

Title

Phylogeography of the *Coccus* scale insects inhabiting myrmecophytic *Macaranga* plants in Southeast Asia

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Abstract

Comparative historical biogeography of multiple symbionts occurring on a common host taxa can shed light on the processes of symbiont diversification. Myrmecophytic *Macaranga* plants are associated with the obligate mutualistic symbionts: *Crematogaster* (subgenus *Decacrema*) ants and *Coccus* scale insects. We conduct phylogeographic analyses based on mitochondrial Cytochrome Oxidase I (COI) from 253 scale insects collected from 15 locations in Borneo, Malaya and Sumatra, to investigate the historical biogeography of the scales, and then to draw comparisons with that of the symbiotic, but independently dispersing *Decacrema* ants which are not specific to different *Coccus* lineages. Despite the different mode of ancient diversification, reconstruction of ancestral area and age estimation on the *Coccus* phylogeny showed that the scales repeatedly migrated between Borneo and Malaya from Pliocene to Pleistocene, which is consistent with the *Decacrema* ants. Just as with the ants, the highest number of lineages in the scale insects was found in the northern northwest Borneo, suggesting that these regions were rain forest refugia during cool dry phases of Pleistocene. Overall, general congruence between the Plio-Pleistocene diversification histories of the symbiotic scales and ants

suggests that they experienced the common history of extinction/migration despite their independent mode of dispersal and host-colonization.

Keywords

biogeography · *Cytochrome Oxidase* · *Decacrema* · myrmecophyte · rain forest · scale insects

Introduction

Phylogeography provide a good opportunity to identify the historical evolutionary processes, the glacial refugia and postglacial migration routes of organisms (Avice 2000).

Several studies have compared the phylogeny between host and symbiont organisms (reviewed in Nieberding and Olivieri 2007), but there are currently few studies that compared phylogeography of co-occurring and distantly related symbiotic and parasitic taxa (e.g., Althoff et al. 2007; Whiteman et al. 2007). Comparative historical biogeography of multiple symbionts occurring on a common host taxa can shed light on the evolutionary processes of symbiont diversification (Whiteman et al. 2007).

Tropical rainforests in Southeast Asia harbor some of the greatest concentrations of biodiversity on earth. In proportion to this biodiversity, however, there is a dearth of phylogeographic studies on the biota of the region. In Plio-Pleistocene, sea levels largely fluctuated through the glacial and interglacial cycles, and repeatedly created connection and disconnection among the islands and mainland in vast areas of the SE Asia. These land bridges may have enabled migration of many organisms across the Sunda region (Medway 1972). In the Pleistocene, the distribution of the rainforest was reduced by the

influence of cool dry climates of the glacial cycles, and these changes might have contracted rainforest to isolated refugia (Morley 2000). These geologic events would have influenced the current geographic distribution of genetic and taxonomic diversity in rainforest biota.

Obligate mutualisms between ants and myrmecophytes (ant-plants) are a phenomenon generally restricted to rain forests, and thus present an excellent system in which to study the generation of diversity in these ecosystems. In Southeast Asian tropics, 26 species of myrmecophytic *Macaranga* trees engage in an obligate mutualism with *Crematogaster* (subgenus *Decacrema*) ants. The ants gain nest sites in hollow stems (domatia) and food bodies secreted by stipules and/or young leaves while the plants gain protection against vines and herbivores from the ants (Fiala et al. 1989). In most cases, the ants also tend *Coccus* scale insects within the hollow stems and these provide additional nutrients for the ants in the form of excreted plant sap, or honey-dew (Heckroth et al. 1998). The distribution of this tripartite symbiosis is strictly limited to the everwet rain forest in western Malesia (Sumatra, the Malay Peninsula and Borneo, Fiala et al. 1999; Davies et al. 2001), and thus, their evolutionary history might illuminate some of the history of the Southeast Asian rain forests.

Several authors suggest that the presence of scale insects plays an important role in the evolution of myrmecophytes (Benson 1985; McKey 1989; Ward 1991), and also in the successful establishment of an ant colony on a host plant (Moog et al. 2005). Heckroth et al. (1998) discovered twenty-two *Coccus* morphospecies from 19 species of myrmecophytic *Macaranga*, they are highly specific to the genus *Macaranga* while ranging from being monophagous to polyphagous towards individual host species of *Macaranga*, Ueda et al. (2008) further reported that the association of scales' mtDNA lineages with ants' was not specific but dictated by opportunity. Whereas the mode of host colonization among the scales is not known, it is known that ants and scales colonize *Macaranga* independently of each other. Scales have not been observed to disperse in tandem with dispersing ant queens attempting to found new colonies, and the nymphs of the scales most probably disperse by wind drift and, on their arrival, ant workers carry them into the interior of the stem (Fiala and Maschwitz 1990; Gullan 1997). The *Coccus* scales inhabiting *Macaranga* appear to constitute a monophyletic group (P. J. Gullan, and T. Kondo, personal communication), but molecular phylogenetic studies based on mtDNA are inconclusive (Ueda et al. 2008).

Quek et al. (2007) investigated the phylogeography of *Decacrema* ants on

Macaranga, and elucidated that the ants originated 20 - 16 Ma (million years ago), drastically diversified during Pliocene, and migrated from Borneo (or Sumatra) to Malaya repeatedly through Plio-Pleistocene. Ueda et al. (2008) subsequently reconstructed gene phylogeny of *Coccus* scale insects collected from the same trees of myrmecophytic *Macaranga* as sampled by Quek et al. (2007) for the ants. The minimum age of the scales was estimated to be half that of the ants, at 9 - 7 Ma in late Miocene, suggesting that they were latecomers in the evolutionary history of the symbiosis. However, the phyllogeography of the scales has yet to be ascertained in comparison with the ants.

Have the scale insects experienced the common historical biogeography with the ants and plants? Because of the obligate symbiosis of *Macaranga* - *Decacrema* - *Coccus*, we can simply expect that the distribution of the scales and ants are restricted to that of their host plants, and that they share common historical biogeographical processes. However, the facts that the scales from *Macaranga* are occasionally found with phytoecious (*i.e.*, dwelling in live plant cavities) *Cladomyrma* ants (Moog et al. 2005) and further that a myrmecophytic *Macaranga* species (*M. puncticulata*) is not inhabited by any scale insects (Federle et al. 1998), both suggest that common history (co-phylogeography) of

the scales and ants is not necessarily expected. In these and other cases, regional extinctions of either scales or ants might have occurred, and this may cause disagreement of their phylogeography, location of glacial refugia, and/or migration routes.

The aim of the present study is to investigate the historical biogeography of the *Coccus* scale insects associated with myrmecophytic *Macaranga* plants in SE Asia, and then to compare it with the phylogeography of another obligate symbionts of *Macaranga* plants, *Decacrema* ants reported by Quek et al. (2007) who used the same DNA fragment as the scales in this study. We expand on the study by Ueda et al. (2008), in combination with new data and the data used therein, and set the focus to (i) infer the time frame of the migration/vicariance events on the *Coccus* phylogeography, (ii) identify the glacial refugia of the *Coccus*, and (iii) compare these results with those of *Decacrema* ants reported by Quek et al. (2007). Results were discussed in the context of the history of Sundaland's rain forest and the extant host plant distribution.

