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ORIGINAL ARTICLE

Biogeographical history and coalescent species delimitation of Pacific island skinks (Squamata: Scincidae: *Emoia cyanura* species group)

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ABSTRACT

Aim A prevailing hypothesis for how Pacific islands organisms have obtained their extant distributions is that of a stepping-stone model, in which populations originate from Papua New Guinea in the western Pacific and gradually disperse eastward. Here, we test this model using a spatiotemporal framework for *Emoia cyanura* and *E. impar*, two species within the *Emoia cyanura* species group (ECSG; Family: Scincidae). We further assess species limits within the group, utilizing novel coalescent methods.

Location Pacific Islands.

Methods We obtained DNA sequence data from one mitochondrial and three nuclear markers for 117 individuals, representing seven of the nine species within the ECSG. These data were analysed for concordance with the stepping-stone model using estimation of population structure, divergence dates, and historical biogeographical range. To assess hypotheses of independent lineages within each widespread species, we also employed the Bayesian Phylogenetics & Phylogeography (BPP) program to define operational taxonomic units in *BEAST.

Results Population structure analyses consistently found individuals from western island groups representing divergent populations, with central and eastern populations demonstrating minimal genetic variation. Phylogenetic hypotheses support a western origin for *E. cyanura* and *E. impar*, while biogeographical and divergence time estimations predict a recent and rapid expansion out of the western Pacific. The BPP and *BEAST analyses found evidence for five independent lineages within *E. impar* and five independent lineages within *E. cyanura*/*E. pseudocyanura*.

Main conclusions In contrast to the expectations of a stepping-stone model, *E. cyanura* and *E. impar* each exhibit the genetic signature of a rapid radiation during the mid to late Pleistocene, with evidence for newly identified lineages, mainly on western islands. Of these recovered lineages, we propose three to be elevated to species status. These findings expand our understanding of endemic Pacific biota, which are subject to conservation threats from human impacts and climate change.

Keywords
BioGeoBEARS, coalescent species delimitation, dispersal, divergence dating, *Emoia*, Pacific islands, phylogenetics, Scincidae

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INTRODUCTION

Organisms distributed across islands in the Pacific Ocean serve as dramatic embodiments of evolutionary principles and have stimulated the development of biogeographical predictions that continue to guide contemporary studies (Mayr, 1942; Wilson, 1961; Diamond, 1972). Colonization of the Pacific islands by terrestrial biota is thought (Emerson, 2002; Gillespie *et al.*, 2012) to occur via dispersal, generally from New Guinea eastward into the islands of the south-west Pacific (western Melanesia) and the hotspot islands of Polynesia (see Fig. 1 for reference). A gradual, stepping-stone dispersal model is supported by some taxonomic and phylogenetic studies of Pacific biotic diversity (reviewed in Gillespie *et al.*, 2008a), while other studies provide support for long-distance dispersal events (reviewed in Keppel *et al.*, 2009).

Under the stepping-stone mainland-to-island colonization hypothesis, biodiversity results from *in situ* diversification or multiple colonization events. Closely related lineages with an extensive distribution through the Pacific provide model systems with which to test these hypothesized processes of dispersal, based on resulting patterns of genetic divergence.

Within Pacific skinks, morphological stasis in the presence of ongoing molecular evolution has historically resulted in the designation of species complexes; however, detailed analyses of both genetic and morphological data have begun to uncover these skinks' diversity (cf. Donnellan & Hutchinson, 1990; Ineich & Zug, 1991; Austin, 1995; Keogh *et al.*, 2008). The ability of coalescent-based species delimitation methods (reviewed in Fujita *et al.*, 2012) to identify cryptic lineages is especially promising in the case of Pacific skinks. When morphological crypsis is prevalent, lineages found to be genetically divergent by population-level analyses may be used to generate initial alternative species delineation hypotheses, which can then be statistically evaluated in a multi-locus species tree framework (Knowles & Carstens, 2007; Carstens & Dewey, 2010).

Squamates are an ideal group with which to study Pacific biogeography. Despite their low vagility across oceanic barriers, lygosomine scincid and gekkonid lineages represent the dominant native terrestrial vertebrates on islands of the Pacific. Studies of Pacific lizards have found that biogeographical patterns, and concomitant inferred means of dispersal, can vary even between or within closely related species (Fisher, 1997; Austin, 1999; Rocha *et al.*, 2006; Tonione *et al.*, 2015). Evidence from the *Emoia samoensis* species group is more ambiguous, suggesting a complex history of historical dispersal and *in situ* speciation events (Austin & Zug, 1999; Hamilton *et al.*, 2010).

