. J. Avian Biol. 38:409–414.

Ho, S. Y. W., and M. J. Phillips. 2009. Accounting for calibration uncertainty in phylogenetic estimates of evolutionary divergence times. Syst. Biol. 58:367–380.

Ho, S. Y. W., M. J. Phillips, A. Cooper, and A. J. Drummond. 2005. Time dependancy of molecular rate estimates and systematic overestimation of recent divergence times. Mol. Biol. Evol. 22:1561–1568.

Huxley, T. H. 1868. On the classification and distribution of the Alectromorphae and Heteromorphae. Proc. Zool. Soc. Lond. 1868:294–319.

Kluge, A. G. 1989. A concern for evidence and a phylogenetic hypothesis for relationships among *Epicrates* (Boideae, Serpentes). Syst. Zool. 38:7–25.

Knowles, L. L. 2010. Sampling strategies for species tree estimation. Pp. 163–172 *in*: L. L. Knowles and L. S. Kubatko, eds. Estimating species trees: practical and theoretical aspects. John Wiley & Sons, Inc., Hoboken, NJ.

Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodriguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115–2118.

Lydekker, R. 1896. A geographical history of mammals. Cambridge Univ. Press, Cambridge, U.K.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, NJ.

Maddison, D. R., and W. P. Maddison. 2001. MacClade: analysis of phylogeny and character evolution version 4.03. Sinauer Associates, Sunderland, MA.

Mayr, E. 1944. Wallace's line in the light of recent zoographic studies. Quart. Rev. Biol. 29:1–14.

Mayr, E., and J. M. Diamond. 2001. The birds of northern Melanesia: speciation, ecology, and biogeography. Oxford Univ. Press, Oxford, U.K.

Mercer, J. M., and V. L. Roth. 2003. The effects of Cenozoic global change on squirrel phylogeny. Science 299:1568–1572.

Middlebach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allan, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol. Lett. 10:315–331.

Moore, B. R., and M. J. Donoghue. 2007. Correlates of diversification in the plant clade Dispicales: geographic movement and evolutionary innovations. Am. Nat. 170:S28–S55.

Moore, B. R., and M. J. Donoghue. 2009. A Bayesian approach for evaluating the impact of historical events on rates of diversification. Proc. Natl. Acad. Sci. USA 106:4307–4312.

Morley, R. J. 2000. Origin and evolution of tropical rain forests. John Wiley and Sons Ltd., New York.

Morlon, H., T. L. Parsons, and J. B. Plotkin. 2011. Reconciling molecular phylogenies with the fossil record. Proc. Natl. Acad. Sci. USA 39:16327–16332.

Muellner, A. N., C. M. Pannell, A. Coleman, and M. W. Chase. 2008. The origin and evolution of Indomalesian, Australian and Pacific island biotas: insights from Aglaieae (Meliaceae). J. Biogeogr. 35:1769–1789.

Müller, K. 2006. Incorporating information from length-mutational events into phylogenetic analysis. Mol. Phylogenet. Evol. 38:667–676.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Nagao, T., and U. Selya. 1995. Heat-flow distribution in Southeast Asia with consideration of volcanic heat. Tectonophysics 251:153–159.

Nixon, K. C., and J. M. Carpenter. 1996. On simultaneous analysis. Cladistics 12:221–242.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Phillips, O. L., P. Hall, A. H. Gentry, S. A. Sawyer, and R. Vásquez. 1994. Dynamics and species richness of tropical rainforests. Proc. Natl. Acad. Sci. USA. 92: 2805–2809.

Posada, D. 2008. jModelTest: Phylogenetic model averaging. Mol. Biol. Evol. 25:1253–1256.

R Core Team (2012). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3–900051-07-0. Available at http://www.R-project.org

Rabosky, D. L. 2006. LASER: a maximum likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. Evol. Bioinf. Online 2:247–250.

———. 2009. Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. Ecol. Lett. 12:735–743.

Rabosky, D. L., and R. E. Glor. 2010. Equilibrium speciation dynamics in a model adaptive radiation of island lizards. Proc. Natl. Acad. Sci. USA 107:22178–22183.

Ree, R. H., and S. Smith. 2008a. LAGRANGE: likelihood analysis of geographic range evolution. Version 2.0 Software. Available at http://code.google.com/p/lagrange

———. 2008b. Maximum-likelihood inference of geographic range evolution by diserpsal, local extinction, and cladogenesis. Syst. Biol. 57:4–14.

Ree, R. H., B. R. Moore, C. O. Webb, and M. J. Donoghue. 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. Evolution 5:2299–2311.

Revolution Analytics (2012). doMC: for each parallel adaptor for the multicore package. R package version 1.2.5. Available at http://CRAN.R-project.org/package=doMC

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. Science 235:167–171.

Roncal, J., J. Fransisco-Ortega, C. B. Asmussen, and C. E. Lewis. 2005. Molecular phylogenetics of tribe Geonomeae (Arecaceae) using nuclear DNA sequences of phosphoribulokinase and RNA polymerase. Syst. Bot. 30:275–283.

