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Deep divergence and structure in the Tropical Oceanic Pacific: a multilocus phylogeography of a widespread gekkonid lizard (Squamata: Gekkonidae: *Gehyra oceanica*)

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ABSTRACT

Aim The islands of the Tropical Oceanic Pacific (TOP) host both local radiations and widespread, colonizing species. The few phylogeographical analyses of widespread species often point to recent human-aided expansions through the Pacific, suggesting that the communities are recently assembled. Here we apply multilocus data to infer biogeographical history of the gekkonid lizard, *Gehyra oceanica*, which is widespread, but for which prior analyses suggested a pre-human history and *in situ* diversification.

Location Tropical Oceanic Pacific.

Methods We generated a data set including mtDNA and diagnostic SNPs for 173 individuals of *G. oceanica* spanning Micronesia, Melanesia, and Polynesia. For a subset of these individuals, we also sequenced nuclear loci. From these data, we performed maximum likelihood and Bayesian inference to reveal major clades. We also performed Bayesian clustering analyses and coalescence-based species delimitation tests to infer the number of species in this area.

Results We found evidence for six independent evolutionary lineages (candidate species) within *G. oceanica* that diverged between the Pliocene and the early Pleistocene, with high diversity through northern Melanesia, and pairing of northern Melanesian endemic taxa with widespread lineages across Micronesia and Polynesia.

Main conclusions The islands of northern Melanesia not only have unrecognized diversity, but also were the source of independent expansions of lineages through the more remote northern and eastern Pacific. These results highlight the very different evolutionary histories of island faunas on remote archipelagos versus those across Melanesia and point to the need for more intensive studies of fauna within Melanesia if we are to understand the evolution of diversity across the tropical Pacific.

Keywords

cytochrome *c* oxidase, *Gehyra*, island biogeography, island evolution, Melanesia, Micronesia, Pacific biogeography, Polynesia, SNPs, Tropical Oceanic Pacific

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INTRODUCTION

The islands of the Tropical Oceanic Pacific (TOP) represent a fascinating system to study the interacting effects of long-distance dispersal, genetic isolation, *in situ* radiation and the impacts of invasive species (Lowe *et al.*,

2004; Meyer, 2004b; Gillespie *et al.*, 2008a,b, 2012). The TOP includes islands from Micronesia, Melanesia, and Polynesia. Geological histories and scales of isolation vary between these geographical groupings. These distinct histories can be expected to affect current patterns of diversity.

Micronesia includes the Mariana Islands, the Caroline Islands, the Marshall Islands, and Palau. The islands in Micronesia are generally composed of low-lying islands, atolls, and reefs that are often inhabited by widespread colonists with a few hotspots of diversity (Craib, 1983; Stoddart, 1992; Crombie & Pregill, 1999). Conversely, the Polynesian and Melanesian regions are characterized by high volcanic islands and raised reef islands with endemic faunas (Stoddart, 1992; Allison, 1996; Gillespie & Roderick, 2002; Steadman, 2006). These high islands and fragmented arcs are typically centres of speciation as well as recipients of colonists (Allison, 1996; De Boer & Duffels, 1997). Melanesia, which has mostly high islands, consists of the islands of the Admiralty, Bismarck, Solomon, Vanuatu, and New Caledonia archipelagos and represents either old Gondwanan fragments or elements of geologically dynamic arcs at the boundary of the Australian and Asian plates (Hall, 2002). Biologically, the border between Polynesia and Melanesia is indistinct, with strong Melanesian influences extending as far as Vanuatu or Fiji, depending on the taxon in question. Polynesia continues eastwards to Easter Island, north to Hawaii and includes New Zealand in the south.

The most common dispersal route suggested across the TOP is a south-eastwardly migration from Melanesia or Australia, consistent with a pattern of steadily decreasing species diversity eastwards of New Guinea (Steadman, 2006). However, for some taxa a westwards colonization from the Americas to the easternmost TOP islands is also evident (Gillespie *et al.*, 2012). Some terrestrial systems in the Pacific have high endemism that is associated with local radiations (Brown, 1991; Goodacre & Wade, 2001; Gillespie, 2002; Steadman, 2006). These endemics can also have lower genetic diversity compared to continental taxa because of founder events (e.g. Sarno *et al.*, 2001; Boessenkool *et al.*, 2006). In addition, there is evidence that some taxa spread from proto-Asia or Australia prior to formation of the islands within the Sunda and Sahul Shelves in the Pacific (e.g. geckos, crocodiles, meiolanid turtles, blind snakes; Worthy & Clark, 2009; Vidal *et al.*, 2010; Heinicke *et al.*, 2011).

Long-distance dispersal of organisms across the Pacific is supported by several molecular studies, including studies of spiders (Gillespie, 2002), plants (Wright *et al.*, 2000), iguanas (Keogh *et al.*, 2008), snakes (Austin, 2000) and geckos (Fisher, 1997). For reptiles, it has been suggested that the entire fauna of the more remote islands is derived from human-assisted colonization (Case *et al.*, 1992). Several species are thought to have been transported as the first canoes made their way across the Pacific: for example, *Gehyra mutilata* (Fisher, 1997), *Emoia cyanura/impar* (Bruna *et al.*, 1996), and *Lipinia noctua* (Austin, 1999). Subsequently, several taxa were spread in association with European colonization and later transport: putative examples include *Hemidactylus frenatus* (Tonione *et al.*, 2011), *Lepidodactylus* (Radtkey *et al.*, 1995) and *Hemidactylus garnotii* (Moritz *et al.*, 1993). In the case of the snakes and geckos, it appears that ocean currents play a role in diversity patterns (Fisher,

1997; Austin, 2000). Parthenogenesis is a common feature of reptiles that have colonized the Pacific Islands, occurring in taxa such as, *Nactus pelagicus* (Moritz, 1987), *Lepidodactylus lugubris* (Cuellar & Kluge, 1971) and *Hemidactylus garnotii* (Cuellar, 1977). Although several widespread TOP lizard species have been examined genetically, these studies have typically been limited in scope in terms of geographical and/or genetic sampling.