Materials and methods

Sampling of *Coccus* scale insects

Two hundred and fifty-three scale insects were collected from 235 trees representing 22 *Macaranga* species (including the data from Ueda et al. (2008) and new data). We sampled from 15 locations, of which one was in Sumatra, seven were in Malaya and seven in Borneo. Most of the scales reported here were collected from ant colonies used in Quek et al. (2007). We concentrated the sampling on myrmecophytic *Macaranga* trees because the *Coccus* scales in *Macaranga* are known to be highly specific to the genus *Macaranga* (Heckroth et al. 1998). Usually, one scale's individual per one *Macaranga* tree was basically analyzed. In some exceptional cases when two morphologically different types of scale insects were detected on a tree (18 out of the 235 *Macaranga* trees sampled), each was individually analyzed. For the outgroups, we sequenced (1) four free-living *Coccus* species (*C. celatus*, *C. hesperidum*, *C. pseudomagnoliarum* and *C. viridis*) which are assumed to be close relatives of the *Coccus* on *Macaranga* (P. J. Gullan, and T. Kondo, personal communication), and (2) two genera, *Eulecanium* and *Parthenolecanium*, in the subfamily Eulecaninae within Coccidae (Hodgson 1994). Host species, collection localities, elevation and GenBank accession numbers of the samples are presented in Table S1 in Electronic Supplementary Material (ESM), Supplementary

material.

Molecular datasets

The methods of DNA extraction and sequencing are reported in Ueda et al. (2008). We used two nucleotide sequence datasets in this study. Dataset 1 includes 521 bp of a mitochondrial Cytochrome Oxidase I (COI) for 253 ingroup samples, and was used for age estimation and migration-vicariance analysis. Dataset 2 includes 1021 bp of COI for 20 ingroup exemplars representing the major clades from Dataset 1 phylogeny, and was used for confirming the monophyly of *Coccus* on *Macaranga*. The 20 samples represent the 7 lineages out of 8 from Dataset 1 phylogeny, and within each lineage, all the monophyletic clades from different geographic region (Sumatra, Malaya or Borneo) were sampled, with one sample per clade being used for sequencing. The polymerase chain reaction (PCR) primers were shown in Table 1. The PCR temperature profile of Dataset 1 is reported in Ueda et al. (2008), and that of Dataset 2 was: 35 cycles of 95°C for 30s, 45°C for 30s and 72°C for 90s.

Phylogenetic analysis

Maximum likelihood (ML) analysis was performed with PHYML version 2.4.4 (Guindon and Gascuel 2003). Best-fitted substitution model was selected for each dataset based on hierarchical likelihood ratio tests (hLRT, Huelsenbeck and Rannala 1997) using Modeltest version 3.7 (Posada and Crandall 1998). GTR + I + G substitution model was used as selected by hLRT in both datasets. Clade support was assessed with 1000 bootstrap pseudoreplications. In addition, Bayesian posterior probabilities and maximum parsimony (MP) bootstrap support were obtained using MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001) and PAUP* 4.0b10 (Swofford 2002), respectively. The GTR + I + G substitution model was also used in Bayesian analysis, using the default run settings that perform two independent analyses with four chains each (one cold and three heated). The Bayesian analysis was run for five million generations, with a burn-in of four million generations, well after stationarity was reached. The parsimony bootstrap support was assessed with 1000 bootstrap replicates, using 10 random addition replicates each.

To test whether the *Coccus* on *Macaranga* are the monophyletic group or not in ML

tree of Dataset 2, the Shimodaira-Hasegawa (SH, Shimodaira and Hasegawa 1999) test was conducted with PAUP using 1000 bootstrap replicates and full optimization. In SH-test, the likelihood score of given topology was compared to the score of constrained topology in which the ingroup (L1-L8) is assumed to be monophyletic.

Operational lineages and age estimation

Operational lineages in the mtDNA tree were defined based on well-supported monophyly and on obvious phylogenetic breaks (i.e., large distances between clades) in order to infer the historical biogeography of the mtDNA lineages as in Ueda et al. (2008). To estimate the ages of divergence within the COI phylogeny of Dataset 1, we used 1.5% divergence per million years (uncorrected pairwise distance). As COI exhibits the least rate heterogeneity in arthropods (Gaunt and Miles 2002), it has been widely used for dating within arthropods (e.g., Degnan et al. 2004) with the substitution rate being about 1.5% per million years (Quek et al. 2004). Homogeneity of substitution rate on the ML phylogeny of Dataset 1 of the scale insects was tested using the LRT (Huelsenbeck and Rannala 1997) with the GTR + I + G model using PAUP 4.0b10. All duplicate haplotypes

were removed in the LRT test. Because the LRT showed significant deviations from rate constancy ($P < 0.01$), branch lengths were subjected to nonparametric rate smoothing (Sanderson 1997) implemented in TreeEdit 1.0 (Rambaut and Charleston 2002). Three well-supported nodes of varying genetic divergences (5.9-13.9%) were used as calibration points to obtain the ages of the other nodes. This approach produces a range of ages, rather than a point estimate and is thus more conservative. Mean uncorrected pairwise distances between sister taxa were calculated using MEGA 2.1 (Kumar et al. 2001).

Migration-vicariance analysis

A dispersal (migration)-vicariance analysis was conducted using DIVA version 1.1 (Ronquist 1997) to examine the historical biogeography of the *Coccus* scale insects and to generate hypothesis for migration or vicariance events in the given phylogeny. DIVA infers ancestral distributions based on a three-dimensional cost matrix that applies a cost of 1 to migration/extinction and no cost to vicariance, and that does not require a general hypothesis of area relationships (Ronquist 1997). Because DIVA analysis requires a

bifurcating tree, we used summary topology of Dataset 1 containing geographically informative clades; each clade consists of OTUs sampled from the same distributional area. Each sample was coded as present or absent in each of two distributional areas: Borneo and/or Sumatra and Malaya. Because of the insufficiency of Sumatran samples ($n = 3$) and the sharing of the same haplotypes between Borneo and Sumatra, Borneo and Sumatra were tentatively pooled as a region in this study.

Results

Phylogeography and geographical distribution of lineages

Eight operational lineages were detected in the mtDNA phylogeny from Dataset 1 (Figure 1A). Here, we detected two new lineages that were not reported in Ueda et al. (2008): L5 ($n = 2$) from Lambir in Borneo and L7 ($n = 1$) from Berastagi in Sumatra. The phylogeny from Dataset 2 (Fig. 1B) provides a better support for each lineage than that from Dataset 1 (Fig. 1A), and it does not support the monophyly of the *Coccus* on *Macaranga*: L1-L7 fall into a clade, whilst L8 fall outside the L1-L7 clade (Fig. 1B). The monophyly of the

L1-L7 clade and the outgroup *C. hesperidum* was well-supported by Bayesian posterior probability (93%), but was poorly supported by ML bootstrapping (68%) and not supported by MP bootstrapping (Fig. 1B). In addition, the SH-test indicated that there is not a significant disagreement between the ML topology of Dataset 2 and the constrained topology in which the ingroup (L1-L8) is assumed to be monophyletic ($P > 0.05$).

In Fig. 1A, L1, L2, L3 and L8 distributed both in Malaya and Borneo; in L1, well-supported Bornean clade is nested within Malayan samples; in L2, L3 and L8, well-supported Malayan clades are nested within Bornean samples. L4 and L5 are exclusively Bornean, and L7 is exclusively Sumatran lineage. L6 is distributed both in Borneo and Sumatra; Sumatran haplotypes in L6 do not form a monophyletic group.