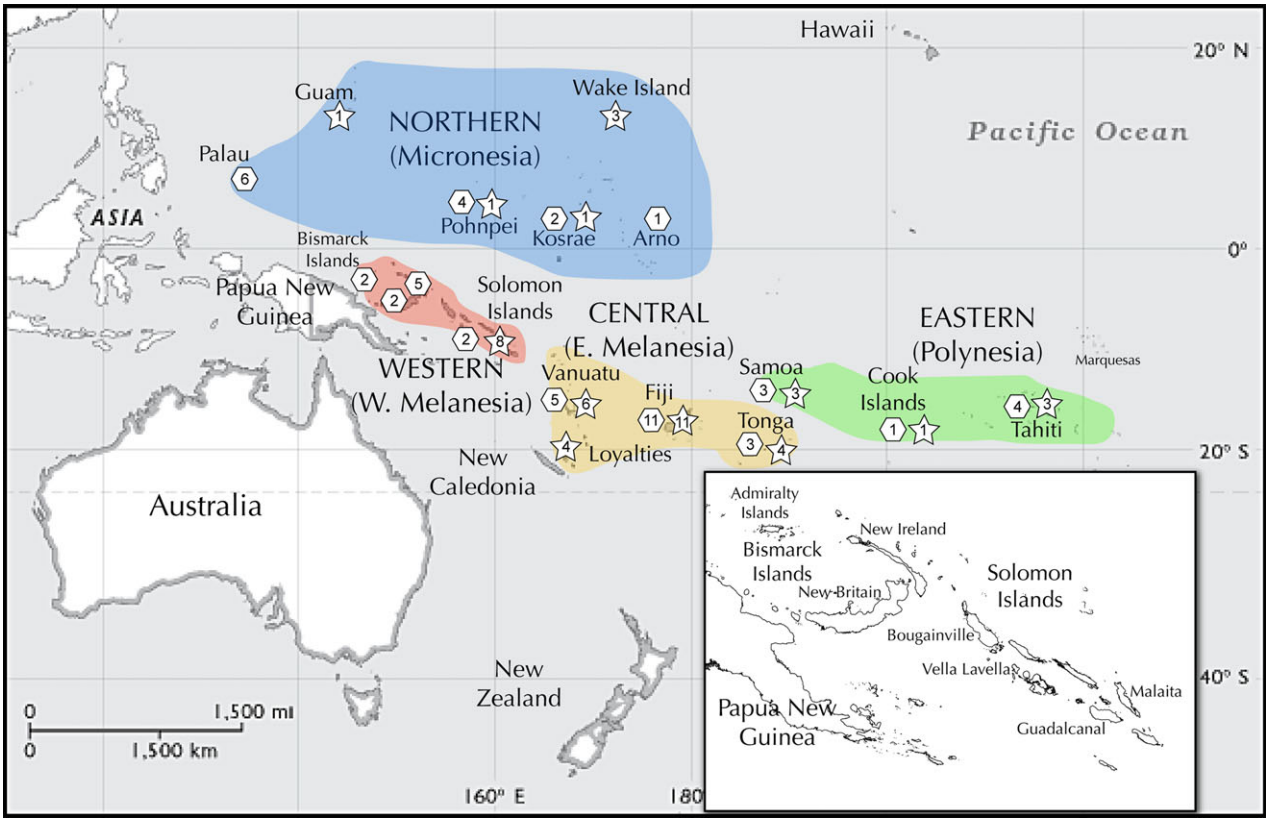

Figure 1 Molecular sampling of the two focal species for this study. Colours indicate Pacific biogeographical regions (Stoddart, 1992). Stars and hexagons represent *Emoia cyanura* and *Emoia impar* respectively; values indicate the number of individuals sampled. The inset shows details of the western biogeographical region.

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Preliminary work in another species group of *Emoia* (Bruna *et al.*, 1996a) points towards the possibility of a similarly complex biogeographical and taxonomic history, and is the focus of this study. The *Emoia cyanura* species group (ECSG; see Brown, 1991 for details on the group's distinguishing morphological features) is composed of nine species, seven of which are endemic to the Solomon Islands. The full ranges for the other two species, *E. cyanura* and *E. impar*, span 12,000 km from the Bismarck Archipelago near New Guinea to the Clipperton Islands south-west of Mexico (Ineich & Zug, 1991), and 40 latitudinal degrees from Guam to the Loyalty Islands.

These two species, despite their morphological and distributional similarities, are ecologically and physiologically divergent (Bruna *et al.*, 1996b; McElroy, 2014) and have been resolved as evolutionarily independent lineages (Guillame *et al.*, 1994; Bruna *et al.*, 1995), with *E. impar* found to represent the sister taxon to all other ECSG species (Bruna *et al.*, 1996a). Bruna *et al.* (1996a) found *E. cyanura* as paraphyletic with respect to *E. pseudocyanura* from the island of Guadalcanal in the Solomon Islands, with very low genetic divergence between cytochrome-*b* mitochondrial DNA (mtDNA) lineages. This finding, in conjunction with the sympatry of *E. cyanura* and *E. pseudocyanura* in the Solomon Islands, suggests that the two species may have undergone a recent speciation or hybridization event. Additionally, populations within both *E. impar* and *E. cyanura* exhibit high levels of molecular divergence (Bruna *et al.*, 1996a) and morphological variability (Brown, 1991; Ineich & Zug, 1991), suggesting that each species may actually consist of multiple independently evolving lineages.

E. cyanura and *E. impar* are not sister taxa (Bruna *et al.*, 1996a) and could therefore represent independent invasions of Pacific islands, providing an exemplary system with which to estimate mechanisms of dispersal. Under the eastward stepping-stone model (due either to human-mediated or natural colonization), the following patterns would be expected from the multiple analyses employed in this study: (1) multiple populations or incipient species that represent island or latitudinal regional groupings and an overall high level of divergence between populations; (2) inferred phylogenetic relationships and range estimates of ancestral nodes that exhibit a nested pattern of time-ordered clades, corresponding to a west–east geographical distribution; and (3) support for a gradual west–east adjacent dispersal and cladogenesis in tandem with island colonization in biogeographical analyses. Alternatively, a rapid radiation scenario would be signified by: (1) population structure or incipient species found in western populations, with overall little divergence between eastern populations; (2) rapidly diverged clades with geographical distributions that span the Pacific; and (3) support for a biogeographical model of widespread dispersal, with limited association between cladogenesis and range expansion.

This study utilizes multiple analyses in a novel combination to estimate the evolutionary history for the focal taxonomic group. Encompassing population structure analyses of intraspecific diversity, coalescent phylogenetic methods to estimate relationships and timing of divergences within the ECSG, and model-based comparison of populations' genetic structure with their geographical distributions, we infer the mode and tempo of dispersal history. Concurrently, we utilize methods of coalescent species delimitation to test species limits for hypothesized new lineages within the group.

METHODS

Taxon sampling and molecular methods

A total of 117 individuals were used in this study. For intraspecific analyses, we obtained tissues from 46 *E. cyanura* and 53 *E. impar*, from across their ranges (see Appendix S1 for locality information and Genbank accession numbers). Interspecific analyses also included 15 individuals representing five other species in the ECSG. Sequence data representing the species *E. ponapea* and *E. caeruleocauda* were employed as outgroups.

Genomic DNA was extracted from tissues using the NucleoSpinTissue kit (Macherey-Nagel, Bethlehem, PA, USA) and PCR (polymerase chain reaction) was used to amplify three nuclear gene regions (PRLR, BZW1, SELT) and one mtDNA gene region (ND2). PCR procedures were performed according to published protocols (as described in references cited in Table S1, Appendix S2), while a 'touchdown' protocol was used to amplify the regions specific to this study (see Appendix S2 for details). PCR templates were purified and subjected to automated DNA sequencing with an ABI 3730 capillary sequencer.