We use the oceanic gecko, *Gehyra oceanica* (Lesson, 1830) to examine patterns of diversity within the TOP. The genus *Gehyra* is diverse across Australo-Papua, Melanesia and Southeast Asia, and a recent molecular analysis suggests divergence of *G. oceanica* from its sister taxon approximately 10 Ma (Heinicke *et al.*, 2011). *G. oceanica* is the most widespread gecko endemic to the Pacific (Beckon, 1992). It is an entirely 'oceanic' species, not occurring on any continental land masses (and not occurring on the large island of New Guinea). On Tonga in the south-central Pacific, *G. oceanica* fossils have been dated to the late Quaternary (Pregill, 1998), while in the Marianas, fossil records indicate that *G. oceanica* is a more recent addition to the herpetofauna (Pregill & Steadman, 2009).

Consistent with the fossil record, both phenotypic and genetic (allozyme) analyses of *G. oceanica* have pointed to *in situ* divergence, especially in Melanesia. Beckon (1992) reported three phenotypically distinct forms: Micronesia, Oceanic (spanning Polynesia and Melanesia), and a third Bougainville morphotype (found on Bougainville and Buka Island in Papua New Guinea). Using allozyme analyses, Fisher (1997) uncovered a northern form found in Micronesia and a southern form found across Melanesia and the Pacific. These data are consistent with the hypothesis that *G. oceanica* was naturally dispersed across the western Pacific prior to human arrival, with the equatorial currents acting as a barrier to gene flow between the northern and southern forms. In a broad phylogenetic analysis of the genus and with sparse sampling of *G. oceanica*, Heinicke *et al.* (2011) observed four deeply divergent lineages (mtDNA and two nuclear genes): three of these lineages were within Melanesia in the western Pacific and one occurred in Micronesia. Based on these previous genetic and morphological studies, it appears that, as currently described, *G. oceanica* is, in fact, a complex of species.

Differences in the geological histories and faunal composition of archipelagos make the TOP a promising arena to understand evolutionary and assembly processes that determine patterns of diversity. However, the Polynesia–Micronesia transition zone lacks rigorous phylogeographical information; for most biota, this information is non-existent (Beheregaray, 2008), severely limiting our understanding of the biogeography of the region. In this paper, we build on previous allozyme, phylogenetic and morphological studies of *G. oceanica* via phylogeographical analyses with more comprehensive sampling of genes and populations across the species range. Hypotheses to be tested are (1) that the western Pacific, especially Melanesia, has the highest diversity

and contains undescribed species, and (2) that south-eastern Pacific beyond Tonga was colonized either recently (as for most other terrestrial reptiles) or by island hopping during periods of lower sea levels in the late Quaternary.

MATERIALS AND METHODS

Sampling

We sampled from islands across the three major geographical subregions of TOP: Polynesia, Micronesia, and Melanesia. A total of 173 individuals of *G. oceanica* were sampled, including 48 samples from islands in Melanesia, 25 samples from islands in Micronesia and 100 samples from islands in Polynesia (Fig. 1a). Samples were sourced from various collections. Field-collected samples consisted of tail tips of released

individuals or of liver from voucher specimens. Some samples were identical to those previously used in Fisher (1997). See Table S1 in Appendix S1 in Supporting Information for voucher information.

This project is an outgrowth from a barcoding initiative, the Moorea Biocode Project (<http://www.mooreabiocode.org>). Consequently, initial genotyping of samples within Moorea was done using the mitochondrial cytochrome *c* oxidase subunit I (COI) gene. We then included samples from Fisher's (1997) previous allozyme study as well as additional samples never before genotyped. From this initial genotyping, we established the general mitochondrial phylogeographical pattern and then chose individuals based on their geographical location and mitochondria lineage to corroborate lineage identities via multiple unlinked nuclear loci. We identified and screened putative diagnostic SNPs (fixed among major

