

Range eclipse leads to tenuous survival of a rare lizard species on a barrier atoll

JONATHAN Q. RICHMOND, ELIJAH WOSTL, ROBERT N. REED and ROBERT N. FISHER

Abstract Rediscovery of living populations of a species that was presumed to be extirpated can generate new narratives for conservation in areas suffering from losses in biodiversity. We used field observations and DNA sequence data to verify the rediscovery of the Critically Endangered scincid lizard *Emoia slevini* on Dãno', an islet off the coast of Guam in the southern Mariana Islands, where for > 20 years it had been considered possibly extirpated. Endemic to the Marianas, *E. slevini* has declined throughout its range and no longer occurs on as many as five islands from which it was historically known, most likely because of interactions with invasive species and loss of native forest. Our results show that individuals from Dãno', the type locality for *E. slevini*, are genetically similar but not identical to *E. slevini* on Sarigan and Alamagan to the north, and that *E. slevini* is a close evolutionary relative to another congener in the southern Marianas that is currently recognized as *Emoia atrocostata* but probably represents an undescribed species in this archipelago. We also show that other, more broadly distributed species of *Emoia* occurring on Dãno' are distant relatives to *E. slevini* and the Mariana lineage of *E. atrocostata*, providing further evidence of the distinctiveness of these taxa. The rediscovery of *E. slevini* on Dãno' following rodent eradication and culling of a population of monitor lizards suggests that management of invasive species is key to the recovery of this skink in the Mariana Islands, and that a range eclipse on the larger neighbouring island of Guam best explains why the rediscovery took place at the periphery of the species' historic range. A Chamorro abstract can be found in the supplementary material.

Keywords Critically Endangered, *Emoia slevini*, extinction, invasive species, Mariana Islands, Mariana skink, range eclipse

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Introduction

Rediscoveries of species once considered extinct or extirpated provide rare opportunities for positive messaging about biodiversity and add to a growing list of examples of successful management outcomes for indigenous species affected by non-indigenous invaders (Ladle et al., 2011; Jones et al., 2016). Rediscoveries may be particularly likely for secretive taxa that occur in under-surveyed or remote areas (Scheffers et al., 2011; Caviedes-Solis et al., 2015), where habitat loss has resulted in scattered populations of a formerly widespread species (Fisher & Blomberg, 2011), where detection probabilities are low to begin with (Durso et al., 2011; Lee et al., 2017; Thompson et al., 2017; Butchart et al., 2018), and where invasive species may be suppressing the densities of individuals below thresholds of detectability but without causing extirpation or extinction (Morrison et al., 2004).

The 540 km² Pacific island of Guam is well known for its high proportion of non-indigenous species and the environmental and socio-economic damage they cause (Rodda et al., 1997). The ecosystem of this small island is regarded as an example of invasional meltdown, a self-reinforcing mutualism in which the presence of certain non-indigenous species promotes the establishment of other non-indigenous species (Simberloff & Von Holle, 1999; Christy et al., 2007; Rogers et al., 2012). Among the numerous non-indigenous animals now present on Guam, some of the most notorious and damaging are the brown treesnake *Boiga irregularis*, invasive rats *Rattus* spp., house mouse *Mus musculus*, marine toad *Rhinella marina*, musk shrew *Suncus murinus*, curious skink *Carlia ailanpalai*, coconut rhinoceros beetle *Oryctes rhinoceros*, and the little fire ant *Wasmannia auropunctata* (Fritts & Rodda, 1998; Raymundo & Miller, 2011; Marshall et al., 2017). These and other species have contributed to the dramatic decline, extirpation or extinction of Guam's indigenous birds (Savidge, 1987), lizards (Rodda & Fritts, 1992) and mammals (Wiles, 1987).

However, not all species that have been lost from Guam are globally extinct. A small barrier islet known as Dãno' in the local Chamorro language (colloquially known as Cocos Island) is located 1.6 km off the southern tip of Guam and now serves as both a natural and artificial repository for many taxa that no longer survive on Guam (Fig. 1). Dãno' is the raised portion (0.39 km²) of the submerged Merizo Barrier Reef (Tracey et al., 1964). Because of its location on an outer reef, some of the terrestrial invasive species present on Guam have not become established on Dãno', most notably

JONATHAN Q. RICHMOND (Corresponding author, orcid.org/0000-0001-9398-4894) and ROBERT N. FISHER (orcid.org/0000-0002-2956-3240) U.S. Geological Survey, Western Ecological Research Center, 4165 Spruance Rd. Suite 200, San Diego, California 92106, USA. E-mail jrichmond@usgs.gov

ELIJAH WOSTL (orcid.org/0000-0003-0746-007X) St. Edward's University–John Brooks Williams Natural Science Center, Austin, USA

ROBERT N. REED (orcid.org/0000-0001-8349-6168) U.S. Geological Survey, Pacific Island Ecosystems Research Center, Hawai'i Volcanoes National Park, Hawaii, USA