The geographical distribution of each lineage differed quite substantially from that of the others (Fig. 2). Borneo harbored higher number of *Coccus* lineages (7) than Malaya (4) and Sumatra (2). Malaya was dominated by L1 whilst Borneo and Sumatra were dominated by L6. L1, L2 and L3 are distributed from Malaya to western Borneo across the South China Sea; L4 was limited to Crocker Range and Kuching and L5 to Lambir; L6 is widespread from Borneo to Sumatra; L7 is endemic to Sumatra; L8 is patchily distributed in four locations (Johor, Crocker, Lambir and Meratus) in both Malaya and

Borneo (Fig. 2). The highest number of lineages was found in Lambir (five lineages) in northern northwest Borneo, and in Johor and Tioman (three lineages each) in Malaya.

Biogeography

The reconstruction of ancestral area (Fig. 3) suggests that the scale's major axis of diversification (L4 - L7) was in Borneo and/or Sumatra. The scales were inferred to have first diversified in Borneo and/or Sumatra 8.6 - 7.2 Ma (million years ago) in late Miocene (node a in Fig. 3, Table 2). If we assume that L8 represents an independent colonization of *Macaranga* by *Coccus* (Fig. 1B), the minimum estimate of the first diversification of the scales is even younger at 6.8 – 5.7 Ma (node b in Fig. 3, Table 2). The DIVA analysis inferred no vicariance and five migration events: four migrations in Pliocene at node g (4.1 - 3.4 Ma), node j (2.2 - 1.8 Ma), node k (2.3 - 1.9 Ma) and node l (2.1 - 1.7 Ma), and one migration in Pleistocene at node i (1.3 - 1.1 Ma).

Discussion

Our aim in this paper is to infer the evolutionary and population history of the mtDNA of *Coccus* scale insects associated with *Macaranga* trees in Southeast Asia, in order to make comparisons with a similar study by Quek et al. (2007) of the *Decacrema* ants that tend them. Quek et al. (2007), based on COI phylogeography, showed that (i) the main diversification of the ants occurred in Borneo in Miocene, (ii) a number of lineages of ants dispersed to Malaya via Sumatra in Plio-Pleistocene, and (iii) historical rain-forest refuges for the ants probably existed in northern northwest Borneo and the mountain ranges of Malaya and Sumatra (Quek et al. 2007).

The single gene analysis of mitochondrial COI in this study and Quek et al. (2004, 2007) may not reflect species (or population) tree due to introgression or incomplete lineage sorting (Avise 1994; Sota and Vogler 2001; Linnen and Farrell 2007). In fact, mtDNA phylogeny in this study disagreed with a preliminary nrDNA phylogeny using wingless gene and with morphology (S. Ueda, unpublished data). Therefore, in order to elucidate the species boundaries of *Coccus* on *Macaranga* in the future, several independently segregating loci should be used to infer the phylogeny of *Coccus* (e.g., Beltran et al. 2002). However, for the present study, the objective is to infer the historical biogeography of the mtDNA of *Coccus* scales on *Macaranga*, and to draw comparisons

of these results of scales with that of the co-habiting *Decacrema* ants.

The exemplar phylogeny from Dataset 2 indicated that the *Coccus* scale insects are non-monophyletic group (Fig. 1B). The non-monophyletic pattern of dataset 2 may support the hypothesis that multiple clades of the *Coccus* scales independently colonized to *Macaranga*, just like as Attine ants acquired fungal cultivars (Mueller et al. 1998, 2001). However, because the SH-test did not reject the monophyly of the scales, it remains ambiguous whether the *Coccus* scales have colonized *Macaranga* multiple times. To resolve this issue, a further exhaustive sampling of free-living *Coccus* species and analyses of several additional neutral genes will be needed.

Ancestral area reconstruction on the *Coccus* phylogeny (Fig. 3) suggested that they originated in Borneo and/or Sumatra and subsequently dispersed to Malaya, which is consistent with the historical biogeographic picture emerging for their host *Macaranga* plants (Bänfer et al. 2006) and *Decacrema* ants based on DNA studies. However, the lack of enough samplings of *Coccus* from Sumatra warrants caution for inferences of origination and dispersal in or between the regions. The timeline of the migration events (Fig. 3) also correspond with that in the *Decacrema* ants reported in Quek et al. (2007); the four of five migration events in the scales (nodes g, j, K and l in Fig. 3) occurred

synchronously in Pliocene and the other one occurred in Pleistocene (node i in Fig. 3), whilst the *trans*-Sunda migration events in the *Decacrema* ants also occurred primarily in Pliocene and less frequently in Pleistocene (Quek et al. 2007). Migrations across the Sunda shelf in Pliocene were also documented in SE Asian rain-forest rodents and some frogs (Gorog et al. 2004; Inger and Voris 2001). These facts suggest that ancient land bridges of Sunda shelf, created during periods of low sea level (Hall 2001), permitted extensive migrations of rain-forest elements across the South-China sea, and that the migrations primarily occurred in Pliocene rather than Pleistocene. Whether the repeated and extensive exposures of the Pleistocene Sunda shelf facilitated the spread of tropical evergreen rainforest in the region is controversial (Kershaw et al. 2001; Quek et al. 2007).

Just as with their host *Decacrema* ants, the higher number of lineages in Borneo was situated in northern northwest Borneo, the Crocker range and Lambir (Fig. 2), suggesting that, as for the ants, these locations represented rain forest refugia during cool dry Pleistocene phases in which everwet rain forests became fragmented, pending plentiful data accumulation from Sumatra. However, it is also possible that the high number of scale lineage in these two locations may be contributed by high sampling intensities there; further sampling in the other locations are needed to confirm this trend.

A further parallel between ants and scales can be seen in Samarinda, which exhibits the lowest number of lineages (only one lineage) of scales among all the locations in Borneo (Fig. 2). This is also true for their tending ants, in which Samarinda ties with Siduk and Kuching for the bottom rank with two lineages. In contrast, an incongruence pattern between the scales and ants is found in Kuching, which harbors the second highest number of *Coccus* lineages (four lineages), but the lowest number of ant lineages (two lineages).

We were able to obtain only few samples from Sumatra (3 samples in one site), where myrmecophytic *Macaranga* and their *Decacrema* ants occur. Further sampling in Sumatra is desirable, and likely to reveal many more haplotypes, and also possibly more lineages. Further sampling in the weakly sampled localities in Borneo and Malaya are also needed to reduce the artifacts of uneven sampling intensities among locations. Nevertheless, the parallels seen between the ants and scales suggest sampling artifacts do not contribute worrisome error to the patterns observed.

The overall congruence between the diversification histories of the symbiotic scales and ants suggests that they experienced the common history of extinction/migration despite their independent mode of dispersal and host-colonization. Common historical

biogeography of multiple parasites occurring on a common host taxa is favored by high level of specificity and vertical transmission of parasites among hosts (cf. Nieberding and Olivieri 2007; Nieberding et al. 2008). On the contrary to this, Whiteman et al. (2007) reported a case where three parasites on a single host species differed in their population genetic, phylogeographical structure and co-divergence with the host in ways that were predicted by the parasites' ecology such as dispersal ability. In this context, the historical congruence of scales and ants suggest that they have not-so-different life history traits such as dispersal ability and survival. Then, what about *Macaranga* plants? Is their historical biogeography similar to the symbionts? Among section *Phachystemon* which contains the majority of *Macaranga* myrmecophytes, 15 species out of 25 are endemic to Borneo (Davies 2001) with others being Sumatran or Malayan species. This suggests their major axis of diversification in Borneo, but extensive phylogeographic study is needed to elucidate the congruence of the history of the three-partner symbiosis.

Because of the strict association of the scales, ants and plants with everwet rain forests in Southeast Asia, this investigation contributes to the small but hopefully growing pool of studies utilizing molecular markers to piece together the historical ecology of this rich, understudied and endangered ecosystem.