Sequences were edited and assembled into contigs using Sequencher 4.7 (Gene Codes Corp., Ann Arbor, MI, USA), and gene sequences were aligned in Muscle using default parameter values (Edgar, 2004). In Mesquite 2.74 (Maddison & Maddison, 2011), the protein-coding regions ND2 and PRLR were manually aligned using identified open reading frames. The 'Find Heterozygous Alleles' feature within the program CodonCode Aligner 3.7.1.1 (CodonCode Corp., 2011) was used to estimate the different allele sequences for heterozygous insertions and deletions in the introns SELT and BZW1.

Population structure analyses

In order to ascertain initial estimates of population structure within *E. impar* and *E. cyanura*, we implemented a number of population genetic structure analyses.

To determine if hybridization has taken place between individuals of *E. cyanura* and *E. pseudocyanura* and to estimate intraspecific relationships within *E. impar,* we generated multilocus nuclear networks for each species using Pofad 1.03 (Joly & Bruneau, 2006). Pofad utilizes the matrix of genetic distances between all alleles for each nuclear locus to create a standardized distance matrix between individuals. We used the NeighborNet algorithm (Bryant & Moulton,

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2003) in SplitsTree 4.11.3 (Huson & Bryant, 2005) to create a visual network.

To statistically evaluate population structure within both widespread species and assign individuals to populations, we used the Bayesian clustering method Structurama 2.0 (Huelsenbeck *et al.*, 2011), which assumes an underlying model of Hardy–Weinberg equilibrium. Rather than relying on a user-defined, fixed value for the estimated number of populations (K), Structurama lets K be a random variable under a Dirichlet process prior. Here, we separately analyse the nuclear data from *E. impair* and *E. cyanura* + *E. pseudocyanura* with multiple permutations and a prior mean $E(k)$ ranging from one to five. Data for *E. impar* were run without admixture, while *E. cyanura* and *E. pseudocyanura* were run both with and without admixture to allow for the possibility of hybridization. All MCMC (Markov chain Monte Carlo) analyses were run with four chains for 5×10^6 generations, sampling every 100 steps and excluding the initial 10,000 steps as burn-in.

Incorporating spatial data into population structure inference may provide greater resolution in certain biological contexts: skinks presently found on different islands can be assumed to be genetically isolated and represent allopatric, discrete populations. Therefore, we used the spatially explicit Bayesian MCMC model executed in Geneland 3.3.2 (Guillot, 2005) as a final method to estimate population structure from all loci. The sampling locality for each individual was converted from geographical coordinates to decimal degrees; in the rare case that specific GPS data were not available for an individual, the geographical centre of the island was used. We conducted three concurrent independent runs for each widespread species for 1×10^6 iterations, with a thinning interval of 1000 and the first 200 iterations discarded as burn-in. We used the uncorrelated alleles model.

Coalescent species delimitation

Recent developments in species delimitation techniques now allow for the joint inference of species relationships and species delimitation. Here, we employ the program Bayesian Phylogenetics & Phylogeography 3.0 (BPP; Yang & Rannala, 2014) in tandem with the Bayesian species tree estimator *BEAST (Heled & Drummond, 2010) to delimit species in a coalescent framework. BPP 3.0, unlike previous versions of the program, incorporates the nearest-neighbour interchange (NNI) algorithm and eliminates the need for a fixed input guide tree. A recent study reanalysed 15 species delimitation studies and demonstrated that the unguided BPP outperforms earlier versions (Caviedes-Solis *et al.*, 2015). Therefore, we choose to use the unguided version of BPP in this study, as it circumvents the issue of the user-specified species tree (Yang & Rannala, 2014).

For BPP analyses, a gamma prior G(2, 2000) was used for both the theta (θ) and tau (τ) priors. Species delimitation within *E. impar* and *E. cyanura* were performed separately using (1) three nuclear loci and (2) mtDNA + nuclear loci. For *E. cyanura*, we used the results from the nuclear only BPP species delimitation analyses, as mitochondrial and nuclear discordance prevented the mtDNA + nuclear analyses from converging. Each analysis was run three times for 5×10^6 generations and convergence was assessed by ensuring the stability of parameter estimates.

*BEAST assumes that terminal taxa are independently evolving lineages, requiring that the terminal taxonomic groupings (operational taxonomic units, or OTUs, which are assigned *a priori*) actually represent independent lineages (Heled & Drummond, 2010; McCormack *et al.*, 2010). We delimited evolutionary lineages within *E. cyanura* and *E. impar* according to the BPP 3.0 results, using a posterior probability (P_p) cut-off of ≥ 0.95. This value is recommended for assessment of speciation probabilities for individual nodes in a guide tree in previous versions of BPP (Leaché & Fujita, 2010). Given the novel methods of BPP 3.0, we also ran an alternative *BEAST tree using a less conservative 0.85 P_p cut-off for probable species (see Fig. S1, Appendix S3 in Supporting Information). These analyses were run concurrently with estimations of lineage divergence dates, as described in the next section.

Phylogenetic analyses & divergence time estimates

For phylogenetic analyses, both PRLR and ND2 were partitioned by codon position, as this was determined to be the best fit for the data by comparing the log-likelihood scores of differently partitioned gene trees (generated in RAxML 7.2.7, Stamatakis *et al.*, 2008; see Appendix S2 for details). Phased (Stephens & Donnelly, 2003; see Appendix S2 for details) sequence data were subsequently input into MrModelTest 2.3 (Nylander, 2004) to determine the appropriate evolutionary model for each locus and codon position. We used beast 1.6.2 (Drummond & Rambaut, 2007) to create Bayesian inference gene trees for each locus, using these best-fit models and a coalescent tree prior. Two to three independent runs of single-chain MCMC analyses were run for 2×10^7 generations, sampling every 1000 generations, and discarding the first 20% as burn-in. Runs were assessed for convergence with Tracer 1.5 (Rambaut & Drummond, 2009). All of the gene regions except for PRLR strongly rejected a strict molecular clock (Drummond *et al.*, 2006); these three loci were subsequently set to a relaxed lognormal clock.

