ORIGINAL ARTICLE

Stochastic faunal exchanges drive diversification in widespread Wallacean and Pacific island lizards (Squamata: Scincidae: *Lamprolepis smaragdina*)

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ABSTRACT

Aim Widespread species found in disturbed habitats are often expected to be human commensals. In island systems, this association predicts that dispersal will be mediated by humans. We investigated the biogeographical relationships among populations of a widespread tree skink that inhabits coastal forest and human-cultivated plantations in Southeast Asia. We sought to determine whether populations of the emerald tree skink, *Lamprolepis smaragdina*, dispersed via mechanisms that were not human-mediated ('natural' dispersal) or whether dispersal was mediated by humans. The latter scenario predicts low levels of genetic differentiation across a species' range, coupled with a genetic signature of recent range expansion.

Location Southeast Asia, the Philippines, Wallacea and the south-western Pacific.

Methods We analysed sequences of mitochondrial DNA from 204 samples collected throughout the range of this species. We use phylogenetic and population genetic methods to distinguish between predicted geographical patterns of genetic variation that might indicate natural or human-mediated dispersal.

Results In contrast to predictions derived from similar studies of taxonomy and natural history, we found *L. smaragdina* to be characterized by highly structured and seemingly geographically stable mitochondrial gene lineages.

Main conclusions Our results demonstrate a novel pattern of widespread species distribution, never before observed in vertebrates of the Indo-Australian Archipelago. Although this widespread and highly dispersive species is capable of long-distance dispersal, and has a clear history of over-water dispersal, it exhibits sharp genetic differentiation across its range. Our results suggest that random waif dispersal has been a pervasive ongoing phenomenon throughout the evolutionary history of this species.

Keywords

Emerald tree skink, human-mediated dispersal, island biogeography, lizard, Pleistocene, sweepstakes dispersal, time tree, waif dispersal.

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INTRODUCTION

The phenomenon of long-distance over-water dispersal has contributed to the assemblage of unique communities of terrestrial vertebrates on isolated oceanic islands (Wallace, 1881; Diamond, 1975). Studies have shown that dispersal across island archipelagos is influenced by island size, distance between islands, distance to continental sources, permanence of physical barriers and the physiology and ecological specificities of the dispersing organisms (MacArthur & Wilson, 1967; Whittaker, 1998). For terrestrial vertebrates in archipelagos, the presence, width and degree of permanence of marine barriers are important factors in the dispersibility of many species (Darlington, 1957; Carlquist, 1965; Lomolino *et al.*, 2010).

Oceanic island communities generally include endemic species and widely distributed non-endemic species (Carlquist, 1965). The more dispersal-prone species are expected to exhibit biogeographical and genetic patterns that differ from less vagile species. This is evinced by the phylogeography of saltwater crocodiles (*Crocodilus porosus*), reticulated pythons (*Python reticulatus*) and volant organisms (bats and birds), all of which disperse readily across marine barriers (MacArthur & Wilson, 1967; Lomolino *et al.*, 2010).

Terrestrial lizards are among the most common land vertebrates of the Pacific (Buden, 2000, 2008), a region composed of islands with unique vertebrate communities, often of exceptionally high biomass (Alcala & Brown, 1967; Losos, 2009). Some species of lizards are capable of long-distance oceanic travel, although the mechanisms by which they achieve this are not always clear (Fisher, 1997; Austin, 1999). Two hypotheses are proposed to explain widespread distributions of taxa in archipelagos: (1) natural dispersal through rafting on vegetative mats (Wallace, 1881; Brown & Alcala, 1957; Darlington, 1957; Schoener & Schoener, 1984; Calsbeek & Smith, 2003), and (2) inadvertent human-mediated passage (Loveridge, 1945; Darlington, 1957; Zweifel, 1979; King & Horner, 1989; Zug, 1991; Beckon, 1992; Fisher, 1997; Brown *et al.*, 2010). On Pacific islands, human-mediated dispersal is considered the primary mode of inter-island dispersal for many species of geckos and skinks (Loveridge, 1945; Darlington, 1957; Zweifel, 1979; King & Horner, 1989; Zug, 1991; Fisher, 1997; Austin, 1999; Austin *et al.*, 2011). Ancient Polynesian settlers and modern humans have had a profound impact on lizard assemblages on Pacific islands through inadvertent introduction via commerce (Fisher, 1997; Austin, 1999). However, some widespread lineages exhibit more ancient histories of colonization not mediated by humans (Keogh *et al.*, 2008; Oliver *et al.*, 2009; Noonan & Sites, 2010).

The emerald tree skink, *Lamprolepis smaragdina* (Lesson, 1826), is an exceedingly common widespread arboreal species that is found in Wallacea, the Philippines, New Guinea, Melanesia and the west Pacific; it may reach the highest biomass of any vertebrate present in some parts of its range (Perry & Buden, 1999). Although widespread, the species also exhibits a biogeographically anomalous pattern of distribution (Fig. 1). Common throughout the Philippines and in Indonesia east of Wallace's Line, *L. smaragdina* is entirely absent from the adjacent continental shelf (i.e. the Sunda Shelf islands of Borneo, Java and Sumatra, as well as the Malay Peninsula). In contrast, other rare species of *Lamprolepis* (*Lamprolepis leucosticta*, *Lamprolepis nieuwenhuisii* and *Lamprolepis vyneri*) are only found on Asian continental shelf islands where they are seldom encountered by field biologists (Lloyd *et al.*, 1968;
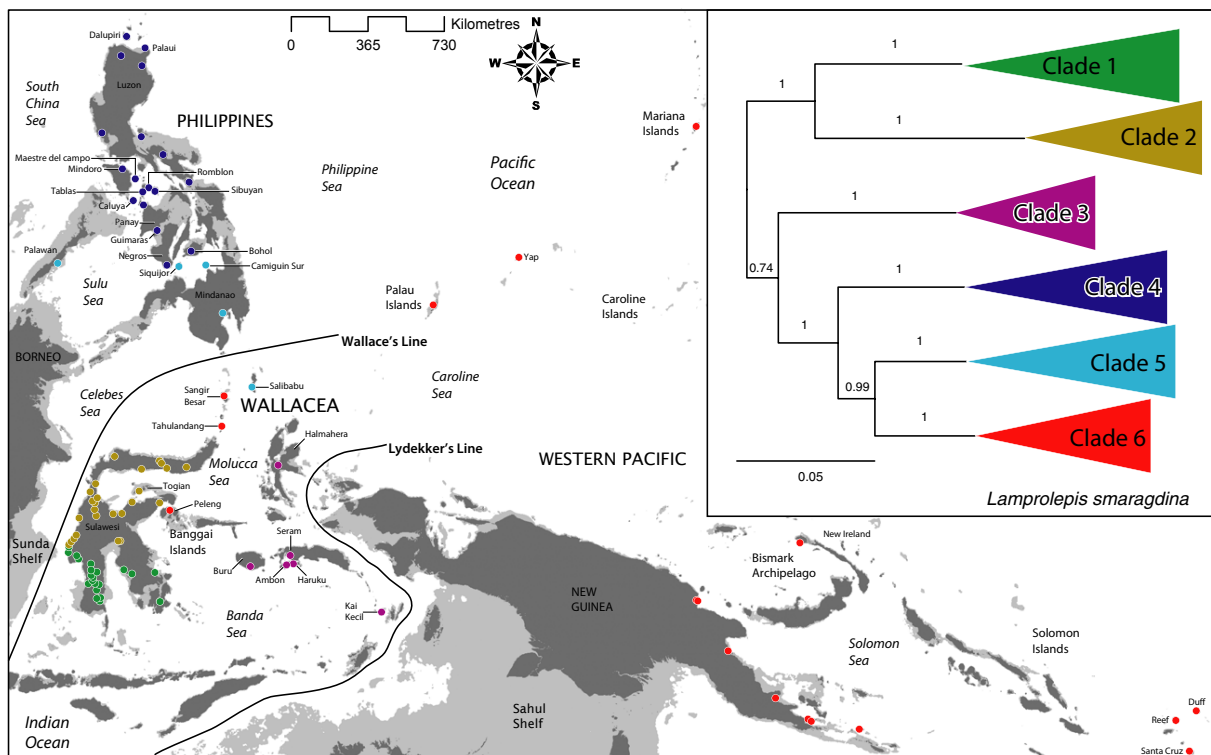