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Table 1 The list of primers used in this study.

Primer				
Locus	name	Sequence	Used for	Reference
COI	mtD-6	5'-GGATCACCTGATA TAGCATTCCC-3'	Dataset 1 and 2	Simon et al. (1994)
COI	CI-N4	5'-CCTGGTAGGATTA AAATATATAC-3'	Dataset 1	Ueda et al. (2008)
COI	CI-N5	5'-TTTTTADTATR TTG TTTGTTA-3'	Dataset 2	this paper
COI	a2761asp	5'-GGTATNCCATTTA ATCC-3'	Dataset 2	Gwiazdowski et al. (2006)
tRNA-L eucine	Pat	5'-TCCAATGCACTAA TCTGCCATATTA-3'	Dataset 2	Simon et al. (1994)

Table 2 Inferred ages of nodes on the *Coccus* chronogram (Fig. 3) obtained by nonparametric rate smoothing, based on a pairwise divergence rate of 1.5% per million years. Fixed ages are indicated in bold font.

Node	mean	Age (Ma)		
	pairwise distance (%)	(node o fixed)	(node c fixed)	(node g fixed)
o	13.9	9.27	7.75	8.85
a	15.0	8.57	7.17	8.18
b	13.7	6.76	5.65	6.45
c	8.0	6.38	5.33	6.08
d	6.9	5.46	4.56	5.21
e	7.6	5.08	4.24	4.85
f	6.2	4.42	3.95	4.51
g	5.9	4.12	3.44	3.93
h	1.7	2.26	1.89	2.15
i	1.5	1.27	1.06	1.21
j	2.1	2.19	1.83	2.09
k	3.3	2.25	1.88	2.15
l	2.2	2.12	1.77	2.02

Figure legend

Fig. 1 (A) Maximum-likelihood tree for *Macaranga*-inhabiting *Coccus* scale insects estimated from Dataset 1 (COI, 521 bp). (B) ML tree for exemplars from Dataset 1 estimated from Dataset 2 (COI, 1021 bp). The numbers above branches indicate ML bootstrap support (left of slash), Bayesian posterior probabilities (right of slash), and MP bootstrap support (below branch). An ‘*’ in the node support values indicates the node was not found recovered in MP bootstrap or Bayesian posterior probability analysis. Shaded clades indicate the Malayan scale insects.

Fig. 2 Approximate distribution of the *Coccus* lineages as inferred by sampling location (colored lines). Pie chart shows the proportional abundance of lineages within each location with sample sizes indicated. The distributional lines and pie charts are color-referenced to the *Coccus* phylogeny at the bottom left.

Fig. 3 Phylogeny of *Coccus* scale insects, showing the reconstruction of the ancestral area optimized by dispersal (migration) -vicariance analysis (DIVA). Branch lengths are proportional to time as inferred by nonparametric rate smoothing. Three timeline is

inferred by fixing the age of nodes o, b or e using 1.5% divergence per million years in COI (Table 2). Branch color indicates the location where each sample inhabits.

The exemplar samples containing geographic information are selected from Fig. 1A (based on Dataset 1, see text for more details), whilst, following Fig. 1B, monophyly of the *Coccus* on *Macaranga* (L1-L8) is denied (shown by dotted branches).

Table S1. List of samples showing locality and associated ants and host plants. Host plant species codes are abbreviated as follows: *aet* = *M. aëtheadenia*, *ang* = *M. angulata*, *ban* = *M. bancana*, *bec* = *M. beccariana*, *gla* = *M. glandibracteolata*, *gri* = *M. griffithiana*, *hos* = *M. hosei*, *hul* = *M. hullettii*, *hyp* = *M. hypoleuca*, *ind* = *M. indistincta*, *kin* = *M. kingii*, *lam* = *M. lamellata*, *mot* = *M. motleyana*, *pea* = *M. pearsonii*, *pet* = *M. petanostyla*, *pru* = *M. pruinosa*, *pse* = *M. pseudopruinosa*, *pub* = *M. puberula*, *tra* = *M. trachyphylla*, *vel* = *M. velutina*, *win* = *M. winkleri*. Ant lineages follow Quek et al. (2007).

scale insect lineage	voucher #	host ant lineage	host plant species	location	elevation (m)	Genbank # COI
L1	SPQ.012	unknown	<i>gri</i>	Singapore, Malaya	< 100	AB439849
L1	SPQ.014	unknown	<i>ban</i>	Singapore, Malaya	< 100	AB439850
L1	SPQ.016	unknown	<i>gri</i>	Singapore, Malaya	< 100	AB476649
L1	SPQ.017	unknown	<i>gri</i>	Johor, Malaya	< 100	AB439851
L1	SPQ.018	unknown	<i>hyp</i>	Johor, Malaya	< 100	AB439852
L1	SPQ.020	K	<i>gri</i>	Johor, Malaya	< 100	AB439853
L1	SPQ.021	K	<i>ban</i>	Johor, Malaya	< 100	AB439854
L1	SPQ.025	K	<i>gri</i>	Johor, Malaya	< 100	AB439855
L1	SPQ.027	K	<i>hyp</i>	Johor, Malaya	< 100	AB439856
L1	SPQ.030	K	<i>hyp</i>	Johor, Malaya	< 100	AB439857
L1	SPQ.031	K	<i>ban</i>	Johor, Malaya	< 100	AB439858
L1	SPQ.032	unknown	<i>hyp</i>	Johor, Malaya	< 100	AB439859
L1	SPQ.034	K	<i>hyp</i>	Johor, Malaya	< 100	AB439860
L1	SPQ.036	unknown	<i>ban</i>	Johor, Malaya	< 100	AB439861
L1	SPQ.037a	unknown	<i>ban</i>	Bauk, Malaya	< 200	AB439862
L1	SPQ.037b	unknown	<i>ban</i>	Bauk, Malaya	< 200	AB439863
L1	SPQ.038	K	<i>hyp</i>	Bauk, Malaya	< 200	AB439864
L1	SPQ.040	K	<i>ban</i>	Bauk, Malaya	< 200	AB439865
L1	SPQ.044	K	<i>gri</i>	Bauk, Malaya	< 200	AB439866
L1	SPQ.045	K	<i>gri</i>	Bauk, Malaya	< 200	AB439867
L1	SPQ.047	K	<i>ban</i>	Kuantan, Malaya	< 300	AB439868
L1	SPQ.050	K	<i>hyp</i>	Kuantan, Malaya	< 300	AB439869
L1	SPQ.052	unknown	<i>hyp</i>	Kuantan, Malaya	< 100	AB439870