Given that single-locus estimates of divergence/coalescence timing may overestimate dates for lineage divergences (McCormack *et al.*, 2010), a species tree approach is appropriate for accurately identifying lineage divergence timing by incorporating the coalescent histories from multiple genes (Edwards & Beerli, 2000; Carstens & Knowles, 2007). Accordingly, the *BEAST multi-species coalescent model (Heled & Drummond, 2010) was implemented within beast v.1.8.2 to estimate divergence dates for all sampled lineages of the ECSG, using the sequence data from all loci, with partitioning, evolutionary, and clock models as described above. Because of the lack of adequate fossils from Pacific

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squamates (Austin & Zug, 1999; Hamilton *et al.*, 2010; Noonan & Sites, 2010), we set the ND2 substitution rate to 0.012 for the ND2 gene region (Smith *et al.*, 2007; Dubey & Shine, 2010), with all other loci set to be estimated relative to the ND2 rate. Population size was set to constant, and we used a coalescent tree prior.

We ran three independent runs of 5×10^9 generations, sampling every 5×10^4 steps and discarding the initial 25% as burn-in. We checked for convergence in Tracer by ensuring that the combined ESS score of all parameters was >200. Then, the three runs were combined using LogCombiner and the maximum clade credibility tree was constructed using TreeAnnotator.

Model-based biogeographical inference

In conjunction with evidence from the above analyses, we assessed dispersal history within *E. cyanura* and *E. impar* using the R (R Core Team, 2015) package BioGeoBEARS (Matzke, 2013a). This analysis enables probabilistic inference of ancestral geographical ranges and statistical comparisons of different models of range expansion (dispersal-extinction-cladogenesis (DEC), dispersal–vicariance analysis (DIVA) and BayArea) using a time-calibrated species tree. Additionally, BioGeoBEARS incorporates founder-event speciation (+J), a process important in island systems, into all models (Matzke, 2013b).

As the input tree for this analysis, we used the *BEAST species tree for the entire ECSG, with OTUs within the two focal lineages based on the BPP v.3.0 groupings with >95% P_p support. Ancestral range was estimated for all nodes. Putative taxa were coded as belonging to one of four biogeographical regions of the Pacific (Northern, Western, Central, or Eastern, as indicated on Fig. 1; Stoddart, 1992), and all nodes were allowed to occupy all possible ranges (num_areas = 4). Analyses constrained direct dispersal to adjacent biogeographical areas only. The likelihoods for each model tested in BioGeoBEARS were then compared for the best fit to the data using an AIC_c (Akaike information criterion corrected for small sample size) approach (Burnham & Anderson, 2002).

RESULTS

Population structure analyses

Results from the Pofad networks based on combined nuclear data are shown in Fig. 2. *Emoia impar* demonstrated a high degree of allelic divergence, with individuals from the western end of the species' range generally representing island-specific clusters. Exceptions to this pattern are four samples from the Admiralty Islands in the Bismarcks and two individuals from the Solomon Islands, which group with widespread *E. impar*.

For the *E. cyanura* complex, the majority of sampled individuals cluster, indicating minimal genetic distance. Two individuals from Bougainville Island (north of the Solomon Islands, Fig. 1 inset), however, form a divergent cluster with *E. pseudocyanura*. One representative of *E. pseudocyanura*, from Malaita in the central Solomon Islands, also exhibits divergence. The remaining eight samples of *E. cyanura* from the Solomon Islands (including two from Guadalcanal, where putative hybridization with *E. pseudocyanura* is hypothesized to have taken place) belong to the geographically widespread cluster.

Within both species, most individuals were assigned by Structurama to one geographically widespread population, with the same western individuals noted above representing divergent populations (Tables 1 & 2). Structurama generated equivocal population assignments for these divergent individuals, however, and were influenced by the different values for the Dirichlet process prior (cf. Evans *et al.*, 2011). Otherwise, for *E. impar*, the estimated number of populations, based on the highest posterior probability value (P_p = 0.36–0.47), varied between $K = 4$ and $K = 5$ (Table 1). The only difference between these populations was if one individual from New Ireland (im-2-nir) belonged to its own population or was assigned to a population of other New Ireland individuals (see Table S2, Appendix S3 for details on all sampled individuals' assignments, according to all three population structure analyses).

Similarly, the estimated number of populations within *E. cyanura* and *E. pseudocyanura* varied between $K = 4$ and $K = 6$ (P_p = 0.37–0.47; Table 2), with different prior values affecting the assignment of all *E. pseudocyanura* and the individuals from Malaita and Bougainville that were noted in the Pofad networks. When analyses for the *E. cyanura* clade were replicated, allowing for admixture between individuals on different island groups, results demonstrated very low posterior support for a high number of populations (P_p = 0.12–0.19; K = 15–28), with the prior mean for the Dirichlet process strongly influencing these results. This finding provides evidence against the admixture model, and suggests that there is not significant gene flow between *E. cyanura* and *E. pseudocyanura*.

For *E. impar*, the optimal Geneland analysis (Table 1) supported $K = 3$, with one population consisting of individuals from New Britain and the Solomon Islands, a second consisting of all of the New Ireland skinks, and a third containing all remaining *E. impar* individuals. As observed in all other analyses, the *E. impar* from the Admiralty Islands (proximal to New Ireland and New Britain) grouped with the widespread lineage.