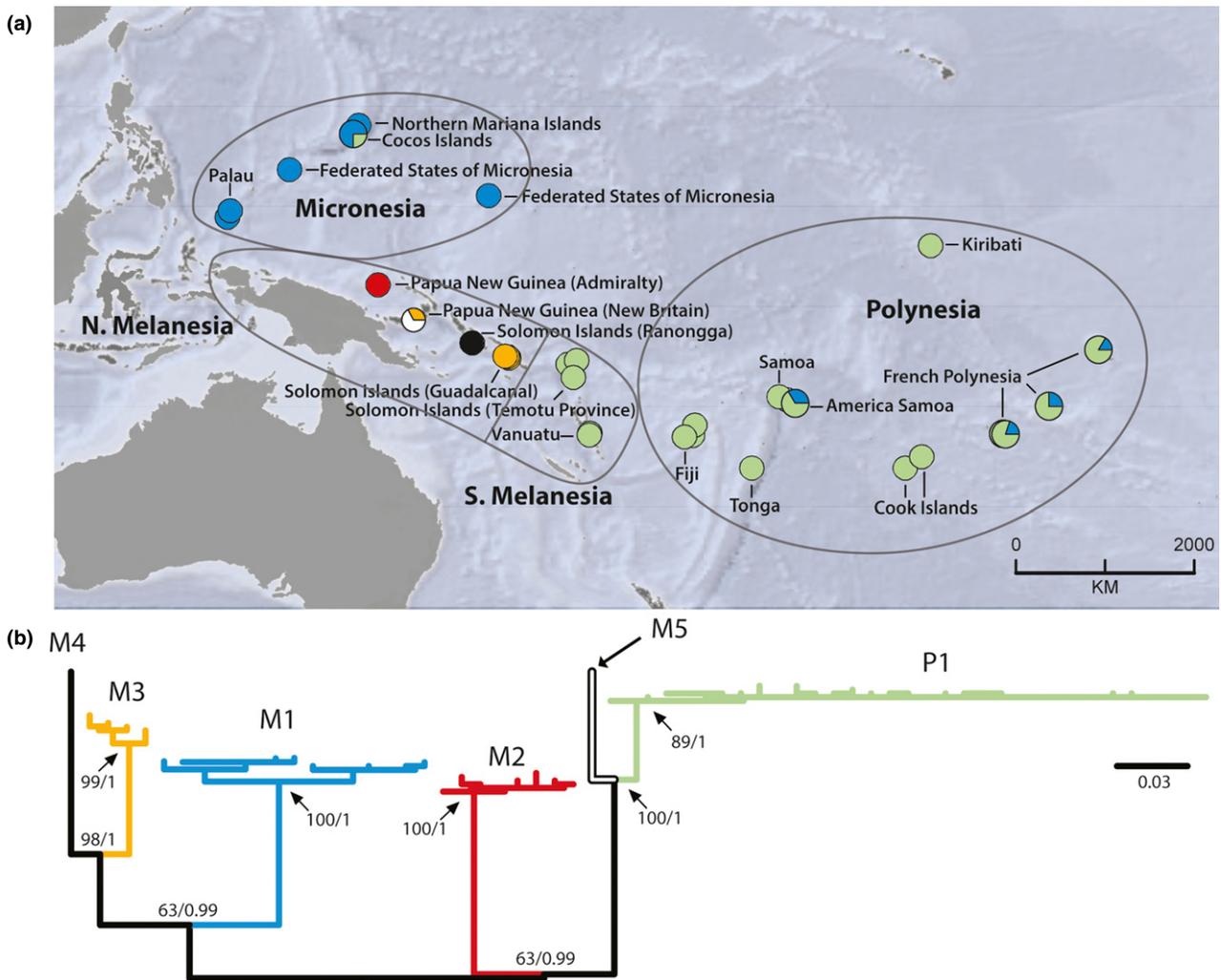


Figure 1 Sampling of this study and the major mitochondrial lineages in *Gehyra oceanica* within the Tropical Oceanic Pacific (TOP). (a) The map projection is World Cylindrical Equal Area (WGS84). Colours correspond to the major mitochondrial lineages (M1, M2, M3, M4, M5, P1). Coloured dots on the map represent the lineage as determined by the mitochondria ($N = 173$ individuals). A locality in which more than one lineage is represented is indicated by a pie chart on the map; pie chart slices are proportional to the actual number of samples represented. (b) COI maximum likelihood tree based on 62 unique mitochondria haplotypes. Values left of the slash are RaxML bootstrap values; values right of the slash are Bayesian posterior probabilities. Scale bar indicates substitutions/site.

mtDNA clades in an initial pilot study) to cluster individuals to genetic populations. However, as this set of markers has strong ascertainment bias, we then Sanger-sequenced eight nuclear loci across a subset of individuals ($N = 46$) representing both the geographical range and major mtDNA clades for formal testing of lineage boundaries and diversity/demography analyses.

Marker development and sequencing

Whole genomic DNA was extracted from either liver or tail tissue that was stored in 95% ethanol or RNAlater using a salt extraction (Miller *et al.*, 1988) and diluted to final concentrations of $20 \text{ ng } \mu\text{L}^{-1}$ prior to PCR amplification. Approximately 650 base pairs of COI were amplified following a previously published protocol (Tonione *et al.*, 2011) and primers (Meyer, 2004a).

To obtain SNPs and nuclear sequence data, we developed markers *de novo* from high-throughput sequencing of a transcriptome library derived from *G. oceanica* liver that was from the mtDNA P1 lineage (CM193; Table S1 in Appendix S1). The transcriptome was sequenced, assembled and analysed as in Singhal (2013). After completing the final assemblies, we identified sequence exon boundaries by computational annotation (e.g. Reciprocal BlastX) against the *Anolis* genome (Flicek *et al.*, 2012).