Figure 1 Map of Southeast Asia and the west Pacific showing the distribution of samples of the widespread species *Lamprolepis smaragdina*, the extent of current islands (dark grey) and the maximum extent of islands during the Pleistocene (light grey). Wallace's Line and Lydekker's Line are shown for reference. Colours of the samples follow the colours of the clades in the inset phylogeny. The phylogeny is a summary of the major relationships found from a Bayesian analysis of the mitochondrial DNA gene *ND2* (see methods).

Manthey & Grossmann, 1997; Das, 2004). The natural history and distribution of *L. smaragdina* suggest that the species may have obtained its current distribution through human-mediated dispersal (Perry & Buden, 1999). This primarily arboreal, diurnal species prefers the trunks of large trees in open, coastal areas and is rarely seen in dense primary forest. It is commonly found close to human settlements (Alcala & Brown, 1966) in highly modified vegetation communities such as coconut palm plantations (C.W.L., R.M.B., J.A.M., C.D.S., B.J.E., D.T.I., C.C.A., A.C.D., pers. obs.).

Very few, if any, of the oceanic islands in Southeast Asia and the Pacific have a geological history of fragmentation that could serve as the basis of vicariant scenarios to explain current species distributions (Hall, 1996, 1998). Dispersal across marine barriers must therefore have occurred multiple times in *L. smaragdina*. The timing and frequency of dispersal events may be influenced by humans, the climatic and geological history of Southeast Asia or a combination of these factors (Hall & Holloway, 1998; Hall, 2001, 2002; Sun *et al.*, 2000; van den Bergh *et al.*, 2001; Woodruff, 2003).

Natural and human-mediated dispersal scenarios have distinct genetic signatures that can be inferred from phylogenetic relationships and population genetic patterns. Widespread species that underwent human-mediated dispersal will show low levels of genetic variation across populations on distant islands (Austin, 1999), recent diversification consistent with the occurrence and spread of human populations in Southeast Asia (< 50,000 years; Bellwood, 1985), and genetic evidence of recent population range or demographic expansion. Alternatively, rare stochastic natural dispersal will produce pronounced genetic differences among islands, substantial geographical structure with clear historical signal, and an age of the group that pre-dates human colonization of the region. Herein, we test these alternative scenarios.

MATERIALS AND METHODS

Taxon sampling and DNA sequence data

Tissue samples were obtained from 204 specimens of *L. smaragdina* representing the breadth of the distribution of this species (see Appendix S1 in Supporting Information). Multiple samples were obtained from each locality where possible to assess haplotype diversity. Outgroup samples comprised the lygosomine skinks *Carlia beccarii*, *Cryptoblepharus keiensis*, *Dasia grisea*, *Dasia olivacea*, *Dasia vittata*, *Emoia atrocostata*, *Emoia caeruleocauda*, *Euprepis auratus*, *Eutropis multifasciata*, *Eutropis rudis*, *Lipinia relicta* and *Lygosoma bowringii*.

Genomic DNA was extracted from liver or muscle tissue using the DNeasy Tissue Kit (Qiagen, Inc., Valencia, CA, USA). We sequenced the mitochondrial gene NADH dehydrogenase subunit 2 (*ND2*) using overlapping primers developed by Macey *et al.* (1997). The primers amplify a 1434 base pair (bp) region including the entirety of the *ND2* coding region and the following tRNAs: tryptophan, alanine,

asparagine, tyrosine and cysteine. Amplification followed standard protocols for polymerase chain reaction (PCR). Amplified samples were purified using exonuclease I and shrimp alkaline phosphatase (ExoSAP-IT, USB, Cleveland, OH, USA). Purified PCR products were sequenced directly using BigDye Terminator sequencing reaction mix (Applied Biosystems, Carlsbad, CA, USA), following the manufacturer's protocols. Cycle-sequencing products were visualized on either an ABI 377 or an ABI 3730 automated sequencer. All DNA sequences generated for this study have been deposited in GenBank (accession numbers JQ610685–JQ610904).

Sequence alignment was performed using Muscle 3.6 (Edgar, 2004) with the default settings. Mesquite 2.0 (Maddison & Maddison, 2010) was used to verify that the protein-coding region remained in frame throughout its length. Alignment of tRNAs and stem–loop regions was manually adjusted and three ambiguous regions totalling 43 bp were excluded from analyses. The data matrices used for the phylogenetic analyses have been deposited in Dryad (http://datadryad.org).

Phylogenetic analyses

Bayesian phylogenetic analyses were performed using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001). We evaluated a variety of a priori partitioning strategies including unpartitioned data sets, data sets with two partitions (*ND2* and tRNA) and data sets with four partitions (each *ND2* codon position and tRNA) to accommodate differences between the protein-coding region and tRNAs. The best partitioning strategy was determined a posteriori through Bayes factors (Brandley *et al.*, 2005). The best-fit model of evolution for each data partition was selected using the Akaike information criterion (AIC), as implemented in MrModeltest 2.2 (Nylander, 2004). To avoid model misspecification we explored alternative strategies of Bayesian tree inference including different partitioning strategies and the incorporation of among-partition rate variation (APRV) through the command 'prset ratepr = variable'. Marshall *et al.* (2006) and Marshall (2010) suggested that use of APRV should be implemented with caution and that branch-length priors may need to be adjusted. Therefore, we ran our partitioned analyses under three different branch-length priors: mean = 10 (default), 50 or 100. Four independent analyses were performed for each partitioning strategy, each with four Markov chain Monte Carlo (MCMC) runs. Each MCMC run was performed for 6 million generations and sampled every 1000 generations. We examined the output in Tracer 1.4 (Rambaut & Drummond, 2007) to determine the number of generations to exclude as burn-in. Additionally we used Are We There Yet? (awty; Wilgenbusch *et al.*, 2004; Nylander *et al.*, 2008) to determine whether the independent runs had converged on the same state space and, if so, whether sampling was sufficient, and also to compare the effect of varying branch-length priors.