Analysis of *E. cyanura* and *E. pseudocyanura* estimated that the group consisted of three populations, with *E. pseudocyanura* from Guadalcanal grouping with the *E. pseudocyanura* from Malaita, the other *E. pseudocyanura* and *E. cyanura* from Bougainville forming a population, and all other *E. cyanura* (including other individuals from the Solomon Islands) as a third population. However, the average posterior probability for individuals' assignments to these populations was relatively low (P_p = 0.61). When all *E. pseudocyanura* except for the Malaita individual were excluded in a subsequent run, individuals were assigned with significantly higher

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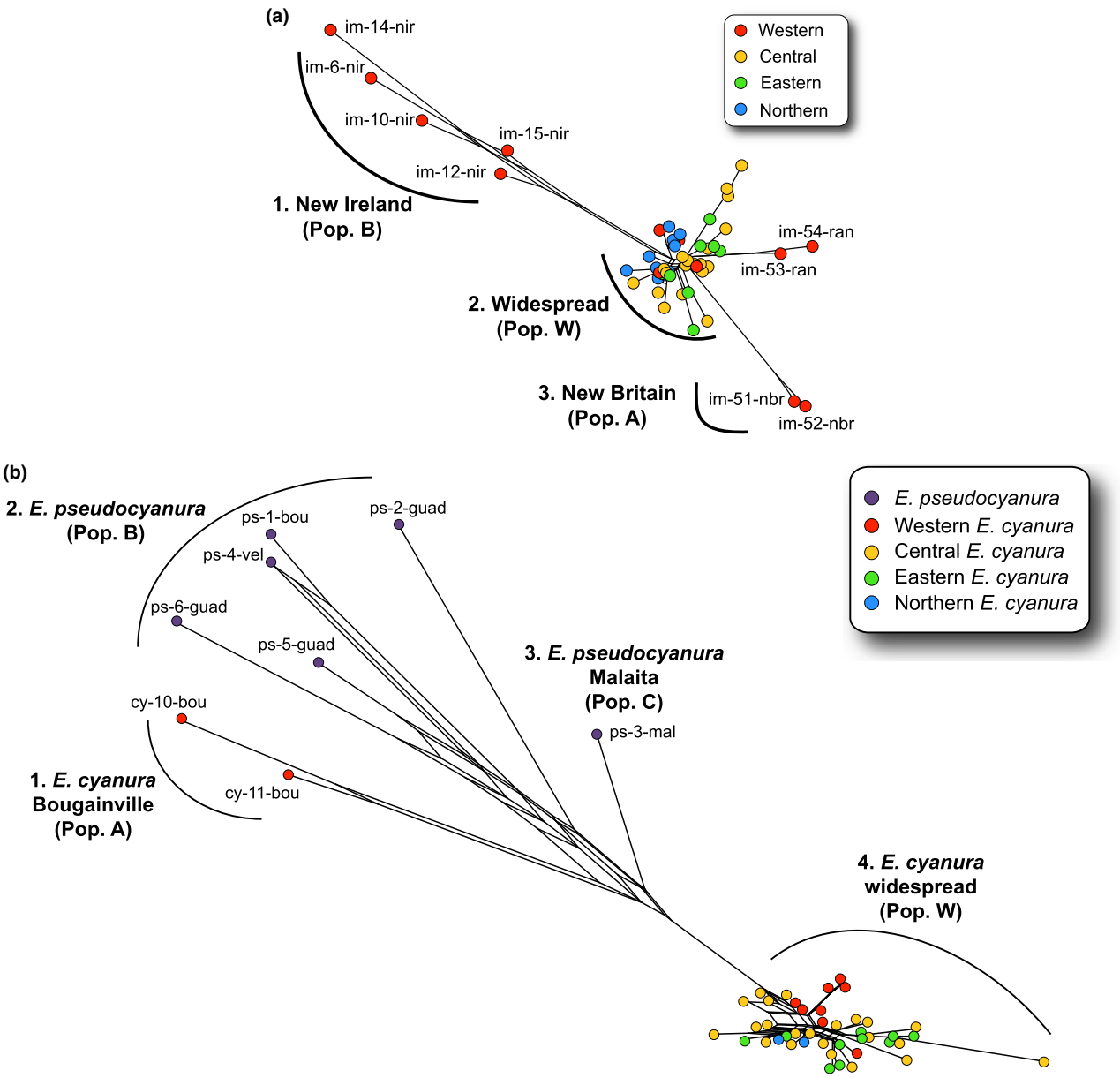

Figure 2 a) Multi-locus nuclear Pofad network for *Emoia impar* and b) for *Emoia cyanura*/*Emoia pseudocyanura*. Groupings of divergent individuals are labelled parenthetically as in Table S2, Appendix S3.

probability values ($P_p > 0.99$). This analysis found evidence for the three Bougainville *E. cyanura* and *E. pseudocyanura* from Malaita as one population and all other individuals as a second population.

Coalescent species delimitation

As estimated by BPP 3.0, the posterior probabilities of species assignments for different populations are shown in the final column of Table S2 in Appendix S3, with the *BEAST species tree depicting all OTUs with ≥ 0.95 P_p support in Fig. 3. As in the population structure analyses of *E. impar*, species identified by this method represent western island groups, with the addition of the population from Vanuatu as its own species. Within *E. cyanura* and *E. pseudocyanura*, species are generally reflective of those identified from population structure analyses. Notably, the population of *E. cyanura* from Tahiti (Eastern region) is also recovered as a novel species. Within both clades, nodal support values on the *BEAST species tree were low ($P_p < 0.95$) for estimation of some of these putative species' relationships, suggesting that data from more loci and/or more intensive sampling may help to clarify their species status and evolutionary relationships.

Timing of lineage divergences

The *BEAST estimated ages for ECSG divergences are shown on the species tree in Fig. 3, with Table 3 listing the 95%

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Table 1 Structurama and Geneland assignment analyses for *Emoia impar*. Values represent the mean of the posterior probability (P_P) distribution for each value of K (estimated number of populations). Bold values indicate the most likely number of populations under each prior setting E(k).

Emoia impar							
	Structurama E(k) Mean Value						Geneland
K	1	2	3	4	5	Gamma (1,10)	
1	K = 53	–	–	–	–	–	–
2		.02	.01	–	–	.03	.05
3		.32	.13	.06	.03	.32	**.61**
4		**.47**	**.40**	.27	.18	**.43**	.20
5		.17	.11	**.39**	**.36**	.18	.14
6		.02	.01	.21	.30	.04	–
	Average P_P of individuals belonging to assigned population:						.57

HPD ranges for nodes of interest. The entire ECSG group split *c.* 13.3 Ma, while the *E. impar* lineage and *E. cyanura*/*E. pseudocyanura* complex were found to be similar in age, dating to *c.* 5.5 and 5.0 Ma respectively. Divergence of both of these clades was found to pre-date the evolution of the four Solomon Island endemic species: *E. rufilabialis* and *E. taumakoensis* are estimated to have diverged *c.* 3.7 Ma and *E. isolata* and *E. schmidti c.* 1.7 Ma. Finally, there is remarkable concordance in the estimated timing for diversification of *E. impar* and *E. cyanura* out of the western end of their ranges, as both of the geographically widespread clades date to *c.* 0.1 Ma.