Given putative exon boundaries, we designed primers with the online Primer3 interface (Rozen & Skaletsky, 2000) off the *G. oceanica* transcriptome within the exons. To identify SNPs specific to major mtDNA lineages, we Sanger-sequenced 20 randomly selected loci (*c.* 500 bp) across a small panel of individuals based on their mtDNA lineage: two from Micronesia, two from Melanesia, and two from the Polynesia group. Once several fixed SNPs were identified, we sent the sequence information to the University of Minnesota BMGC Sequencing and Genotyping Facility where they designed an array to genotype 15 SNPs – all from separate loci – across all our individuals using the Sequenom MassArray iPLEX platform (SNP information can be found in Tables S2 and S3 in Appendix S1).

For an overlapping set of suitably sized (360–843 bp) exons, we Sanger-sequenced eight nuclear exons from the 20 above, selected because they have polymorphisms within the initial sampling set (see Table S3 in Appendix S1). All DNA sequences used for analyses are accessioned in GenBank (KR857724–KR858258; Table S4 in Appendix S1).

MtDNA phylogenetic structure

For the complete COI data set, maximum likelihood (ML) and Bayesian inference were used to estimate the mtDNA genealogy and reveal major clades. ML analyses were implemented in the RAXML BlackBox webserver (Stamatakis *et al.*, 2008), using the GTRGAMMA model, and partitioned by codon position. The optimal partition scheme was assessed by PARTITIONFINDER 1.1.1 (Lanfear *et al.*, 2012). ML node

support was calculated by analysing 100 bootstrap replicates. Bayesian phylogenetic analyses were conducted using MRBAYES 3.1.2 (Huelsenbeck & Ronquist, 2001). Appropriate models of sequence evolution were determined for each codon position using MRMODELTEST 2.2 (Nylander, 2004). We produced posterior probability distributions by allowing four incrementally heated Markov chains to run for 50 million generations, sampling every 5000 generations, with a burn-in of 10,000. The Bayesian posterior probability values were estimated from the sampled trees that remained after burn-in. The final output was examined visually in TRACER 1.6 (Rambaut & Drummond, 2007) to determine if the run had reached convergence (ESS values > 200).

BEAST 1.8 (Drummond *et al.*, 2012) was used to estimate a time-calibrated tree under a rate-estimated strict clock model with COI. See Table S5 for partition schemes and models of evolution in Appendix S1. Parameters included a Yule speciation process, with a random starting tree, for 50,000,000 generations, saving trees every 5000 generations, with a burn-in of 1000. The mutation rate of COI was estimated to be between 2% and 2.8% per million years (Pasoni *et al.*, 2008).

Population structure

To infer the number and composition of populations based on nuclear markers, we combined the full SNP data set (coded as integers) with previously published allozyme data (Fisher, 1997) in the program STRUCTURAMA (Huelsenbeck *et al.*, 2011). Preliminary runs using the SNP data set alone did not produce stable results. STRUCTURAMA allows the number of populations (K) to be a random variable that follows a Dirichlet process prior (Pella & Masuda, 2006; Huelsenbeck & Andolfatto, 2007). Many of our individuals had both SNP and allozyme data ($N = 83$). We ran 1,000,000 MCMC cycles, with the first 1000 cycles discarded as burn-in and let the prior of the mean of the number of populations be a random variable. We also ran STRUCTURAMA twice with fixed population numbers for comparison to the K with the highest probability (see Fig. S1 in Appendix S1).

Multilocus sequence analyses

Problems with species-tree inference based on concatenating independent nuclear loci are widely recognized (Degnan & Rosenberg, 2006; Edwards, 2009). However, for those interested in the boundaries of phylogeographical lineages and species, one strategy has been to use information from clustering individuals by either a phylogenetic analysis of concatenated sequences or majority-rule approach to estimate plausible topologies, and then use coalescent approaches (e.g. BPP, Rannala & Yang, 2013) to infer lineage boundaries and relationships among those (Leaché, 2009).

To obtain an alternative topology to our mtDNA phylogeny, we ran a partitioned Bayesian analysis of the concatenated

nuclear data implemented in MRBAYES 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; Fig. S2 in Appendix S1). We used SPLITS TREE 4.6 (Huson, 1998; Huson & Bryant, 2006) to display conflicts in the data by taking into account incompatible phylogenetic signals that might be present due to incomplete lineage sorting or admixture. A pairwise (uncorrected) distance matrix for each locus was generated using PAUP* 4.0b10 (Swofford, 2002). The genetic distance matrices for separate loci were combined into a single distance matrix using the program POFAD v1.03 (Joly & Bruneau, 2006). A genetic network among specimens was constructed using the Neighbor-Net algorithm (Bryant & Moulton, 2004), and we visualized phylogenetic patterns in a net-like scheme in SPLITS TREE (see Table S6 in Appendix S1). To infer haplotypes from heterozygous individuals, we used PHASE 2.1 (Stephens *et al.*, 2001; Stephens & Donnelly, 2003). Only haplotypes with support ≥ 0.95 were used in the following analyses.