Divergence time estimation

Divergence time analyses were conducted using BEAST 1.5.3 (Drummond & Rambaut, 2006, 2007). The data set was reduced to a single haplotype per population (found during preliminary analyses) for a total of 72 individuals. We then used a relaxed lognormal clock with a 95% normal distribution prior (mean 0.00895, standard deviation 0.0025) for a rate distribution of 0.483–1.31% Myr^{-1}, which was used by Rabosky *et al.* (2007) for mitochondrial genes in Australian skinks. Without a fossil record for *Lamprolepis* or any close relatives, it is impossible to calibrate a molecular clock based on fossil placement. One possible source of information that could provide maximum ages for populations is the ages of various islands within the range of *L. smaragdina*. However, this type of calibration suffers from only providing a maximum age with no minimum bound. For this reason we instead rely on using a rough molecular rate for divergence dating. We judge that even a very general or vague time calibration can assist us in distinguishing between human-mediated and natural dispersal and that this temporal framework can then be evaluated a posteriori with the estimates of island age from the geological record.

We used a Yule prior on speciation rates and used our preferred model (based on Bayes factors) of four partitions with a GTR + I + Γ model for each partition. All other priors were left with their default distributions. Two independent analyses were run for 30 million generations, sampling every 5000 generations. Output files were analysed using TRACER (Rambaut & Drummond, 2007). A maximum clade credibility tree for the two analyses, excluding the first 10 million generations, was summarized with TREEANNOTATOR 1.7.2 (Drummond & Rambaut, 2007).

We estimated dispersal events on the time tree using an ordered parsimony reconstruction in MESQUITE (Maddison & Maddison, 2010), treating each island as a unique area. If islands were connected during any part of their history then we may assume that over-water dispersal was not required and so we considered them as one unit for the reconstruction. The maximum parsimony estimate of inferred dispersal events was mapped onto the stems of the tree. We chose the stems because we do not expect that dispersal occurred at the cladogenetic (branching) event, but rather before it. We place inferred dispersal events at the most basal stem position with the realization that dispersal could occur anywhere along the branch.

Inference of demographic history

Under a human-mediated dispersal hypothesis, we expect low genetic differentiation among populations on different islands (Moritz *et al.*, 1993; Glor *et al.*, 2005) and evidence of recent population expansion. In contrast, under natural dispersal, we expect sharp phylogenetic structure among populations on different islands. Within large islands, we may also potentially observe genetic subdivision among populations isolated by current or former barriers to dis-

persal. To evaluate these predictions, we used a variety of population genetic analyses implemented by ARLEQUIN 3.1 (Excoffier *et al.*, 2005). For these analyses, samples were grouped by biogeographical region: Philippines, Wallacea and West Pacific (Fig. 1). The Philippine group includes all oceanic islands north of Wallace's Line and west of the Philippine Sea, including Palawan; the Wallacea group includes all islands between Wallace's Line and Lydekker's Line; and the west Pacific group includes all islands east of Lydekker's Line and the oceanic Pacific islands.

Mismatch distributions were calculated and qualitatively assessed for multimodality, which potentially stems from population structure, as contrasted with unimodality which is suggestive of recent population expansion or sudden panmixia. We calculated raggedness indices and their significance via coalescent simulations of a large, neutrally evolving population of constant size in the context of assumed selectively neutral nucleotide substitutions (Rogers & Harpending, 1992; Slatkin & Hudson, 1992). We also calculated Tajima's D as a test for selective neutrality, and we employed Fu's F_S neutrality test (Fu, 1997) to examine our data for indications of changes in population size. This method assumes neutrality and may diagnose recent population or demographic expansion via a highly negative value of F_S (Fu, 1997). To elucidate the amount of genetic variation that could be explained among and within our three regions, we performed an analysis of molecular variation (AMOVA) with 1000 permutations (Excoffier *et al.*, 2005).

RESULTS

Phylogeny

The unambiguously aligned data set included 808 parsimony-informative characters, 446 constant characters and 137 variable but uninformative characters, for a total of 1391 characters. Among the alternative partitioning strategies, the four-partition analysis resulted in a significantly better likelihood based on Bayes factors (Table 1). Mixing in the four-partition Bayesian analysis was poor when the APRV was set to variable and the default branch-length prior was used. Mixing improved dramatically with branch-length priors changed to 50 and 100. The Bayes factor comparison between the branch-length priors of 50 and 100 was marginally significant. The posterior distribution of the likelihood was best in the analysis with the branch length prior of 100, but only moderately significant (BF = 7.22). The independent runs of the four-partition analysis converged after 1 million generations and these were discarded as burn-in. We therefore focus our discussion on the phylogeny resulting from the partitioned Bayesian analysis with a branch length prior of 50, which was selected as the preferred topology (Table 1). This phylogeny is presented in Figs 1 & 2.

The two separate BEAST analyses converged on the same parameter space and were combined for further analysis.

Table 1 Comparison of Bayes factors between the three different partitioning strategies and varying branch-length priors calculated from the harmonic mean log-likelihood output by MRBAYES: ln(hm*L*). Model of evolution for each DNA partition estimated using the Akaike information criterion in MRMODELTEST.

	4 br 100	4 br 50	4 br 10	2	0	ln(hm*L*)	Model of evolution
4 br 100	—	7.22	392.72	1349.82	1543.20	−27799.29	GTR+I+Γ (all)
4 br 50		—	385.50	1342.60	1535.98	−27802.90	GTR+I+Γ (all)
4 br 10			—	957.10	1150.48	−27995.65	GTR+I+Γ (all)
2				—	193.38	−28474.20	GTR+I+Γ (all)
0					—	−28570.89	GTR+I+Γ (all)

br: branch rate prior setting in MRBAYES.

Many maximum clade credibility intervals on node dates are broad, especially those deep in the tree (Fig. 3). However, under the assumption that the mutation rate deployed in this analysis roughly approximates the actual mutation rate, some conclusions can be drawn.