Biogeographical reconstruction

Results from the BioGeoBEARS analysis of the *BEAST species tree based on the 0.95 P_P BPP species assignment supports a western origin for both the *E. impar* and the *E. cyanura* clades, as well as for the entire ECSG (Fig. 4). As estimated by the program, the simple DEC model had the strongest statistical support (Table 4). Given that this model does not account for cladogenesis in tandem with range expansion (Ree & Smith, 2008), this lends support to the findings of limited speciation from the population structure and species delimitation analyses, despite obvious dispersal of the two focal lineages to oceanic islands. Furthermore, the additional +J parameter provided by the BioGeoBEARS package to account for founder-event speciation was not statistically supported to fit the data.

On an intraspecific level, the *E. impar* radiation out of the western Pacific region was reconstructed to have occurred rapidly, with cladogenesis occurring simultaneously with a radiation across all four biogeographical areas. Similarly, extant lineages of widespread *E. cyanura* were estimated to have dispersed rapidly from a biogeographical origin in the western region.

DISCUSSION

With more intensive sampling of individuals than in previous studies and the use of DNA sequence data from multiple, independent loci, we are able to accurately assess intraspecific diversity as well as the timing and tempo of lineage divergences within the ECSG. Based on intraspecific analyses of population structure, coalescent species delimitation, estimated dates of lineage divergence, and methods of historical biogeographical reconstruction, *E. impar* and *E. cyanura* show evidence of independent rapid radiations out of the western end of their ranges. The elements that would accompany a stepping-stone model of dispersal (genetic populations or incipient species that represent island or regional groupings, a nested series of time-ordered clades corresponding to west–east geographical distribution, and statistical support for a biogeographical model indicating gradual dispersal) are not apparent for either widespread lineage.

Table 2 Structurama and Geneland assignment analyses for *Emoia cyanura* and *Emoia pseudocyanura*. Values represent the mean of the posterior probability (P_P) distribution for each value of K (estimated number of populations). Bold values indicate the most likely number of populations under each prior setting E(k).

Emoia cyanura & *Emoia pseudocyanura*								
	Structurama E(k) Mean Value						Geneland	
K	1	2	3	4	5	Gamma (1,10)	With All *E. pseudocyanura*	Excluding Non-Malaita *E. pseudocyanura*
1	K = 55	–	–	–	–	–	–	–
2		–	–	–	–	–	.03	**.60**
3		.17	.05	.02	.01	.15	**.66**	.21
4		**.47**	.28	.16	.09	**.41**	.19	.08
5		.29	**.41**	**.37**	.30	.30	.13	.12
6		.06	.20	.32	**.37**	.10	–	–
7		.01	.04	.10	.19	.02	–	–
	Average P_P of individuals belonging to assigned population:						.61	.99

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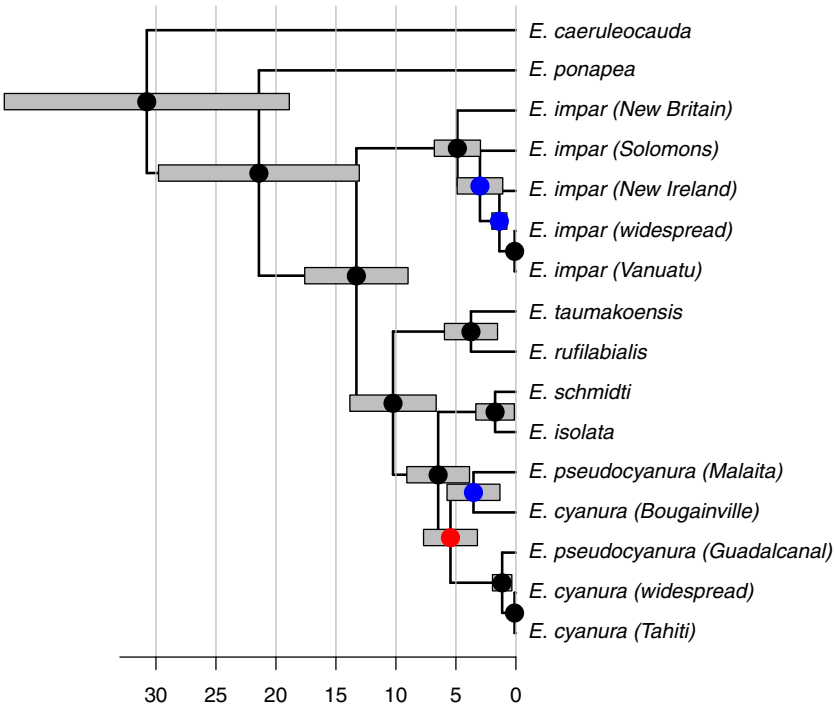

Figure 3 Bayesian chronogram produced by *BEAST analyses for the *Emoia cyanura* species group, using the BPP posterior probability (P_p) ≥ 0.95 species probabilities as OTU designations for *Emoia impar*, *Emoia. cyanura*, and *Emoia pseudocyanura* (see Table S2, Appendix S3 for reference). Nodal scale bars indicate the 95% highest posterior density interval for divergence time estimates in mya. Black nodes: $P_p \geq 0.95$; blue nodes: P_p between 0.75–0.95; red nodes: $P_p < 0.75$.

Table 3 *BEAST estimated divergence dates for certain lineages within the *Emoia cyanura* species group (ECSG).