Species-tree reconstruction

We used the hierarchical Bayesian model implemented in *BEAST 1.8 (Drummond *et al.*, 2012) to estimate the species tree based on nuclear sequences. We included nuclear DNA sequences for only those samples that contained information for all the genes and removed three individuals that were placed in conflicting clusters between STRUCTURAMA and SPLITS TREE (see Results) as such individuals likely reflect the results of recent introgression and can bias the result of species-tree analyses (Leaché *et al.*, 2014). The optimal partitioning scheme and model choices were assessed with PARTITIONFINDER 1.1.1 (Lanfear *et al.*, 2012) using the greedy algorithm and Bayesian Information Criterion, considering only models available in BEAST (see Table S5 for partition schemes and models of evolution in Appendix S1). Unlinked parameters were used for all loci. We used the mtDNA topology as the input for *a priori* assignment of clade membership for the *BEAST analysis. We employed a strict molecular clock with a uniform substitution rate for each locus, and a Yule speciation process with a random starting tree, for 100,000,000 generations, saving trees every 10,000 generations. The final output was examined visually in TRACER 1.6 (Rambaut & Drummond, 2007) to determine if the run had reached convergence (ESS values > 200). The final tree was produced after 1000 samples (10%) were removed as burn-in using TREEANNOTATOR 1.8 (Drummond *et al.*, 2012).

Bayesian species delimitation

We generated the posterior probabilities of species assignments using a Bayesian modelling approach implemented in BPP 2.2 (Rannala & Yang, 2013). We assigned samples to one of six clusters based on their mitochondrial clade. Analyses were run for 500,000 generations, sampling every five, with a burn-in of 100,000 with the full phased data set of

eight loci. Following the methods of Leaché & Fujita (2010), we explored the effect of varying ancestral population sizes (θ) and root ages (τ) on speciation probabilities. We used both the mtDNA topology from RAXML and BEAST (and alternative root placements) and the nDNA topology from the *BEAST as guide trees (see Table S7 in Appendix S1). Each result was confirmed with two runs and random starting seeds.

Diversity and demographic analyses

Using ARLEQUIN 3.1 (Excoffier *et al.*, 2005), we estimated nucleotide diversity (θ_π and θ_s) for each geographical region (Melanesia, Micronesia, and Pacific) and net sequence divergence (D_a) among the six major mitochondrial lineages for both COI and the combined phased nuclear markers using the Tamura-Nei model of sequence evolution (Tamura & Nei, 1993). We also calculated Tajima's D and Fu's F_s values for COI in order to test for population expansion within each geographical region and within the major lineages. For each genetic population found by SPLITS TREE, we estimated diversity and divergence as described above.

RESULTS

Mitochondrial phylogeography and diversity

The mitochondrial phylogeny recovered strong geographical structuring of diversity with six major lineages (Fig. 1). Net sequence divergence (D_a) between all six major lineages ranged from *c.* 7–18% (Table 1). Geographically, one major mitochondrial lineage spans Micronesia (M1) and another extends from southern Melanesia across Polynesia (P1). Northern Melanesia has several lineages confined to single islands or a few individuals: M2 is only found on Admiralty island, M3 is found on New Britain and Guadalcanal, M4 is only found on Ranongga Island, and M5 is only on New Britain (Fig. 1a). There is an especially abrupt geographical transition between the northern and southern elements of the Solomon Islands. Individuals on Guadalcanal fall into mtDNA lineage M3, while those south of Guadalcanal have the widespread P1 mtDNA (Fig. 1a). Based on the BEAST analysis of the COI sequences, these lineages diverged 3.25–4.61 Ma, *i.e.* during the Pliocene (see Fig. S3 in Appendix S1). While this sets a reasonable overall time-scale for the divergence, we note that the mtDNA-based topology is incongruent with the species-tree analysis using nDNA loci (see below).

Within northern Melanesia nucleotide diversity is high ($\theta_\pi = 8.3\%$) compared to diversity across Polynesia ($\theta_\pi = 1.4\%$), and across Micronesia ($\theta_\pi = 1.4\%$). This is expected given that northern Melanesia harbours four lineages: M2, M3, M4 and M5. Some admixture between the divergent M1 and P1 clades is evident, with one of the 25 Micronesian samples having the P1 mtDNA and seven of the 120 Polynesian samples having the M1 mtDNA. Expansion

Table 1 Population differences (Tamura-Nei D_a) for mitochondrial DNA (below diagonal) and combined nuclear sequences (above diagonal, grey) between the major *Gehyra oceanica* lineages in the Tropical Oceanic Pacific.

| | M1 | M2 | M3 | M4 | M5 | P1 |
|----|--------|--------|--------|--------|--------|--------|
| M1 | | 0.0035 | 0.0028 | 0.0010 | 0.0009 | 0.0061 |
| M2 | 0.1152 | | 0.0022 | 0.0021 | 0.0029 | 0.0015 |
| M3 | 0.1203 | 0.1353 | | 0.0030 | 0.0023 | 0.0018 |
| M4 | 0.1241 | 0.1313 | 0.1062 | | 0.0038 | 0.0031 |
| M5 | 0.1522 | 0.1537 | 0.1593 | 0.1834 | | 0.0046 |
| P1 | 0.1332 | 0.1498 | 0.1494 | 0.1625 | 0.0694 | |

tests based on Fu's F_S suggest expansion in all three geographical regions. However, the more conservative Tajima's D results suggest expansion is only occurring in Micronesia and Polynesia ($P < 0.05$, Table 2). Diversity within the major mtDNA clades is relatively low ($\theta_\pi = 0.4$ – 0.76%) and expansion tests suggest expansion is occurring in the M2, M3, and P1 lineages, however, only Fu's F_S suggests expansion in the M1 lineage (Table 2).