The phylogenies (Figs 2 & 3) are well resolved and supported (posterior probability ≥ 0.95) for almost all major nodes. *Lamprolepis smaragdina* is sister to *Lygosoma bowringii*, which was shown previously (Honda *et al.*, 2000; Reeder, 2003; Skinner *et al.*, 2011). *Lamprolepis vyneri* from Borneo is not closely related to its congener *L. smaragdina*, but rather is placed with *Dasia*. *Lamprolepis smaragdina* is an old clade (Fig. 3), having first diversified approximately 16 Ma [95% highest posterior density (HPD) 9–33 Ma]. The phylogeny of *Lamprolepis smaragdina* can be divided into six major clades diversifying 10–15 Ma (Figs 1–3). Clades 1 and 2 represent two Sulawesi assemblages, constituting morphologically distinct southern and northern populations, respectively. Clade 3 consists entirely of sequences from the Maluku Islands. Clade 4 consists of a subset of Philippine samples representing 15 Philippine islands in the northern and eastern portions of this archipelago. Clade 5 consists of sequences obtained from individuals from four additional Philippine islands from the southern and western portion of this archipelago, and also from individuals from the island of Salibabu in the Talaud group, which is located between Sulawesi and the Philippines. The Philippine clade 5 is sister to clade 6, and not sister to clade 4, rendering Philippine *L. smaragdina* paraphyletic. Clade 6 is primarily composed of sequences obtained from individuals from Papua New Guinea, the Solomon Islands, Palau and the Caroline Islands. Also included in clade 6 are sequences from Sulawesi's eastern and northern satellite islands of Peleng, Sangir Besar and Tahulandang (Fig. 2).

The two mitochondrial DNA clades on Sulawesi (clades 1 and 2) correspond to two distinct colour morphs found on the island. Lizards with mitochondrial DNA in clade 2 are brown with large black dorsal blotches, and lizards with mitochondrial DNA in clade 1 are uniformly bright green. These two sister clades represent morphologically distinct colour morphs and are deeply divergent (15% uncorrected sequence divergence; Table 2). The Maluku clade (clade 3) is well differentiated from other clades and comprises five subclades, which correspond to island groups separated by deep-water barriers, including the Kai Islands, Halmahera, Buru and the Pleistocene land bridge island complex that includes Seram, Ambon and Haruku. The Philippine populations are paraphyletic, and the internal structures of clades 4 and 5 depart completely from expectations based on Pleistocene connectivity of islands (Heaney, 1985; Voris, 2000; Brown & Diesmos, 2002, 2009). In contrast with clades 1–5, clade 6, which corresponds primarily to New Guinea and west Pacific populations, comprises geographically widespread populations that are fairly genetically homogeneous. Perhaps most surprising from a geographical perspective is the observation that Peleng, Sangir Besar and Tahulandang populations of *Lamprolepis* are placed in clade 6 rather than with adjacent Sulawesi, Maluku or Philippine populations (Figs 2 & 3).

Population structure and demographic history

We observed strikingly high genetic diversity in *L. smaragdina* (Table 3). The number of unique haplotypes ranged from 33 to 124 for the three regions (Wallacea, the Philippines and the west Pacific). Wallacea and the Philippines have the highest number of polymorphic sites (P_N = 553 and 286, respectively) whereas the number of polymorphic sites in the west Pacific is 129 (Table 3). Haplotype diversities (h) within individual biogeographical regions were all high (Table 3). Nucleotide diversity was lowest in the west Pacific (π = 0.0271) and highest in Wallacea (π = 0.1015).