L1	SPQ.053	K	<i>gri</i>	Kuantan, Malaya	< 100	AB439871
L1	SPQ.054	K	<i>hyp</i>	Kuantan, Malaya	< 100	AB439872
L1	SPQ.056	K	<i>gri</i>	Kuantan, Malaya	< 100	AB439873
L1	SPQ.059	K	<i>ban</i>	Kuantan, Malaya	< 100	AB439874
L1	SPQ.062	unknown	<i>pru</i>	Kuantan, Malaya	< 100	AB439875
L1	SPQ.063	unknown	<i>pru</i>	Kuantan, Malaya	< 100	AB439876
L1	SPQ.064	K	<i>pru</i>	Kuantan, Malaya	< 100	AB439877
L1	SPQ.066	K	<i>hyp</i>	Kuantan, Malaya	< 100	AB439878
L1	SPQ.067	K	<i>hyp</i>	Kuantan, Malaya	< 100	AB439879
L1	SPQ.068	unknown	<i>gri</i>	Johor, Malaya	< 100	AB439880
L1	SPQ.069	K	<i>gri</i>	Johor, Malaya	< 100	AB439881
L1	SPQ.072	K	<i>gri</i>	Pasor, Malaya	< 100	AB439882
L1	SPQ.073	K	<i>gri</i>	Pasor, Malaya	< 100	AB439883
L1	SPQ.075	K	<i>hyp</i>	Pasor, Malaya	< 100	AB439884
L1	SPQ.076	K	<i>hyp</i>	Pasor, Malaya	< 100	AB439885
L1	SPQ.085b	K	<i>hyp</i>	Tioman, Malaya	< 400	AB439886
L1	SPQ.088	K	<i>ban</i>	Singapore, Malaya	< 100	AB439887
L1	SPQ.089	unknown	<i>ban</i>	Singapore, Malaya	< 100	AB439888
L1	SPQ.090	K	<i>hyp</i>	Singapore, Malaya	< 100	AB439889
L1	SPQ.091	K	<i>hyp</i>	Singapore, Malaya	< 100	AB439890
L1	SPQ.092	K	<i>gri</i>	Singapore, Malaya	< 100	AB439891
L1	SPQ.093	unknown	<i>gri</i>	Singapore, Malaya	< 100	AB476650
L1	SPQ.094	unknown	<i>hyp</i>	Singapore, Malaya	< 100	AB439892
L1	SPQ.095	K	<i>gri</i>	Singapore, Malaya	< 100	AB439893
L1	SPQ.175	K	<i>hul</i>	Johor, Malaya	< 100	AB439894
L1	SPQ.178	K	<i>gri</i>	Johor, Malaya	< 100	AB439895
L1	SPQ.180	K	<i>pru</i>	Johor, Malaya	< 100	AB439896
L1	SPQ.182	K	<i>hyp</i>	Johor, Malaya	< 100	AB439897
L1	TI.9825	unknown	<i>tra</i>	Kuching, Borneo	< 50	AB476651
L1	TI.9826	unknown	<i>bec</i>	Kuching, Borneo	< 50	AB476652
L1	TI.9827	unknown	<i>tra</i>	Kuching, Borneo	< 50	AB476653
L1	TI.9830	unknown	<i>hyp</i>	Kuching, Borneo	< 50	AB476654
L1	TI.9831	unknown	<i>bec</i>	Kuching, Borneo	< 50	AB476655
L1	TI.9835	unknown	<i>ban</i>	Kuching, Borneo	< 50	AB476656
L1	TKom.L01	unknown	<i>unknown</i>	Gombak, Malaya	250	AB439898

L1	TKom.L02	unknown	<i>unknown</i>	Gombak, Malaya	250	AB439899
L1	TKom.L04	unknown	<i>unknown</i>	Gombak, Malaya	250	AB439900
L1	TKom.L10	unknown	<i>unknown</i>	Gombak, Malaya	250	AB439901
L2	KM.s05	unknown	<i>bec</i>	Lambir, Borneo	150	AB439912
L2	KM.s06	D	<i>bec</i>	Lambir, Borneo	150	AB439913
L2	KM.s07	D	<i>bec</i>	Lambir, Borneo	150	AB439914
L2	KM.s09	D	<i>bec</i>	Lambir, Borneo	150	AB439915
L2	KM.s11	G	<i>hos</i>	Lambir, Borneo	150	AB439916
L2	SPQ.041	unknown	<i>ban</i>	Bauk, Malaya	200 - 300	AB439902
L2	SPQ.085a	K	<i>hyp</i>	Tioman, Malaya	< 400	AB439903
L2	SPQ.099	H	<i>ang</i>	Crocker, Borneo	1200	AB439904
L2	SPQ.109	G	<i>pub</i>	Crocker, Borneo	500	AB439905
L2	SPQ.123	G	<i>ind</i>	Crocker, Borneo	600	AB439906
L2	SPQ.133	H	<i>ang</i>	Crocker, Borneo	1100	AB439907
L2	SPQ.152	C	<i>hyp</i>	Crocker, Borneo	450	AB439908
L2	SPQ.156	H	<i>ang</i>	Crocker, Borneo	1200	AB439909
L2	SPQ.172	H	<i>tra</i>	Crocker, Borneo	300	AB439910
L2	SU.L16	unknown	<i>hos</i>	Lambir, Borneo	150	AB439911
L2	SU.L20	H	<i>lam</i>	Lambir, Borneo	150	AB461425
L2	TI.s29	H	<i>hul</i>	Lambir, Borneo	150	AB439917
L2	TI.s30	E	<i>hul</i>	Lambir, Borneo	150	AB439918
L2	TI.s31	H	<i>win</i>	Lambir, Borneo	150	AB439919
L2	TI.s32	H	<i>tra</i>	Lambir, Borneo	150	AB439920
L2	TI.s33	H	<i>tra</i>	Lambir, Borneo	150	AB461426
L2	TI.s34	H	<i>tra</i>	Lambir, Borneo	150	AB439921
L2	TI.s35	H	<i>tra</i>	Lambir, Borneo	150	AB439922
L2	TI.s37	H	<i>ban</i>	Lambir, Borneo	150	AB439923
L2	TI.s39	D	<i>bec</i>	Lambir, Borneo	150	AB439924
L2	TI.s42	G	<i>hos</i>	Lambir, Borneo	150	AB439925
L2	TI.s45	unknown	<i>bec</i>	Lambir, Borneo	150	AB439926
L2	TI.s49	unknown	<i>hos</i>	Lambir, Borneo	150	AB439927
L2	TI.s50	G	<i>hos</i>	Lambir, Borneo	150	AB439928
L2	TI.s52a	G	<i>hos</i>	Lambir, Borneo	150	AB439929
L2	TI.s64	Cam	<i>lam</i>	Lambir, Borneo	150	AB439930