Lineage divergence	Mean node age (Ma)	95% HPD
ECSG	13.3	9.3–17.8
E. impar	5.0	3.2–7.3
Widespread *E. impar*	0.1	0.01–0.2
E. cyanura & *E. pseudocyanura* clade	5.5	3.0–7.5
Widespread *E. cyanura*	0.1	0.02–0.2

Instead, genetic data for both species across their ranges reveal divergence mainly in western island groups only, recently diverged clades with geographical distributions spanning the Pacific, and the simple DEC analysis as the best-fit biogeographical scenario.

It is worth noting, however, that there is evidence for non-Western incipient species within both widespread lineages. BPP recovered the Vanuatu population of *E. impar* and the Tahiti population of *E. cyanura* as likely ($P_p > 0.95$) species, suggesting unique genetic lineages are starting to evolve outside of the Western region.

Rapid radiation: human-mediated or natural?

The low amount of genetic variability between widespread populations as compared to western populations suggests that both *E. impar* and *E. cyanura* were subject to a founder effect caused by a rapid dispersal event. Both the root ages and timing for these radiations are concordant (Table 3), suggesting extrinsic geological and environmental factors may have played a role in both lineages' dispersal histories.

However, even the lower ranges of the 95% HPDs (*c.* 0.01–0.02 Ma) for the *BEAST estimated dates of the radiations of the widespread clades considerably pre-date human settlement of the Polynesian region of the Pacific, which is estimated to have occurred only 3000–5000 years ago (Ricaut *et al.*, 2010). Initial dispersal events out of the species' respective ancestral regions most likely happened by natural means, either through waif dispersal of a small number of skinks or even a single gravid female. The similar timing for these initial radiations of *E. impar* and *E. cyanura* could be due to the relative stability of the Pacific region since the early to mid-Pliocene; most island groups throughout central and eastern Pacific have been emergent or geologically stable since at least this era (Hall, 2002; Neall & Trewick, 2008). Human movements, from early settlers of the Polynesian region to American and Japanese troops during World War II, most likely have played a key role in producing the current extant ranges of *E. impar* and *E. cyanura* (as found for other Pacific squamates; Austin *et al.*, 2011; Zug & Fisher, 2012; Tonione *et al.*, 2015), and have further contributed to the low degree of variability observed between most of the sampled populations.

The consistent findings of New Ireland and New Britain representing separate populations/species suggests that *E. impar* also experienced at least one natural dispersal event to these islands. Geological evidence posits these islands to be some of the oldest in the region, dating to 35 Ma (Neall & Trewick, 2008). Although this hypothesis could not be rigorously tested in this study, the species tree topology presented (Fig. 3) suggests that *E. impar* may have dispersed directly

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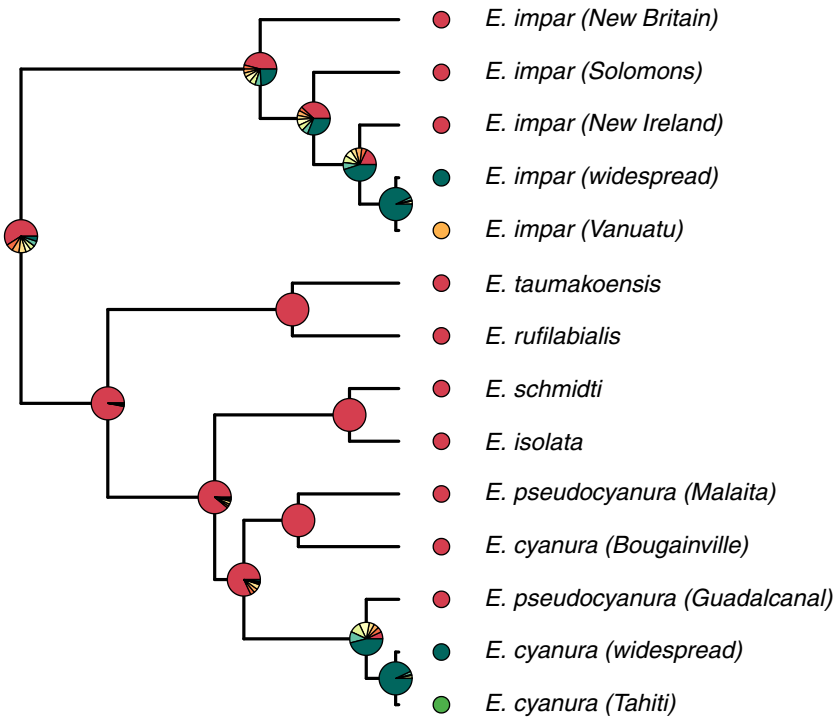

Figure 4 Ancestral range estimation results from the best supported BioGeoBEARS model for the *Emoia cyanura* species group. Colours correspond to regions in Fig. 1; teal represents all four biogeographical regions.

Table 4 Comparison of ancestral range reconstruction models for the *Emoia cyanura* species group, as inferred by BioGeoBEARS. Models are dispersal-extinction-cladogenesis (DEC), dispersal–vicariance analysis (DIVA) and BayArea, as well as each model allowing for founder-event speciation (+J). The relative probability for each biogeographical model was calculated from the AIC_c weight value.

Dispersal model	Ln*L*	No. of parameters	*d*	*e*	*j*	AIC	AIC_c	Relative probability
DEC	−23.01	2	0.0433	0.0000	0.0000	50.01	50.12	74%
DEC+J	−23.01	3	0.0433	0.0000	0.0000	52.01	52.23	26%
DIVA	−34.22	2	0.0660	0.0000	0.0000	72.45	72.56	0%
DIVA+J	−34.23	3	0.0660	0.0000	0.0000	74.45	74.67	0%
BayArea	−46.17	2	0.0518	0.0891	0.0000	96.34	96.45	0%
BayArea+J	−34.93	3	0.0434	0.0000	0.0551	75.87	76.09	0%

Ln*L*, log-likelihood; *d*, rate of dispersal; *e*, rate of extinction; *j*, relative probability of founder-event speciation at cladogenesis; AIC, Akaike's information criterion; AIC_c, Akaike's information criterion corrected for small sample size.

from New Britain throughout the rest of the Pacific. *Emoia cyanura* does not presently occur on islands in the Bismarck Archipelago, and most likely was restricted to the Solomon Islands until radiating across the Pacific region during a similar time frame as *E. impar*. This illustrates that even closely related lineages may, due to the random nature of chance dispersal events, develop disparate ranges. While this can lead to differential evolutionary trajectories, *E. impar* and *E. cyanura* subsequently underwent similar natural and human-mediated radiations, producing their extant distributions and result in sympatry on islands across the Pacific region.