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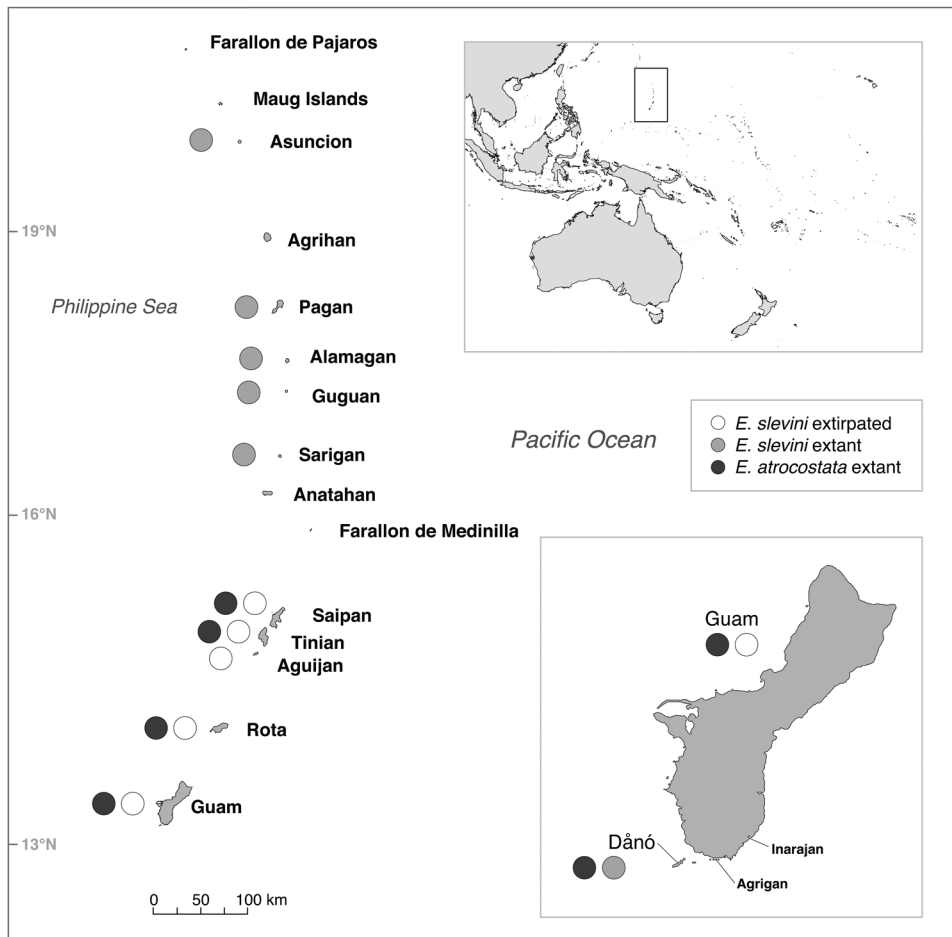


FIG. 1 Distribution of the Mariana skink *Emoia slevini* in the Mariana Islands, showing islands where it is presumed to be extirpated, islands with extant populations, and islands with known extant populations of *Emoia atrocostata*.

the brown treesnake. However, brown treesnakes have been sighted, hand captured, or caught in snake traps on Dãno' since 1988, suggesting that the islet remains vulnerable to introductions (U.S. Geological Survey, unpubl. data.).

Human land use has drastically altered the habitat on Dãno' but much of it remains forested (Neubauer & Neubauer, 1981; McCoid et al., 1995; Ehrhard, 2016). The islet harbours seven habitat types; resort/horticulture, *Casuarina* forest, mixed strand forest, *Pemphis acidula* scrub, *Scaevola* scrub, sand/open areas, and an interior that supports two small wetlands (c. 0.1 ha in total) maintained by subterranean freshwater (Ayers & Vacher, 1986). Native species persisting on the island but that are now absent or at low densities on Guam include the Micronesian starling *Aplonis opaca*, an introduced population of the Guam rail *Hypotaenidia owstoni* (categorized as endangered under the U.S. Endangered Species Act; U.S. Fish & Wildlife Service, 1984, and Critically Endangered on the IUCN Red List; BirdLife International, 2019), breeding seabirds, and several lizard species that have declined or been extirpated on Guam. The island also supports or has supported several invasive and/or predatory species including *Rattus exulans*, the monitor lizard *Varanus tsukamotoi* (recently identified as a

species endemic to the Marianas; Weijola et al., 2019), *R. marina*, *C. ailanpalai* and possibly *M. musculus*.

Prior to the introduction of the Guam rail to Dãno', the Guam Department of Agriculture and the U.S. Department of Agriculture Wildlife Services eradicated *R. exulans* in 2009 (Lujan et al., 2010). The population of *V. tsukamotoi* was also culled via trapping and shooting to promote re-establishment of *H. owstoni*; after 11 months of trapping and shooting in 2011–2012, the estimated density of *V. tsukamotoi* was reduced from 6.3 lizards per hectare to 1.0 per ha (Ehrhard, 2016). Control of monitor lizards has continued at varying levels of intensity since this time.