Mismatch distributions from each of these three regions were qualitatively ragged and multimodal (significant *T* statistics for Wallacea and the West Pacific), suggesting structured populations (Fig. 4; Harpending, 1994). Raggedness index values were non-significant for all three regions, indicating a failure to reject goodness of fit between the simulated frequencies of pairwise nucleotide differences and the observed distribution under the model of sudden population expansion. Non-significant *P*-values for Tajima's *D* indicate a failure to reject neutrality and demographic stability within the three regions. Fu's F_S is significant for all three regions, which is inconsistent with a constant population size. The AMOVA analysis suggests that the majority of observed molecular variation is explained by within-region variation (61.1%), whereas less (38.9%) was found between regions (Fig. 5).
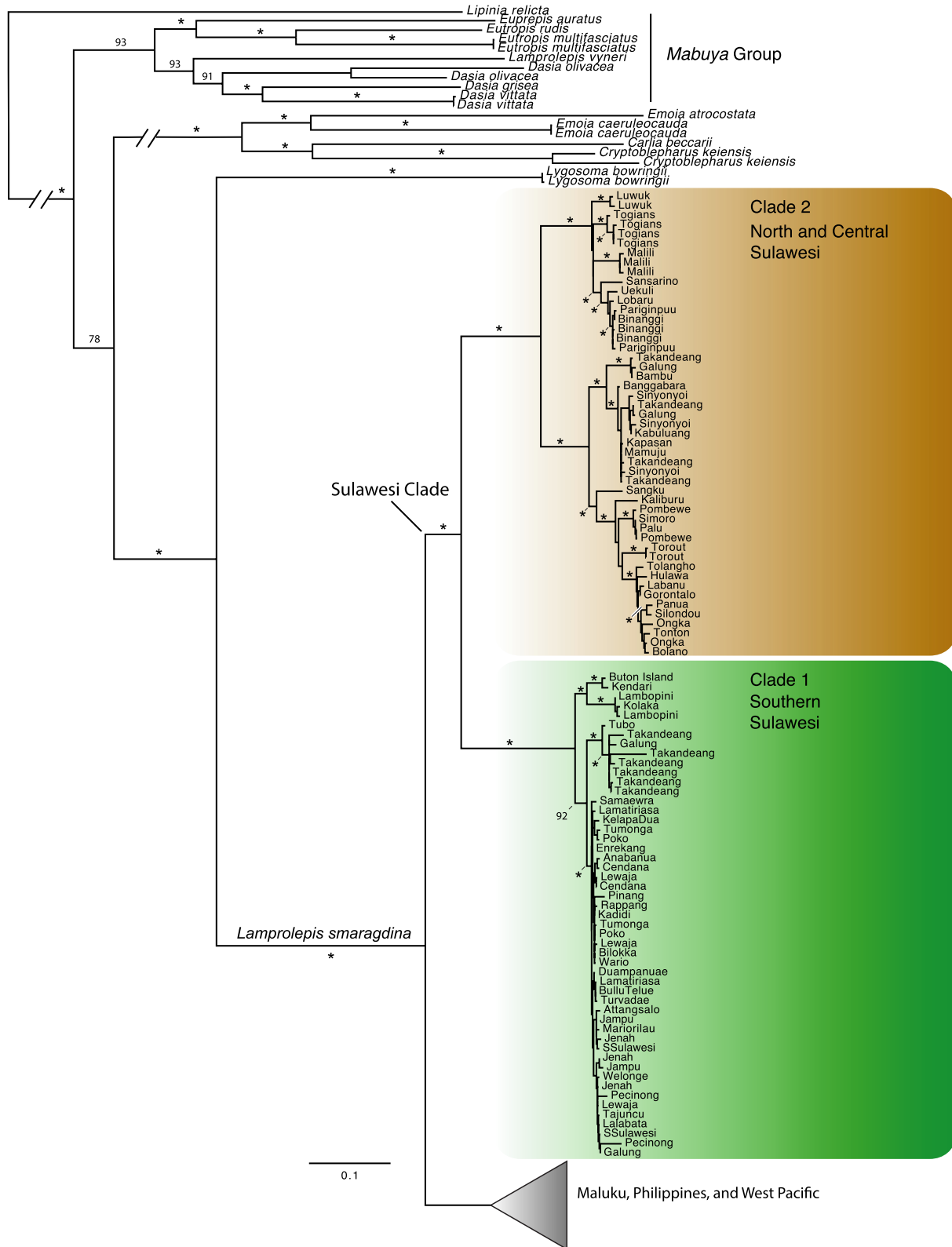
Figure 2 Bayesian majority-rule consensus tree (from 10,000 trees) of *Lamprolepis smaragdina* with major clades highlighted and named according to biogeographical region. Asterisks denote Bayesian posterior probabilities ≥ 0.95 and the scale bar represents the number of substitutions per site.
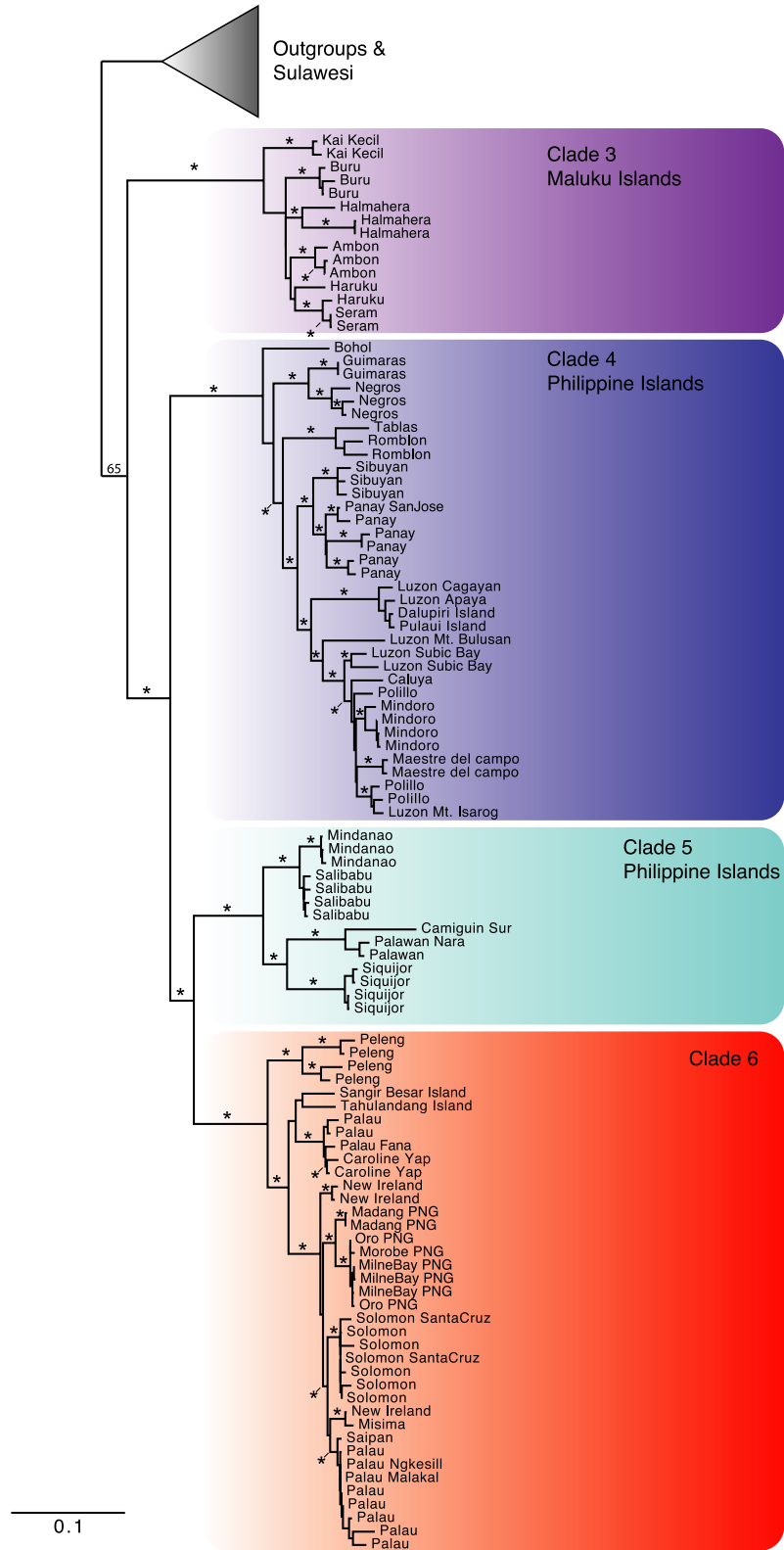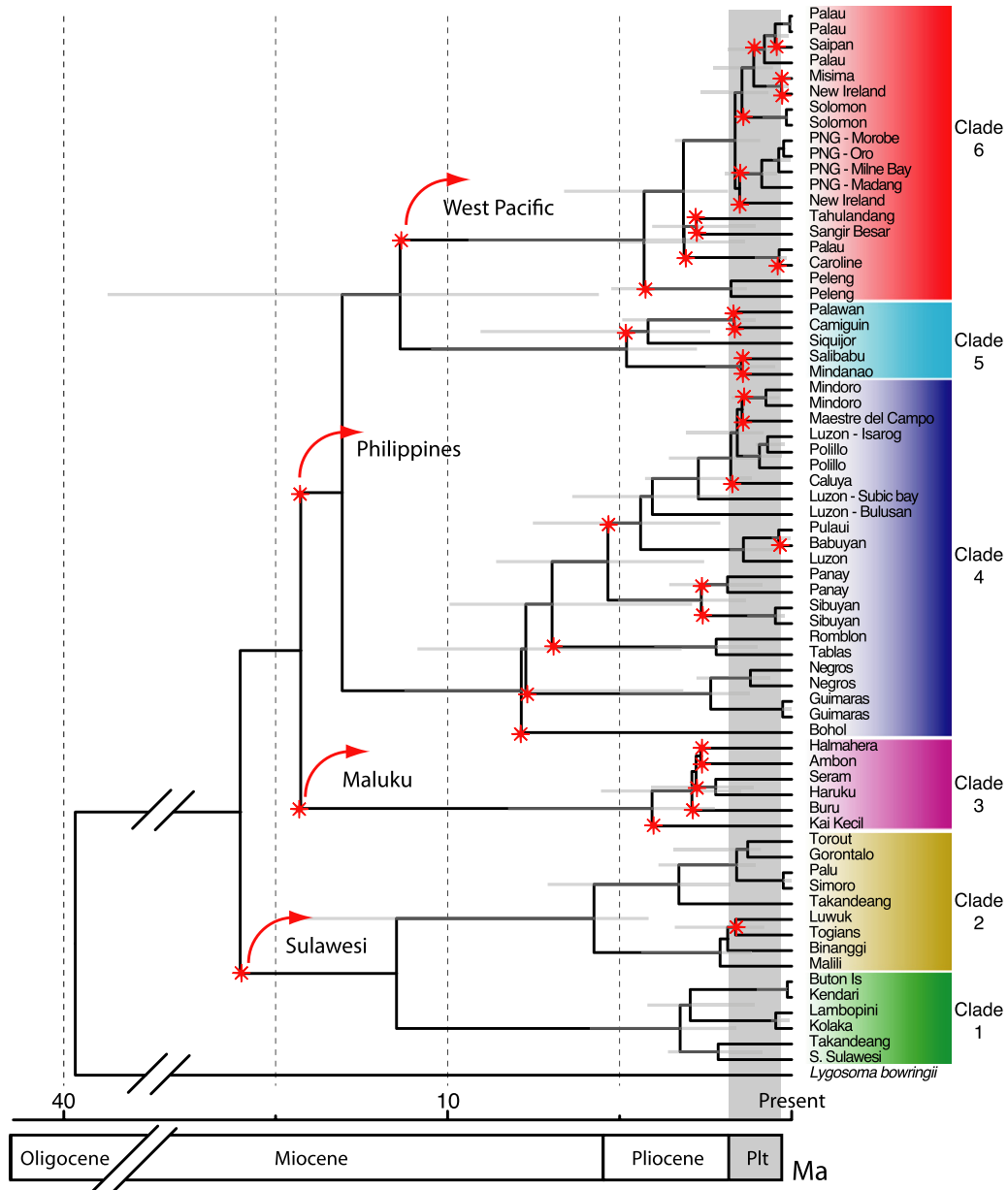
Figure 2 Continued