L2	TI.s66	C. sp. SKY32	<i>win</i>	Lambir, Borneo	150	AB439931
L3	KM.s16b	G	<i>hos</i>	Lambir, Borneo	150	AB461429
L3	KM.s27	F	<i>ban</i>	Lambir, Borneo	150	AB439942
L3	SPQ.015	unknown	<i>ban</i>	Singapore, Malaya	< 100	AB439932
L3	SPQ.028	unknown	<i>ban</i>	Johor, Malaya	< 100	AB439933
L3	SPQ.084	unknown	<i>ban</i>	Tioman, Malaya	< 400	AB439934
L3	SPQ.396	H	<i>ind/vel</i>	Siduk, Borneo	< 100	AB439935
L3	SPQ.417	H	<i>hos</i>	Siduk, Borneo	< 100	AB439936
L3	SPQ.679	unknown	<i>win</i>	Long Ampung, Borneo	700	AB439937
L3	SPQ.710	F	<i>ind</i>	Long Ampung, Borneo	700	AB439938
L3	SU.L15	D	<i>ban</i>	Lambir, Borneo	150	AB439939
L3	SU.L22	D	<i>hav</i>	Lambir, Borneo	150	AB439940
L3	SU.L32a	unknown	<i>bec</i>	Lambir, Borneo	150	AB439941
L3	TI.9802	unknown	<i>tra</i>	Kuching, Borneo	500	AB476657
L3	TI.9803	unknown	<i>ban</i>	Kuching, Borneo	500	AB476658
L3	TI.9812	unknown	<i>hul</i>	Kuching, Borneo	200 - 400	AB476659
L3	TI.s46	unknown	<i>hul</i>	Lambir, Borneo	150	AB439943
L3	TI.s52b	G	<i>hos</i>	Lambir, Borneo	150	AB461431
L3	TI.s53a	unknown	<i>bec</i>	Lambir, Borneo	150	AB439944
L3	TI.s53b	unknown	<i>bec</i>	Lambir, Borneo	150	AB439945
L3	TI.s55	unknown	<i>tra</i>	Lambir, Borneo	150	AB461432
L3	TI.s56	C. sp. SKY32	<i>win</i>	Lambir, Borneo	150	AB439946
L3	TI.s57a	F	<i>kin</i>	Lambir, Borneo	150	AB439947
L3	TI.s57b	F	<i>kin</i>	Lambir, Borneo	150	AB439948
L4	SPQ.098	G	<i>pub</i>	Crocker, Borneo	1000	AB439949
L4	SPQ.114	H	<i>ang</i>	Crocker, Borneo	1200	AB439950
L4	SPQ.130	H	<i>ang</i>	Crocker, Borneo	1100	AB439951
L4	SPQ.131a	unknown	<i>ang</i>	Crocker, Borneo	1100	AB439952
L4	SPQ.136a	H	<i>gla</i>	Crocker, Borneo	900	AB439953
L4	SPQ.163	G	<i>pet</i>	Crocker, Borneo	1300	AB439954
L4	SPQ.164	G	<i>pet</i>	Crocker, Borneo	1300	AB439955
L4	TI.9810	unknown	<i>pse</i>	Kuching, Borneo	200 - 400	AB476660
L4	TI.9811	unknown	<i>aet</i>	Kuching, Borneo	200 - 400	AB476661
L5	KM.s15	G	<i>hos</i>	Lambir, Borneo	150	AB461424

L5	KM.s16a	G	<i>hos</i>	Lambir, Borneo	150	AB461428
L6	KM.s03	D	<i>bec</i>	Lambir, Borneo	150	AB440051
L6	KM.s17	G	<i>pse</i>	Lambir, Borneo	150	AB440052
L6	KM.s18	G	<i>pse</i>	Lambir, Borneo	150	AB440053
L6	KM.s19	F	<i>pse</i>	Lambir, Borneo	150	AB440054
L6	KM.s21	G	<i>pse</i>	Lambir, Borneo	150	AB440055
L6	KM.s22	G	<i>pse</i>	Lambir, Borneo	150	AB440056
L6	KM.s24	G	<i>pse</i>	Lambir, Borneo	150	AB440057
L6	SPQ.100	H	<i>pet</i>	Crocker, Borneo	1200	AB439956
L6	SPQ.101	G	<i>pub</i>	Crocker, Borneo	1000	AB439957
L6	SPQ.102	G	<i>mot</i>	Crocker, Borneo	500	AB439958
L6	SPQ.103	G	<i>mot</i>	Crocker, Borneo	500	AB439959
L6	SPQ.105	H	<i>ind</i>	Crocker, Borneo	500	AB439960
L6	SPQ.108	G	<i>ind</i>	Crocker, Borneo	500	AB439961
L6	SPQ.110	G	<i>gla</i>	Crocker, Borneo	500	AB439962
L6	SPQ.111	H	<i>ind</i>	Crocker, Borneo	500	AB439963
L6	SPQ.113	G	<i>pub</i>	Crocker, Borneo	1100	AB439964
L6	SPQ.119	A	<i>hyp</i>	Crocker, Borneo	600	AB439965
L6	SPQ.120	A	<i>mot</i>	Crocker, Borneo	600	AB439966
L6	SPQ.126	G	<i>pea</i>	Crocker, Borneo	650	AB439967
L6	SPQ.127	H	<i>ind</i>	Crocker, Borneo	650	AB439968
L6	SPQ.129	G	<i>gla</i>	Crocker, Borneo	650	AB439969
L6	SPQ.131b	unknown	<i>ang</i>	Crocker, Borneo	1100	AB439970
L6	SPQ.136b	H	<i>gla</i>	Crocker, Borneo	900	AB439971
L6	SPQ.137	H	<i>ang</i>	Crocker, Borneo	900	AB439972
L6	SPQ.139	H	<i>gla</i>	Crocker, Borneo	900	AB439973
L6	SPQ.141	H	<i>ind</i>	Crocker, Borneo	850	AB439974
L6	SPQ.143	H	<i>ban</i>	Crocker, Borneo	300	AB439975
L6	SPQ.145	unknown	<i>ban</i>	Crocker, Borneo	280	AB439976
L6	SPQ.146	H	<i>ban</i>	Crocker, Borneo	250	AB439977
L6	SPQ.147	G	<i>pub</i>	Crocker, Borneo	1200	AB439978
L6	SPQ.148	G	<i>gla</i>	Crocker, Borneo	450	AB439979
L6	SPQ.149	H	<i>gla</i>	Crocker, Borneo	450	AB439980
L6	SPQ.150	H	<i>ind</i>	Crocker, Borneo	450	AB439981

L6	SPQ.151	H	<i>ind</i>	Crocker, Borneo	450	AB439982
L6	SPQ.153	H	<i>ang</i>	Crocker, Borneo	1400	AB439983
L6	SPQ.155	unknown	<i>ind</i>	Crocker, Borneo	> 1000	AB439984
L6	SPQ.157	G	<i>pub</i>	Crocker, Borneo	1200	AB439985
L6	SPQ.158a	H	<i>ang</i>	Crocker, Borneo	1300	AB439986
L6	SPQ.158b	H	<i>ang</i>	Crocker, Borneo	1300	AB439987
L6	SPQ.159	G	<i>pub</i>	Crocker, Borneo	1300	AB439988
L6	SPQ.160	G	<i>pub</i>	Crocker, Borneo	1200	AB439989
L6	SPQ.161a	H	<i>ang</i>	Crocker, Borneo	1200	AB439990
L6	SPQ.161b	H	<i>ang</i>	Crocker, Borneo	1200	AB439991
L6	SPQ.162	unknown	<i>pet</i>	Crocker, Borneo	1300	AB439992
L6	SPQ.165	G	<i>ang</i>	Crocker, Borneo	1250	AB439993
L6	SPQ.166	G	<i>pet</i>	Crocker, Borneo	1200	AB439994
L6	SPQ.168	H	<i>pet</i>	Crocker, Borneo	1200	AB439995
L6	SPQ.170	H	<i>ban</i>	Crocker, Borneo	600	AB439996
L6	SPQ.173	H	<i>tra</i>	Crocker, Borneo	200	AB439997
L6	SPQ.174a	H	<i>ban</i>	Crocker, Borneo	200	AB439998
L6	SPQ.174b	H	<i>ban</i>	Crocker, Borneo	200	AB439999
L6	SPQ.321	G	<i>pea</i>	Samarinda, Borneo	< 100	AB440000
L6	SPQ.324	G	<i>mot</i>	Samarinda, Borneo	< 100	AB440001
L6	SPQ.325	G	<i>pea</i>	Samarinda, Borneo	< 100	AB440002
L6	SPQ.335	G	<i>gla</i>	Meratus, Borneo	900 - 1000	AB440003
L6	SPQ.340	D	<i>mot</i>	Meratus, Borneo	500	AB440004
L6	SPQ.345	H	<i>ban</i>	Meratus, Borneo	380	AB440005
L6	SPQ.346a	H	<i>ban</i>	Meratus, Borneo	380	AB476662
L6	SPQ.346b	H	<i>ban</i>	Meratus, Borneo	380	AB440006
L6	SPQ.351	H	<i>ind/vel</i>	Meratus, Borneo	200	AB440007
L6	SPQ.352	H	<i>ind/vel</i>	Meratus, Borneo	180	AB440008
L6	SPQ.353	H	<i>hul</i>	Meratus, Borneo	173	AB440009
L6	SPQ.354	H	<i>ind/vel</i>	Meratus, Borneo	173	AB440010
L6	SPQ.356a	G	<i>mot</i>	Meratus, Borneo	170	AB440011
L6	SPQ.356b	G	<i>mot</i>	Meratus, Borneo	170	AB440012
L6	SPQ.358	G	<i>mot</i>	Meratus, Borneo	211	AB440013
L6	SPQ.361a	H	<i>ind/vel</i>	Meratus, Borneo	200	AB440014
L6	SPQ.361b	H	<i>ind/vel</i>	Meratus, Borneo	200	AB476663