Nuclear phylogeography and diversity

Clustering of diagnostic SNP and allozyme genotypes using STRUCTURAMA revealed population structure that was broadly consistent with the mtDNA phylogeny and highly geographically structured (Fig. 2). Our data set can be divided into three populations based on the nuclear haplotypes. Putting aside the Palau population momentarily, at $K = 3$, Group 1 corresponds to individuals within Micronesia with mtDNA M1, with the exception of two individuals with P1 mtDNA: one from Micronesia and the other from Polynesia (Fig. 2b, blue). Group 2 includes individuals from within Melanesia and from divergent mtDNA lineages M2, M3, and M4 (Fig. 2b, orange). A caveat here is that STRUCTURAMA has been shown to over-lump recently diverged lineages, especially with small sample sizes (Rittmeyer & Austin, 2012; Carstens *et al.*, 2013). Group 3 is composed of all

individuals within Polynesia, Southern Melanesia, and on New Britain (Fig. 2b, green). While the individuals from Palau are all placed within the M1 lineage mitochondrially, the STRUCTURAMA group from Palau appears heterogeneous: three individuals are placed in Group 1, four in Group 2, and one in Group 3. As with mtDNA, the nDNA clusters detected using STRUCTURAMA indicated an abrupt transition between the northern (Group 2) and southern (Group 3) Solomon Islands (Figs 2, Fig. S3 in Appendix S1).

The eight nuclear exons that were Sanger-sequenced for a subset of individuals of *G. oceanica* spanned a total of 5063 base pairs. Preliminary analyses of individual gene trees indicated incomplete lineage sorting across the entire complex; however, the concatenated tree revealed clusters that are generally consistent with the SPLITS TREE results (see Fig. S2 in Appendix S1).

The SPLITS TREE network from the combined nuclear data display four clusters, termed A to D, that reflect the samples' geographical locations (Fig. 3a). Broadly, cluster A includes southern Melanesian and Polynesian samples with mtDNA lineages P1 and M1, and also the M5 individual from New Britain, and corresponds mostly with the STRUCTURAMA Group 1. Clusters B and C represent the different mtDNA lineages within STRUCTURAMA Group 2; cluster B has the M3 and M4 individuals from northern Melanesia, and cluster C includes the M2 individuals from Admiralty. Cluster D represents individuals from Micronesia, mostly with M1 mtDNA. Three individuals were placed in different groups when comparing the STRUCTURAMA and SPLITS TREE result: two from Palau and one from New Britain (Fig. 3a, grey arrows).

Species delimitation and relationships

As candidate taxa for statistical tests for species boundaries, we used the six mitochondrial clades (M1, M2, M3, M4, M5 and P1) as also evident from the SPLITS TREE network of nDNA divergences. We excluded individuals if they were placed in different clusters or groups between the

Table 2 Diversity and demographic statistics for *Gehyra oceanica* (n , total number of individuals sampled, θ_π and θ_S , nucleotide diversity expressed as percentages). Asterisks denote statistical significance ($P > 0.05$). Lineages M4 and M5 contained too few samples to be included in certain analyses.

| | mtDNA | | | | | nDNA | | |
|------------|-------|--------------|------------|--------------|------------------------|------|--------------|------------|
| | n | θ_π | θ_S | Tajima's D | Fu's F_S | N | θ_π | θ_S |
| Micronesia | 25 | 1.43 | 3.42 | -2.3* | -20.5* | 11 | 0.33 | 0.38 |
| Melanesia | 20 | 8.34 | 6.60 | 1.1 | -3.4* | 17 | 0.41 | 0.54 |
| Polynesia | 128 | 1.35 | 2.60 | -1.5* | -24.7* | 18 | 0.39 | 0.36 |
| M1 | 31 | 0.42 | 0.58 | 1.14 | -26.1* | 17 | 0.58 | 0.61 |
| M2 | 10 | 0.51 | 0.35 | -1.3 | -10.0* | 8 | 0.26 | 0.22 |
| M3 | 7 | 0.76 | 0.58 | -1.2 | -4.0* | 7 | 0.30 | 0.30 |
| M4 | 1 | N/A | N/A | N/A | N/A | 1 | 0.10 | 0.10 |
| M5 | 2 | N/A | N/A | N/A | N/A | 1 | 0.08 | 0.08 |
| P1 | 122 | 0.41 | 0.07 | -2.2* | $-3.4 \times 10^{38*}$ | 12 | 0.46 | 0.46 |

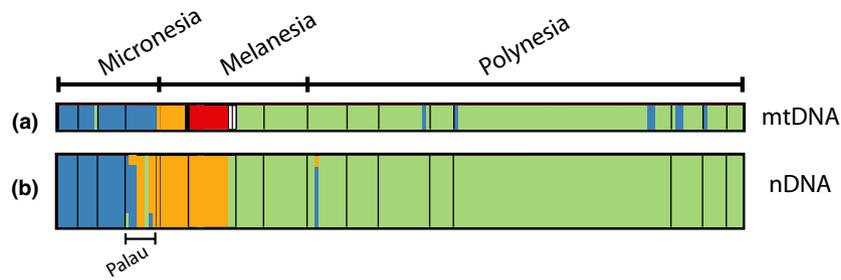


Figure 2 STRUCTURAMA results and comparison to mitochondrial lineage in *Gehyra oceanica*. Black lines denote each island, with vertical separation proportional to the number of individuals sampled ($N = 173$ individuals); coloured bars represent individuals, with the colour of each representing the proportion of that individual's membership in each cluster. (a) Mitochondrial lineages are shown in colours that correspond to Fig. 1. (b) STRUCTURAMA clustering of nDNA genotypes for $K = 3$: blue = Group 1, orange = Group 2, green = Group 3.