Figure 3 Maximum clade credibility tree of *Lamprolepis smaragdina* from two separate BEAST analyses run with a lognormal relaxed molecular clock. Sampling was reduced to one haplotype per island or major population for a total of 72 individuals. Major clades are labelled with clade number and colour (Fig. 1). Oceanic dispersal events necessary to explain the current distribution of species are marked by a red asterisk. These hypothesized events could have occurred at any time along the stem branch. The time-scale of divergence in this group clearly exceeds the Pleistocene, shown in grey, with most major divergences occurring in the Miocene.

	Clade 1	Clade 2	Clade 3	Clade 4	Clade 5	Clade 6
Clade 1	0.1–7.3	10.7–17.4	12.5–16.5	9.0–33.9	10.2–15.6	12.1–18.2
Clade 2		0.1–9.4	12.6–16.7	8.7–21.3	11.7–14.7	12.1–16.6
Clade 3			0.1–6.5	6.3–18.4	9.2–13.7	10.8–14.7
Clade 4				0.0–25.1	6.1–14.6	5.7–29.8
Clade 5					0.1–7.0	7.8–12.8
Clade 6						0.1–7.4

Table 2 Comparison of uncorrected pairwise sequence divergence within and among the major *Lamprolepis smaragdina* clades shown in Figs 1–3.

Table 3 Summary of *Lamprolepis smaragdina* sampling, the three major regions studied, numbers of individuals (n), numbers of mitochondrial DNA haplotypes (N_h), numbers of polymorphic sites (P_N), haplotype diversity (h) and nucleotide diversity (π). See Appendix S1 for full details of sampling and a list of all samples included.

Region/clade	n	N_h	P_N	h	π
Philippines	46	45	286	0.999 ± 0.005	0.0784 ± 0.0382
Wallacea	125	124	553	0.999 ± 0.001	0.1015 ± 0.0485
West Pacific	33	33	129	1.000 ± 0.008	0.0271 ± 0.0135
All samples	204	202	596	0.999 ± 0.001	0.1222 ± 0.0582

DISCUSSION

Natural, ancient, stochastic dispersal

The distribution of *L. smaragdina* in Southeast Asia provides a unique opportunity to explore biogeographical relationships across a matrix of suitable habitat with intervening marine barriers to dispersal. The inferred age of *Lamprolepis*, along with geographically structured population subdivisions, provides a clear indication that natural dispersal has been the primary mechanism by which this species has spread throughout insular Southeast Asia and the west Pacific. In light of its seemingly commensal distribution with humans, it is remarkably diverse with high levels of population substructuring. This diversity could stem from a large effective population size, but in this case we can dismiss this explanation as the sole cause of diversity because the unique lineages of *L. smaragdina* are geographically structured.

Early interpretations of the distribution of *Lamprolepis smaragdina* inferred a centre of origin in the Maluku Archipelago (Mertens, 1929) or the Asian continent (Greer, 1970). Our phylogeny indicates that *L. smaragdina* is not closely related to Sunda Shelf taxa (*Dasia* and *L. vyneri*) as hypothesized by Greer (1970), but our finding of *Lygosoma* as the sister to *Lamprolepis smaragdina* is consistent with a western origin.

Despite clear evidence for a long history of waif dispersal (sweepstakes dispersal), some aspects of biogeography in *L. smaragdina* are consistent with generally accepted hypotheses for the region. For example, the occurrence of Sulawesi and Maluku clades, and a large clade of Philippine populations, are consistent with general expectations of biogeographical provincialism based on studies of other organisms (Lomolino *et al.*, 2010).