Sanmartín, I, and Ronquist, F. 2004. Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. Syst. Biol. 53:216–243.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, Oxford, UK.

Simmons, M. P. 2004. Independence of alignment and tree search. Mol. Phylogenet. Evol. 31:874–879.

Simmons, M. P., and H. Ochoterena. 2000. Gaps as characters in sequence-based phylogenetic analyses. Syst. Biol. 49:369–381.

Simmons, M. P., H. Ochoterena, and T. G. Carr. 2001. Incorporation, relative homoplasy, and effect of gap characters in sequence-based phylogenetic analysis. Syst. Biol. 50:454–462.

Simpson, G. G. 1977. Too many lines; the limits of the oriental and Australian zoogeographic regions. Proc. Am. Philos. Soc. 121:107–120.

Stamatakis, A., T. Ludwig, and H. Meier. 2005. RAxML-III: a fast program for maximum likelihood-based inference of large phylogenetic trees. Bioinformatics 21:456–463.

Stamatakis, A., P. Hoover, and J. Rougemont. 2008. A rapid bootstrap algorithm for the RAxML web-servers. Syst. Biol. 75:758–771.

Steele, K. P., and R. Vilgalys. 1994. Phylogenetic analyses of Polemonianceae using nucleotide sequences of the plastid gene *matK*. Syst. Bot. 19:126–142.

Su, Y. C. F., and R. M. K. Saunders. 2010. Evolutionary divergence times in the Annonaceae: evidence of a late Miocene origin of *Pseudovaris* in Sundaland with subsequent diversification in New Guinea. BMC Evol. Biol. 9:e153.

Swofford, D. L. 2001. PAUP* 4.0: Phylogenetic Analysis Using Parsimony (*and Other Methods). Sinauer Associates, Sunderland, MA.

Urbanek, S. 2011. multicore: parallel processing of R code on machines with multiple cores or CPUs. R package version 0.1-7. Available at http://CRAN.R-project.org/package=multicore

Van Welzen, P. C., J. W. F. Slik, and J. Alahuhta. 2005. Plant distribution patterns and plate tectonics in Malesia. Biologiske Skrifter 55:199–217.

Van Welzen, P. C., J. A. N. Parnell, and J. W. F. Slik. 2011. Wallace's Line and plant distributions: two or three phytogeographical areas and where to group Java? Biol. J. Linnean Soc. 103:531–545.

Wagner, C. E., L. J. Harmon, and O. Seehausen. 2012. Ecological opportunity and sexual selection together predict adaptive radiation. Nature 487:366–369.

Wallace, A. R. 1860. On the zoological geography of the Malay archipelago. J. Proc. Linn. Soc. 4:172–184.

———. 1878. Tropical nature and other essays. Macmillan, New York.

Weber, M. 1902. Der Indo-australische Archipel und die Geschichte seiner Tierwelt. Lydekker, Jena, Germany.

Whitmore, T. C. 1982. Wallace's Line: a result of plate tectonics. Ann. Missouri Bot. Gar. 69:668–675.

Wing, S. L., F. Herrera, C. A. Jaramillo, C. Gómez-Navarro, P. Wilf, and C. C. Labandeira. 2009. Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest. Proc. Natl. Acad. Sci. USA 106:18627–18632.

Wurster, C. M., M. J. Bird, I. D. Bull, F. Creed, C. Bryant, and J. A. J. Dungiat. 2010. Forest contraction in north equatorial Southeast Asia during the Last Glacial Period. Proc. Natl. Acad. Sci. USA 107:15508–15511.

Yang, Z. 2006. Computational molecular evolution. Oxford Univ. Press, Oxford, U.K.

Zona, S., and A. Henderson. 1989. A review of animal-mediated seed dispersal of palms. Selbyana 11:6–21.

Associate Editor: L. Harmon

Supporting Information

Additional Supporting information may be found in the online version of this article at the publisher's website:

Table S1. Table of new sequences generated for this study with taxonomic authorities, voucher, or DNA source information and GenBank accession numbers where blank cells represent sequences not amplified.

Figure S1. Simplified inter-generic relationships inferred from previous studies of the tribe Trachycarpeae (Bacon et al. 2012), compared to each of the ML gene tree partitions generated in this study where likelihood bootstrap support is indicated above and parsimony jackknife support is indicated below each branch.

Figure S2. Basal portion of the simultaneous-analysis parsimony JK tree with parsimony JK values 50% above and likelihood BS values below each branch.

Figure S3. Distal portion of the parsimony simultaneous-analysis with support values and incongruence indicated as in Figure S2.

Table S2. Mean and credible interval (upper and lower) of divergence times for each clade in the Livistoninae with ages in millions of years (Ma).

Table S3. Alternative historical distributions for crown nodes that had more than one likely reconstruction (within 2 log likelihood units of the maximum).