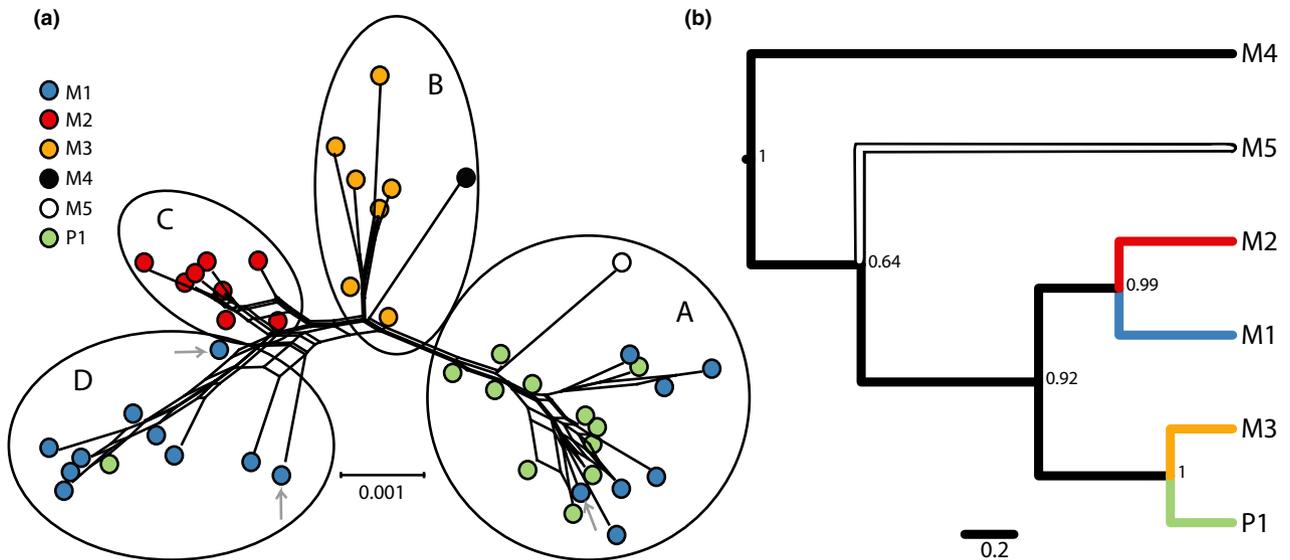


Figure 3 Species delimitation from nuclear haplotypes of *Gehyra oceanica*. (a) SPLITSTREE diagram of nDNA groups within *G. oceanica* ($N = 46$ individuals). Colours correspond to mitochondrial lineage. Circles denote geographical groups. Grey arrows represent discordances between STRUCTURAMA and SPLITSTREE. (b) Bayesian nuclear tree inferred using the partitioned nuclear genes (*Apob*, *Fbxw10*, *Adcy9*, *Larp6*, *Ndst1*, *Clmn*, *Fam193b*, *Usp47*) in *BEAST, numbers on nodes are posterior probability values.

SPLITSTREE network and STRUCTURAMA results (grey arrows; Fig. 3a). The subsequent BPP analysis of phased nDNA sequences, using both the mtDNA (with alternative root placements) and nDNA guide trees, supported the evolutionary independence of each of the six clusters. Varying the sizes (θ) and root ages (τ) did not affect the outcome. All clades were found to have support values of 1.0 (see Table S7 in Appendix S1).

We estimated relationships among the six lineages by applying the species-tree approach in *BEAST to the multi-locus nDNA data, using those samples that appeared to have no discrepancies between the mtDNA and nDNA clustering. The results (Fig. 3b) infer that clusters A (excluding mtDNA clade M5) and B (excluding mtDNA clade M4) are sister taxa with strong support, and that clusters C and D are sister taxa also with strong support. We can also infer mtDNA clades M4 (with strong support) and

M5 (with low support) are basal to the Polynesian and Micronesian clades. Thus, two taxa restricted to northern Melanesia are each related to different, but geographically adjacent, widespread taxa – the more northern Admiralty Island taxon (cluster C; mtDNA = M2) to the Micronesian taxon (cluster D; mtDNA ~ M1), and cluster B (including samples from New Britain and Guadalcanal; mtDNA = M3) to the southern Melanesian and Polynesian taxon (cluster A; mtDNA ~ P1).

DISCUSSION

In this study, we combined mtDNA, allozymes and diagnostic SNPs and, for a subset of samples, sequences from eight exons to investigate the diversity and biogeographical history of *G. oceanica* in the TOP. The combined analyses point to high levels of genetic divergence of *G. oceanica* across the

region. Lineage delimitation tests applied to the multilocus sequence data suggest that there are at least six distinct evolutionary lineages of *G. oceanica*: one widespread in Micronesia, one widespread across southern Melanesia and Polynesia, and four restricted to northern Melanesia. These distinct evolutionary lineages are effectively 'candidate species'.