In contrast to the geographical regionalism revealed at a larger Asian–Pacific scale, fine-scale biogeographical patterns within these regions defy expectations, and differ markedly from those observed in other groups. *Lamprolepis smaragdina* from Sulawesi have two divergent clades of mitochondrial DNA that correspond to the two colour pattern types found on the island. The margins of distributions of these clades do not, in general, correspond with the boundaries of previously defined Sulawesi areas of endemism (AOEs) identified
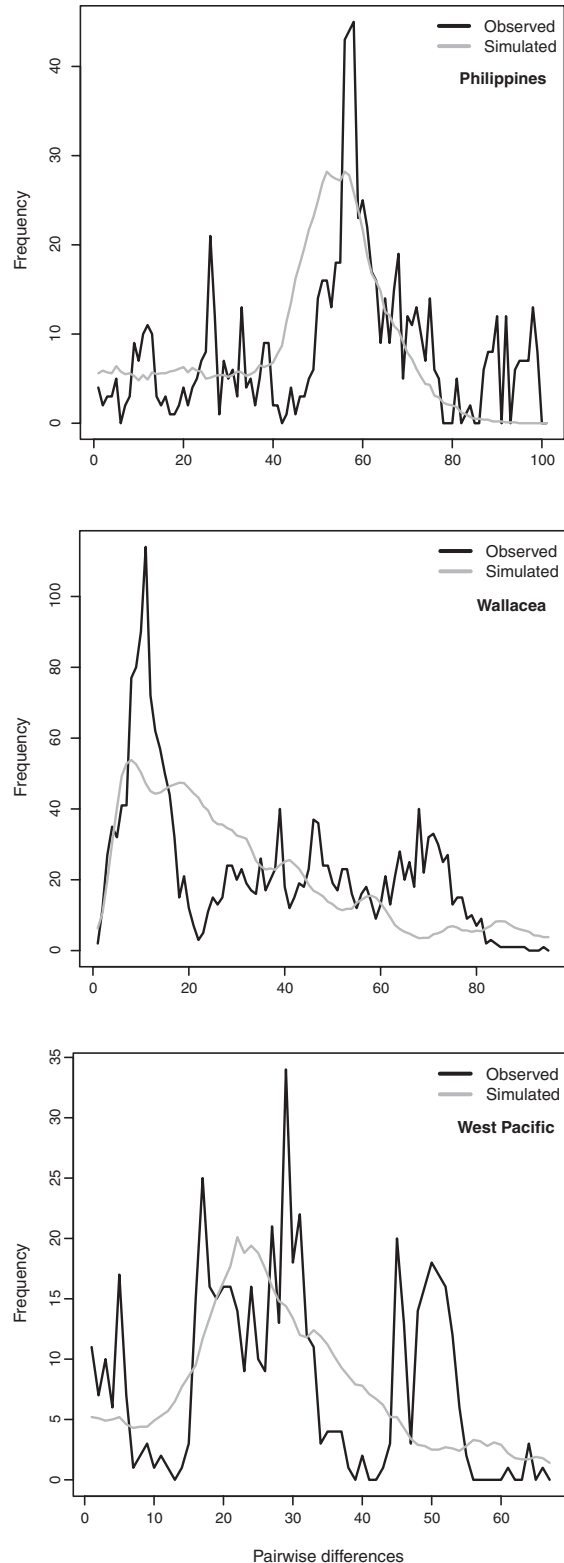

Figure 4 Mismatch distributions (observed pairwise nucleotide differences in black; expected frequencies under a model of sudden population expansion in grey) for populations of *Lamprolepis smaragdina* from the Philippines, Wallacea and the west Pacific.
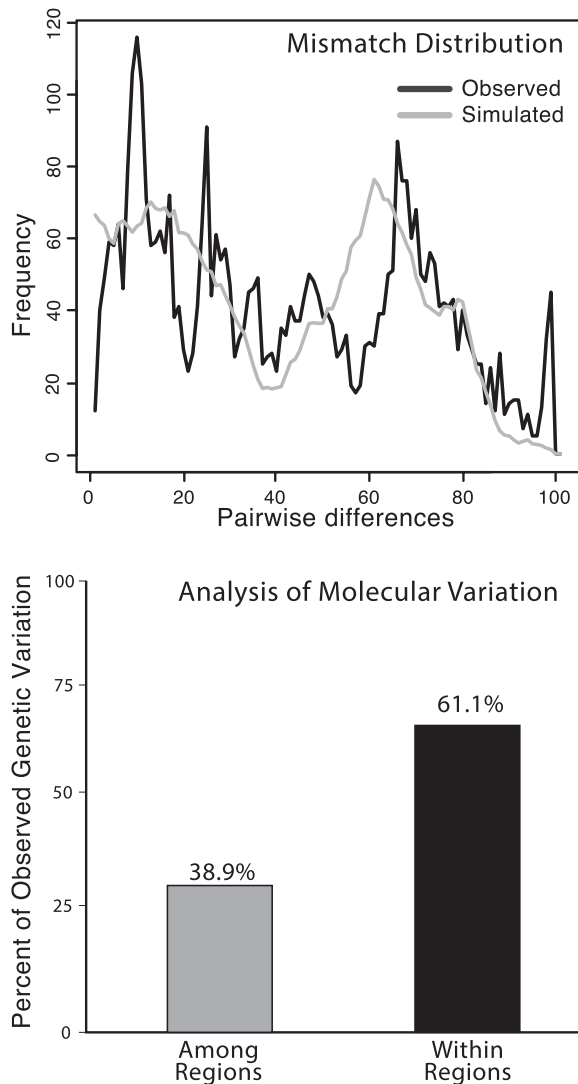
Figure 5 Mismatch distribution (shading as in Fig. 4) and results of analysis of molecular variation (AMOVA) of *Lamprolepis smaragdina* populations from the Philippines, Wallacea and the west Pacific.

for a diversity of taxa including toads, tree frogs, macaques, fanged frogs and flying lizards (Evans *et al.*, 2003a,b; McGuire *et al.*, 2007; Brown *et al.*, 2010). Collections made along a longitudinal transect in the south-western portion of the Sulawesi Selatan Province, as well as along the south-east peninsula of Sulawesi, revealed zones of sympatry between the green and brown morphs of *L. smaragdina* – most notably in the western portion of this zone – not corresponding with the Tempe Depression (a boundary between AOEs for other Sulawesi species). In these zones of overlap of the brown and green Sulawesi morphs of *L. smaragdina*, individuals of each colour type can be found on the same tree, but, based on our sequence data, they appear not to have exchanged mitochondrial DNA; the colour morphs are reciprocally monophyletic at this locus. The occurrence of this zone of

sympatry without evidence of hybridization across colour morphs suggests that reproductive isolation exists between populations in clades 1 and 2.

The green form (clade 1) is found on the two southern peninsulas, but does not have a continuous distribution. Instead, its members on each of the southern peninsulas are separated from one another by a population of the brown form (clade 2), which occurs throughout the central core of Sulawesi including the coastal region on the northern extreme of the Gulf of Boni between the south-west and south-east peninsulas of Sulawesi (Fig. 1). Based on the timing of divergence on Sulawesi and the history of the island's formation, we infer that the brown form reached the northern peninsula and central core between 5 and 10 Ma when these regions probably still represented separate palaeo-islands (Hall, 2002). Early dispersal between these palaeo-islands, followed by a period of isolation, may help to explain the 8–10% sequence divergence observed between populations of the brown Sulawesi *L. smaragdina* in clade 2.

The biogeographical pattern of the Maluku Islands (Fig. 2) shows that Haruku Island is not monophyletic, but, given the proximity to Seram and the possibility that these islands were connected during the Pleistocene, this is not surprising. The inferred polytomy (Fig. 2), short internodes and unique haplotypes between islands (Fig. 3) suggest that *L. smaragdina* dispersed among the islands rapidly, but that once established there was limited gene flow between islands.