L6	SPQ.362	G	<i>mot</i>	Meratus, Borneo	200	AB440015
L6	SPQ.389	unknown	<i>ind/vel</i>	Siduk, Borneo	< 100	AB476664
L6	SPQ.392	unknown	<i>ind/vel</i>	Siduk, Borneo	< 100	AB440016
L6	SPQ.393	H	<i>ind/vel</i>	Siduk, Borneo	< 100	AB440017
L6	SPQ.408	H	<i>ind/vel</i>	Siduk, Borneo	< 100	AB440018
L6	SPQ.412a	H	<i>aet</i>	Siduk, Borneo	< 100	AB440019
L6	SPQ.412b	H	<i>aet</i>	Siduk, Borneo	< 100	AB440020
L6	SPQ.415	H	<i>hos</i>	Siduk, Borneo	< 100	AB440021
L6	SPQ.416	H	<i>hos</i>	Siduk, Borneo	< 100	AB440022
L6	SPQ.418	H	<i>ind/vel</i>	Siduk, Borneo	< 100	AB440023
L6	SPQ.420	unknown	<i>ind/vel</i>	Siduk, Borneo	< 100	AB440024
L6	SPQ.539	K	<i>hul</i>	Berastagi, Sumatra	800	AB476665
L6	SPQ.541	K	<i>ban</i>	Berastagi, Sumatra	500	AB476666
L6	SPQ.689	F	<i>ind</i>	Long Ampung, Borneo	700	AB440025
L6	SPQ.690	F	<i>hul</i>	Long Ampung, Borneo	700	AB476667
L6	SPQ.691	H	<i>hul</i>	Long Ampung, Borneo	700	AB440026
L6	SPQ.695a	F	<i>ind?</i>	Long Ampung, Borneo	700	AB440027
L6	SPQ.695b	F	<i>ind?</i>	Long Ampung, Borneo	700	AB440027
L6	SPQ.696	H	<i>gla</i>	Long Ampung, Borneo	700	AB440029
L6	SPQ.698	D	<i>bec</i>	Long Ampung, Borneo	700	AB440030
L6	SPQ.701	H	<i>aet</i>	Long Ampung, Borneo	700	AB440031
L6	SPQ.703	D	<i>bec</i>	Long Ampung, Borneo	700	AB440032
L6	SPQ.704	H	<i>aet?</i>	Long Ampung, Borneo	700	AB440033
L6	SPQ.705	H	<i>ban/ind</i>	Long Ampung, Borneo	700	AB440034
L6	SPQ.712	F	<i>ind</i>	Long Ampung, Borneo	700	AB440035
L6	SPQ.713	F	<i>hul</i>	Long Ampung, Borneo	700	AB440036
L6	SPQ.714	H	<i>gla</i>	Long Ampung, Borneo	700	AB440037
L6	SPQ.722	G	<i>hos/pea</i>	Samarinda, Borneo	< 100	AB440038
L6	SPQ.723	G	<i>hyp</i>	Samarinda, Borneo	< 100	AB440039
L6	SPQ.724	G	<i>hos/pea</i>	Samarinda, Borneo	< 100	AB440040
L6	SPQ.725	G	<i>hos/pea</i>	Samarinda, Borneo	< 100	AB440041
L6	SPQ.727	G	<i>pea?</i>	Samarinda, Borneo	< 100	AB440042
L6	SPQ.728	G	<i>ban/ind</i>	Samarinda, Borneo	< 100	AB440043
L6	SPQ.729	G	<i>hyp</i>	Samarinda, Borneo	< 100	AB440044
L6	SU.L12	unknown	<i>bec</i>	Lambir, Borneo	150	AB476668

L6	SU.L17	unknown	<i>hul</i>	Lambir, Borneo	150	AB461434
L6	SU.L18	G	<i>pse</i>	Lambir, Borneo	150	AB440045
L6	SU.L19	G	<i>pse</i>	Lambir, Borneo	150	AB440046
L6	SU.L21	G	<i>win</i>	Lambir, Borneo	150	AB461435
L6	SU.L27	D	<i>bec</i>	Lambir, Borneo	150	AB461437
L6	SU.L30a	unknown	<i>bec</i>	Lambir, Borneo	150	AB440047
L6	SU.L30b	unknown	<i>bec</i>	Lambir, Borneo	150	AB440048
L6	SU.L31	D	<i>bec</i>	Lambir, Borneo	150	AB440049
L6	SU.L32b	unknown	<i>bec</i>	Lambir, Borneo	150	AB440050
L6	TI.9823	unknown	<i>hyp</i>	Kuching, Borneo	200-400	AB476669
L6	TI.s38	H	<i>ban</i>	Lambir, Borneo	150	AB440058
L6	TI.s40	unknown	<i>bec</i>	Lambir, Borneo	150	AB461440
L6	TI.s51	unknown	<i>hos</i>	Lambir, Borneo	150	AB440059
L6	TI.s54	D	<i>bec</i>	Lambir, Borneo	150	AB440060
L6	TI.s58	E	<i>hul</i>	Lambir, Borneo	150	AB440061
L6	TI.s62	H	<i>hul</i>	Lambir, Borneo	150	AB440062
L7	SPQ.540	K	<i>hul</i>	Berastagi, Sumatra	800	AB476670
L8	SPQ.023	unknown	<i>hyp</i>	Johor, Malaya	< 100	AB440063
L8	SPQ.024	K	<i>pru</i>	Johor, Malaya	< 100	AB440064
L8	SPQ.116	A	<i>hyp</i>	Crocker, Borneo	600	AB440065
L8	SPQ.142	H	<i>ban</i>	Crocker, Borneo	350	AB440066
L8	SPQ.334	G	<i>ban</i>	Meratus, Borneo	966	AB440067
L8	SU.L14	unknown	<i>lam</i>	Lambir, Borneo	150	AB440068

Outgroups

Species name	Location	Genebank #
<i>Coccus celatus</i>	Tailand	AB476671
<i>Coccus hesperidum</i>	Adana, Turkey	AB440069
<i>Coccus pseudomagnoliarum</i>	California	AB440070
<i>Coccus viridis</i>	Tailand	AB476672
<i>Eulecanium kunoense</i>	California	AB440071
<i>Parthenolecanium pruinsum</i>	Nagano, Japan	AB440072

Reference

Quek SP, Davies SJ, Ashton PS, Itino T, Pierce NE (2007) The geography of diversification in mutualistic ants: a gene's-eye view into the Neogene history of Sundaland rain forests. *Mol Ecol* 16:2045-2062. DOI 10.1111/j.1365-294X.2007.03294.x