Coalescent species delimitation & taxonomic conclusions

For both species, we found obvious divergence of certain western populations that most likely represent independent, evolutionary species (Table 3). Although we undertook the coalescent species delimitation analyses in part to ensure accurate designation of OTUs in the *BEAST species tree estimation, this integrative process is an ideal method with which to hypothesize species limits (Fujita *et al.*, 2012; Grummer *et al.*, 2013). Coalescent-based methods of species delimitation directly incorporate gene coalescence, which accounts for gene tree discordance due to drift and utilizes information from multiple loci to estimate species membership, inter-relationships, population sizes and divergence times (reviewed in Fujita *et al.*, 2012). When performed appropriately (Carstens *et al.*, 2013), these methodologies enable a more objective assessment of species limits than delimiting species based on single-locus data or morphology, and is especially applicable to populations in which loci are subject to incomplete lineage sorting, making reciprocal monophyly in gene trees of independent lineages unlikely (Hudson & Coyne, 2002).

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Based on our results, *E. pseudocyanura sensu stricto* remains a lineage separate from *E. cyanura sensu stricto*. Only the mtDNA gene tree demonstrated shared haplotypes between the two species; these relationships were not supported by the nuclear data. Given the geographical proximity of Solomon Islands individuals that were found to have very similar mitochondrial haplotypes, this finding could be due to historic asymmetrical introgression, but there was no signal of extant gene flow.

In contrast, *E. cyanura* from Bougainville and *E. pseudocyanura* from Malaita were consistently supported as an independent lineage: *E.* sp. nov. Malaita. This finding is concordant with previous work on the group (Bruna *et al.*, 1996a,b), which included mtDNA sequence data from the same individual from Malaita and found strong support for its sister relationship to *E. isolata* rather than other sampled *E. pseudocyanura*.

In their morphological study of *E. cyanura* and *E. impar*, Ineich & Zug (1991) noted that individuals of *E. impar* from the species' type locality (islands off the coast of New Britain) were distinct in size and colour pattern from Central and Eastern populations of the species. The authors refrained from designating these as independent lineages 'until an analysis of the geographical variation of the *impar*-type lizards demonstrates that the Bismarck populations are or are not different from those of Oceania' (p. 1134). This study provides evidence that these lineages are indeed differentiated, with support from the genetic data for two species in the Bismarcks/Solomon Islands region (*E. impar sensu stricto* and *E.* sp. nov. New Ireland), and a third species representing all other populations (*E. schauinslandi*). This latter lineage includes the population from the Admiralty Islands, which, as this island group is also part of the Bismarck Archipelago, presents an intriguing result in terms of biogeography (consistent with findings for the gecko *Nactus pelagicus*, Zug & Fisher, 2012). All of the new lineages proposed here, with descriptions of corollary distinguishing morphological features, will be described in another paper (Klein *et al.*, in prep).

Implications

Through studying the evolutionary histories of *E. cyanura* and *E. impar*, we gain a more accurate approximation of biogeographical history and species biodiversity for squamates occurring in the insular Pacific. In terms of colonization patterns, these lineages demonstrate similarities to those of other Pacific lygosomine skinks (Austin, 1999; Austin & Zug, 1999) and gecko lineages (Fisher, 1997; Rocha *et al.*, 2006). The decreased genetic diversity in eastward populations of the focal lineages is also in accordance with the general attenuation of species richness and endemism proceeding from western archipelagos to eastern islands in the Pacific (Stoddart, 1992; Gillespie *et al.*, 2008b; Keppel *et al.*, 2009), in accordance with the predictions of classic island biogeography theory (MacArthur & Wilson, 1967) and many empirical studies of global island systems (Gillespie & Baldwin, 2009; Losos & Ricklefs, 2009). However, the BPP findings of possible divergent lineages on Vanuatu and Tahiti disrupt this model, given the central and eastern locations of these populations. Although more genetic and morphological data needs to be collected to determine if these populations indeed represent actual species, our overall findings demonstrate that there are still cryptic lineages to be discovered through fieldwork on oceanic Pacific islands. This has implications for understanding true Pacific biodiversity and identifying target areas for conservation management based on recognizing unique genetic lineages (as has been undertaken for Pacific marine protected areas; Carpenter *et al.*, 2011).

Methodologically, this study demonstrates the utility of employing multi-locus data with coalescent-based species delimitation methods to reveal cryptic biodiversity, especially within a morphologically conserved group. For general use of the methodological pipeline described in this study, it may be appropriate to include multiple means of intraspecific clustering, as performed here, unless one has definite *a priori* hypotheses about which individuals represent divergent populations.

In consideration of both the inferred biogeographical history and methods of species delimitation used in this study, *E. cyanura* and *E. impar* have exhibited a propensity to successfully establish on islands across the Pacific, but their nearly homogeneous levels of genetic variability do not bode well for the species' long-term sustainability. The movements of humans and organisms throughout the insular Pacific are complex, and will only intensify as sea levels rise and weather patterns fluctuate due to climate change (Bindoff *et al.*, 2007; Becker *et al.*, 2012). It is therefore vital to undertake studies such as this one, in order to understand historical dispersal processes and ecological factors that can, in turn, help to predict future cascading effects on Pacific Island biodiversity (Gillespie *et al.*, 2008b).

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SUPPORTING INFORMATION

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

Appendix S1 Collection data for study samples.
Appendix S2 Methods details.
Appendix S3 Results: additional tables and figures.

BIOSKETCH

Elaine R. Klein is a PhD student at the Institute for Science & Math Education, University of Washington College of Education. Her work with the co-authors focuses on the evolutionary histories of Pacific herpetofauna and the biological factors influencing species tree interference. See https://sites.google.com/site/todreederslab/ and http://faculty.washington.edu/leache/wordpress/ for more details.

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