We observed two deeply divergent clades in the Philippines that originated approximately 5–12 Ma. Given the age of these divergent lineages, it is unsurprising that they depart from biogeographical expectations based on Pleistocene sea-level changes (Heaney, 1986; Voris, 2000). Although numerous past studies have found exceptions to the predictions of the Pleistocene aggregate island complex diversification model (e.g. Evans *et al.*, 2003a; Linkem *et al.*, 2010), the results of our study not only reveal divergences pre-dating the Pleistocene, but also biogeographical patterns that depart from expectations based on hypothesized land bridges between islands separated today by shallow seas (Brown & Diesmos, 2009). With just a few exceptions, nearly all sister relationships appear to either pre-date the Pleistocene or require dispersal (Figs 2 & 3). Given our divergence dating results, Philippine populations in clade 4 are inferred to have diversified before populations in clade 5, which might explain why clade 4 is more widespread. As observed with populations on Sulawesi, reproductive isolation between new and established populations in this widespread species may in part explain their abutting, allopatric distributions observed today. Based on the timing of divergence, we infer a high level of dispersal between 3 and 7.5 Ma as the species became established on many of the islands. In conjunction, around 5 Ma, clade 5 diversified, but apparently only became established on islands not already occupied by clade 4. This later arrival might explain why clade 5 is primarily found on small satellite islands (Camiguin Sur, Salibabu, Siquijor) and only became established on two major islands (Mindanao

Table 4 Summary statistics and results of tests of population expansion for the three major study regions of *Lamprolepis smaragdina*. For mismatch distributions, T is presented along with P-values for rejection of the sudden expansion model, based on a comparison of the sum of squares of expected and observed distributions (using parametric bootstrapping with 10,000 replicates; Rogers & Harpending, 1992; Excoffier *et al.*, 2005). Additional entries include Harpending's raggedness index (RI) and P-values for rejection of the goodness of fit test comparing simulated vs. observed distribution raggedness, Tajima's D, and Fu's F_S. All tests were implemented separately for each of the three major regions as defined in the text.

Region/clade	T	RI	Tajima's D (P)	F_S (P)*
Philippines	53.312 (0.34)	0.005 (0.22)	−0.045 (0.50)	−10.700 (0.01)
Wallacea	3.881 (0.00)	0.002 (0.36)	0.907 (0.19)	−10.826 (0.03)
West Pacific	17.461 (0.01)	0.009 (0.27)	−0.424 (0.36)	−5.614 (0.01)

*Statistical significance for rejecting a null model of constant population size included in parentheses.

and Palawan), which may not have had *Lamprolepis* populations at the time.

Demographic patterns

Given the ecological preferences of *Lamprolepis* (coastal lowland forest areas, including disturbed regions), we sought to determine whether populations from any of these regions showed demographic expansion following founder-effect-type bottlenecks or other signs of human-mediated range expansion. The timing of divergence in the three biogeographical regions examined here (Fig. 4) suggests that anthropogenic dispersal was not a factor in driving the breadth of the distribution of this species. It is possible, however, that habitat alteration by humans could have provided opportunities for expansion of population size within portions of this expansive range (Brown *et al.*, 2010). The combination of qualitatively ragged mismatch distributions and unique haplotypes among all populations suggest a protracted history of population structure within each of the focal biogeographical regions. Our results from Fu's F_S and mismatch distributions reject constant population size and Tajima's D and Harpending's raggedness index cannot reject selective neutrality (Table 4). With these results we can clearly assert that populations are structured more than would be expected under an assumption of continuous gene flow between islands.

The Tahulandang and Sangir Besar lineages are nested within the west Pacific clade (clade 6), but these two islands are part of an archipelago that extends from Sulawesi towards Mindanao. For this reason, we expected these populations to be most closely related to those from Sulawesi, Mindanao or the nearby Salibabu Island. For example, flying lizards of the genus *Draco* from Sangir Besar and Tahulandang are closely related to Sulawesi species (McGuire & Kiew, 2001). *Lamprolepis smaragdina*, in contrast, shows a unique relationship with the west Pacific. The inferred timing of divergence of populations on Sangir Besar and Tahulandang (2–3 Ma) also pre-dates human colonization. In addition, there are high levels of genetic divergence between these two small islands, even though they are geographically close, suggesting an early dispersal to the islands with prolonged subsequent isolation. Alternatively, we cannot reject the possibility that humans mediated the dispersal of populations

on Sangir Besar, Tahulandang and Peleng islands from unsampled source populations in western New Guinea, which would explain the unexpected occurrence of apparently ancient populations on these islands.

CONCLUSIONS

The biogeography of *L. smaragdina* is striking in that the broad geographical range of these lizards provides clear evidence of the species' excellent dispersal capabilities, yet dispersal has not been so rampant as to prevent the evolution of pronounced geographic structure. The stochastic nature of waif dispersal in *L. smaragdina* has resulted in some unexpected biogeographical relationships, such as the independent invasions of the Sangir Talaud islands (between Sulawesi and the southern Philippines) from the west Pacific, and the early invasion of the Banggai Islands (represented by Peleng) by a clade otherwise restricted to New Guinea, the Solomon Islands and the west Pacific.

Our findings suggest that once *L. smaragdina* reaches an island, it is difficult for subsequent lineages to invade and become established as part of a local community of sympatric, coexisting species. This is most evident in the Philippines, where divergent mitochondrial DNA lineages of *L. smaragdina* occur on virtually every island even though sets of Philippine islands were connected as recently as 10,000 years ago. If these lineages are shown to be reproductively and genetically isolated, then we may soon be left with the possibility that each represents an independent species. Is *L. smaragdina* a single species or a complex of as many as 40 or more species? It would be premature to suggest taxonomic modifications on the basis of a single-locus data set, but clearly this question warrants further investigation with an integrative approach.

Still, the relationships of *L. smaragdina* are anomalous among previous biogeographical studies of Southeast Asian and south-west Pacific island vertebrates. This species represents a unique system with a widespread distribution, spanning several biogeographical regions (a testament to its dispersal abilities), and yet exhibits deep phylogenetic structure, contrary to expectations derived from its ecological preference for palm plantations in disturbed coastal habitat. Finally, the convoluted patterns of relatedness that we

have elucidated demonstrate that *L. smaragdina* has relied primarily on stochastic waif dispersal and that this mode of transport has been pervasive throughout the evolutionary history of the species, contradicting expectations derived from both ancient vicariance and recent human-mediated dispersal scenarios.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Table of samples, localities, and GenBank accession numbers.

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BIOSKETCH

All authors are interested in the fields of historical biogeography, systematics and phylogenetics in Asian reptiles and amphibians. The authors' various research programmes focus on combining fieldwork and modern phylogenetic techniques to elucidate the mechanisms driving diversification in Asian fauna.

Author contributions: C.W.L., J.A.M. and R.M.B. conceived the ideas; all authors participated in the fieldwork; C.W.L collected and analysed the data; C.D.S. assisted in components of analysis; C.W.L. led the writing; all authors approved the writing.

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