Fig. 1

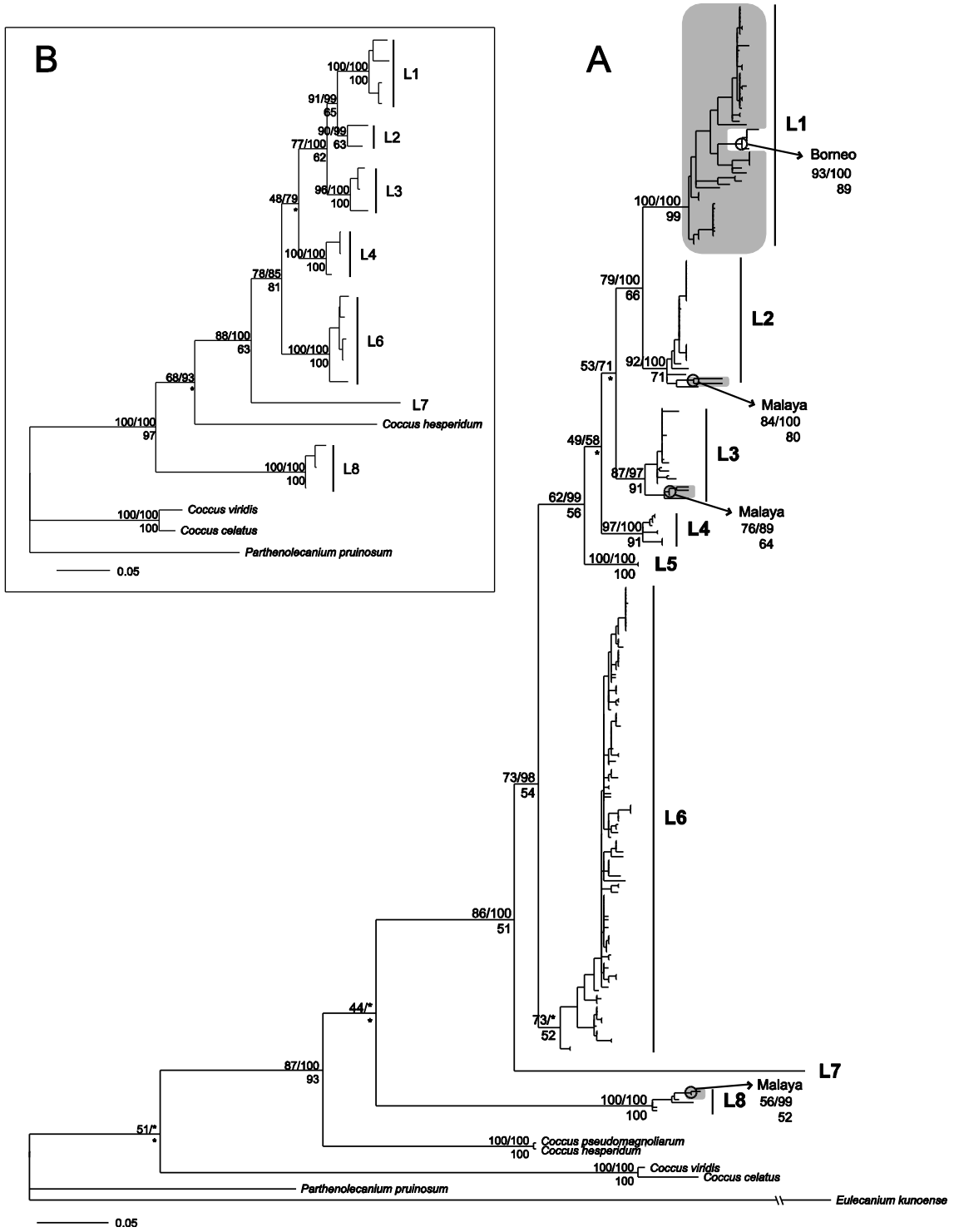


Fig. 2

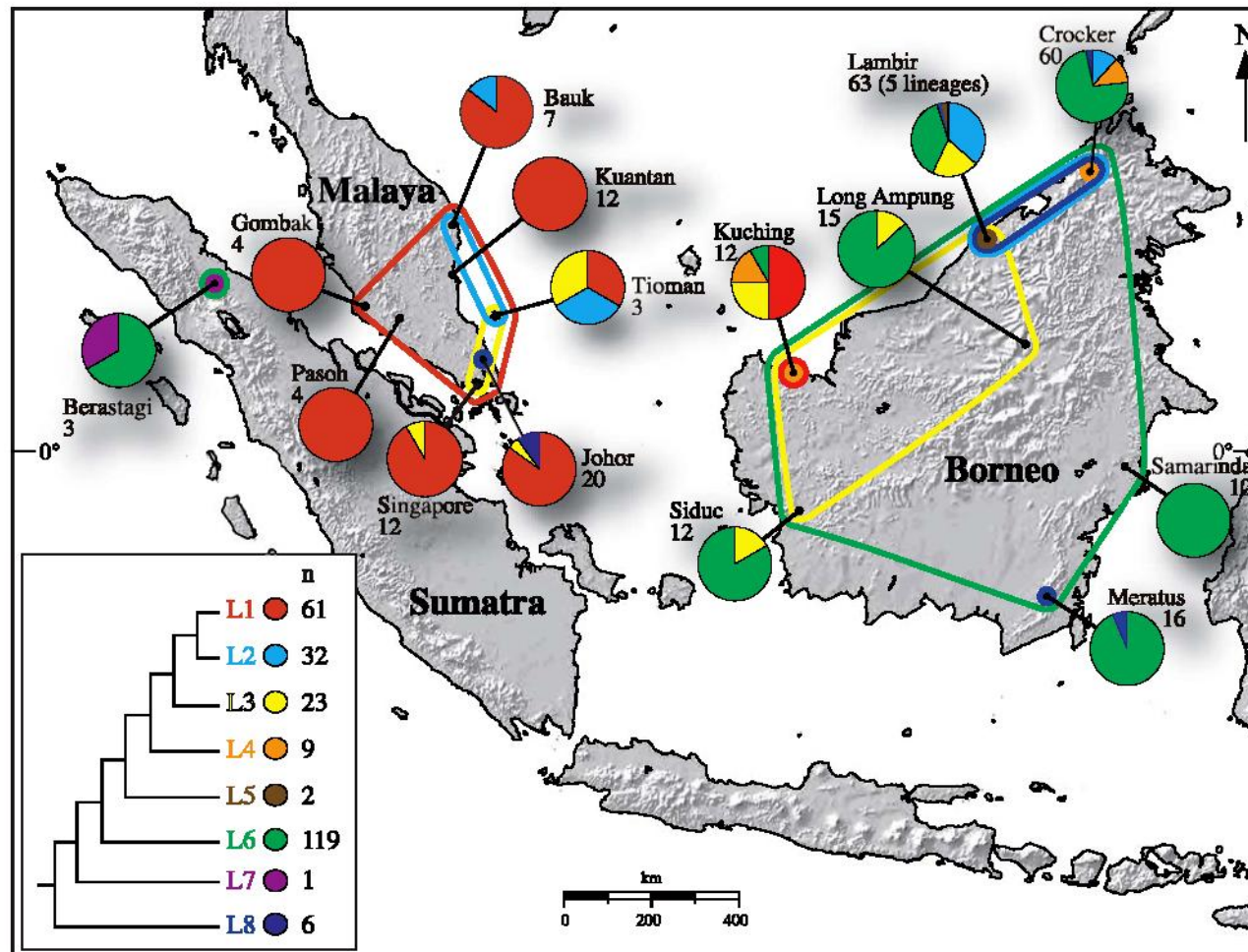


Fig. 3