These results support and extend Fisher's (1997) analyses of allozyme variation across the species' range. That study found a northern form, which corresponds to the M1 lineage in this study and a southern form that corresponds to a combination of the M3 and P1 lineages. No samples from lineages M2, M4 or M5 were examined allozymically in the Fisher (1997) analyses. Taking a phenotypic perspective, Beckon (1992) found that individuals in Micronesia could be distinguished morphologically from other Melanesia and Polynesia individuals. Although he grouped samples from Melanesia and Polynesia, the samples from Micronesia appear to be distinguishable based on the numbers of lamellae under their fourth toe and number of pre-anal-femoral pores in males. Our results reinforce the findings of Heinicke *et al.* (2011), which were based on limited sampling, which indicated deep divergence within *G. oceanica*. Clearly, *G. oceanica* as currently recognized represents at least six species and formal description of these rests on ongoing analyses of phenotypic variation (R. F., in progress) and additional sampling in Melanesia (P. Oliver, pers. comm.).

A key result in this current study is that the widespread Micronesian and Polynesian taxa are closely related to lineages endemic to northern Melanesia. This suggests a northern Melanesian origin for the *G. oceanica* complex, with subsequent expansion to the northern and eastern TOP. Analyses of mtDNA variation indicate demographic expansion in Micronesia and Polynesia, but not Melanesia. The fossil evidence (Pregill, 1998; Pregill & Steadman, 2009) suggests an earlier (before the late Quaternary) expansion through southern Melanesia to western Polynesia than through Micronesia. The distribution and diversity of *G. oceanica* is therefore the result of both vicariant speciation and subsequent dispersal across the Pacific and through Micronesia.

The contrast between northern Melanesia and southern Melanesia is particularly interesting. Northern Melanesia has high endemism with sharp boundaries between species and no evidence of introgression (lineages M2, M3, M4, and M5). This area and the Admiralty Islands in particular have consistently been found to harbour endemic and ancient fauna that is exemplified by this species as well as others (e.g. Dutson & Newman, 1991; Kraus & Allison, 2007; Brown *et al.*, 2015). In southern Melanesia, only the Polynesian lineage (P1) was found. The split between the northern Melanesian lineages and the widespread Polynesian taxon occurs within the Solomon Islands, specifically between Guadalcanal and the Temotu Province (Reef, Santa Cruz, and Duff Islands). Southern Melanesian islands lack many of

the reptiles otherwise endemic to the Solomon Islands and are biologically more similar to islands in the east (McCoy, 2006).

The generally sharp geographical boundaries among lineages within northern Melanesia indicate an old history of isolation and divergence across this archipelago, suggesting that, unlike for some other geckos (e.g. *Hemidactylus frenatus*; Tonione *et al.*, 2011), human-mediated dispersal is not prevalent. This is surprising given that *G. oceanica* is widespread and can be found in disturbed habitats, although some other widespread reptile species have also been found to have this pattern (Linkem *et al.*, 2013). However, the apparent admixture in Palau (south-western Micronesia) and the presence of some mixing of mtDNA lineages between Micronesia and Polynesia suggests some level of recent dispersal and admixture across the range, which could be human-mediated.

This multilocus, multiregional study gives a much more robust view of diversity in the area than have previous studies of the TOP reptile fauna. In fact, it suggests that there is much more diversity in Melanesia than has been previously recognized. As conservationists aim to maximize representation of biodiversity when planning, it is imperative to have a deep understanding of the community assembly in order to plan effectively. It seems there are several important historic areas in the Pacific that are hotspots for divergent *G. oceanica* lineages: Papua New Guinea and the Solomon Islands. Northern Melanesia has long been known as a highly diverse and endemic area (e.g. birds; Mayr & Diamond, 2001). As reptiles frequently show finer scale endemism than do birds, further sampling of *G. oceanica* and other terrestrial taxa across the region is warranted if we are to understand the diversity in the area and historic drivers of its development.

ACKNOWLEDGEMENTS

We thank Michelle Koo for help producing the map, Winifred Tonione, Charles Moritz, Natalie Reeder, and Steven Stones-Havas for assistance in the field. We thank Mike Fay, Jon Richmond, Rafe Brown, Fred Kraus, and George Zug for fresh samples from key sampling gaps, Rayna Bell for help with molecular phylogenetic dating analyses, members of the Moritz lab and members of the Gump Station, especially Neil Davies and Chris Meyer for assistance in Moorea. RNFs fieldwork in Vanuatu and Fiji was supported in part by the Smithsonian Scholarly Studies Program funding to George R. Zug (NMNH), the Critical Ecosystems Partnership Fund, the International Iguana Foundation and the Secretariat of the Pacific Regional Environment Programme. Three anonymous referees and Paul Oliver provided a welcome and useful critique of the manuscript. We thank our funders; the Gordon and Betty Moore Foundation and the Australia Research Council. The use of trade, product or firm names in this publication does not imply endorsement by the U.S. Government.

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SUPPORTING INFORMATION

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

Appendix S1 Supplementary information for sampling and analyses for the phylogeography of *Gehyra oceanica*.

DATA ACCESSIBILITY

All DNA sequences were accessioned in GenBank. GenBank numbers for individual samples can be found in Table S4 in Appendix S1 (KR857724–KR858258). The final SNP data set has been included in Table S2 in Appendix S1.

BIOSKETCH

Maria Tonione is broadly interested in evolution, historical biogeography and phylogenetics.

Author contributions: M.A.T., R.F., and C.M. designed the research; M.A.T., R.F. and C.M. collected samples; M.A.T. and C.Z. collected the data; M.A.T. analysed the data; and M.A.T., R.F. and C.M. wrote the paper.

Editor: Mark Carine