The Mariana skink *Emoia slevini* (Åchi ak in Chamorro; Plate 1a) is endemic to the Mariana Islands and is historically known from Guam and Dãno' (Brown & Falanruw, 1972; Brown, 1991). It has been documented on 10 islands (from south to north: Dãno', Guam, Rota, Aguijan, Tinian, Sarigan, Guguan, Alamagan, Pagan and Asuncion), but a recent summary suggested that it persists on only five of these (Sarigan, Guguan, Alamagan, Pagan and Asuncion; USFWS, 2015; Fig. 1). Both the IUCN and U.S. Fish & Wildlife Service list the species as Critically Endangered because of its limited range, recent extirpations on some islands, and presumed

declines on islands where it still occurs (Allison et al., 2013; U.S. Fish & Wildlife Service, 2015). Prior to our study, the last verifiable records for *E. slevini* on Guam and Dãno' were from 1945 and 1993, respectively (McCoid et al., 1995). Dãno' is also the type locality for *E. slevini*, and prior to recent molecular work, its closest evolutionary affinities based on colour pattern and size were presumed to be with *E. boettgeri* and *E. arnoensis* from the Caroline and Marshall Islands (Brown & Falanruw, 1972; Brown, 1991).

In January 2011, c. 21 months after rodent removal and reduction of the monitor lizard population, we observed what appeared to be *E. slevini* in a small, forested area of Dãno'. Successive visits over the next 2 years resulted in more observations of the species, and in 2014 we non-lethally collected tail tissue from four individuals and used DNA sequence data to verify their identity by comparing results to archived tissue samples of *E. slevini* collected on Sarigan and Alamagan, located 377 and 653 km north of Guam, respectively. Both islands are part of the Commonwealth of the Northern Mariana Islands and are currently uninhabited (Fig. 1). At the time of our study, these samples represented all known tissues available for DNA sequencing of this rare, endemic species in the Mariana Islands.

Methods

Taxon and field sampling

Emoia slevini is one of 78 currently recognized species of *Emoia* and a member of the *Emoia atrocostata* species group (Brown, 1991; Plate 1). Richmond et al. (2021) used DNA sequence data to revise the group's membership to include seven nominal taxa: *E. adspersa*, *E. lawesi*, *E. arnoensis*, *E. atrocostata*, *E. boettgeri*, *E. laobaoense*, *E. nativitatis* and *E. slevini* (Fig. 2). *Emoia adspersa* and *E. lawesi* are endemic to Samoa and nearby islands in Polynesia (Schwaner & Brown, 1984) and *E. arnoensis* and *E. boettgeri* are endemic to the Marshall and Caroline islands in Micronesia (Brown & Marshall, 1953). Brown & Falanruw (1972) speculated that *E. slevini* is most closely related to *E. boettgeri*, based on morphological similarity and proximity of the Caroline and Marshall Islands to the Marianas. *Emoia laobaoense* is known from only two specimens collected at a single locality in Viet Nam but has not been observed since its discovery in 1937 (Bourrett, 1937). *Emoia nativitatis* is endemic to Christmas Island in the Indian Ocean and was last observed in the wild in late 2009 (Andrew et al., 2018; Fig. 2). Richmond et al. (2021) identified four regional clades within the wide-ranging *E. atrocostata*, which they treated as provisional species. One of these is endemic to the Mariana Islands.

For this study, we added sequence data from the 2014 tissue samples of *E. slevini* from Dãno' and Alamagan to



PLATE 1 Representatives of (a) the Mariana skink *Emoia slevini* and (b) the littoral skink *Emoia atrocostata* from Dãno'.

the dataset of Richmond et al. (2021), which included sequences from *E. slevini* previously collected on Sarigan (Smithsonian National Museum of Natural History 536082 and 536083) and from *E. atrocostata* previously collected on Dãno' and Guam. The original dataset had multiple representatives of all members of the *atrocostata* group except for *E. laobaoense*, and multiple representatives of three out-group species in the *E. cyanogaster* group (Brown, 1991).

We also added three new tissue samples of *E. atrocostata* that we collected on Agrigan, a smaller islet c. 7 km east of Dãno', and three tissue samples from two coastal sites on Saipan, c. 190 km north of Guam. To compare amounts of sequence divergence among all *Emoia* occurring on Dãno' and Guam, we sequenced samples of *E. cyanura* and *E. caeruleocauda* from Dãno' and a second sample of *E. caeruleocauda* from Guam; both are common, widespread species of *Emoia* and are members of the *cyanura* species group (Brown, 1991). *Emoia cyanura* is extirpated on Guam, but there is uncertainty as to whether it was native to the Marianas because the only records are from a single locality on Guam and no voucher specimens were ever collected (Rodda et al., 1991).

We captured all newly collected specimens using adhesive traps placed in shaded areas where we observed lizards foraging (Trapper Max Free, Bell Laboratories,

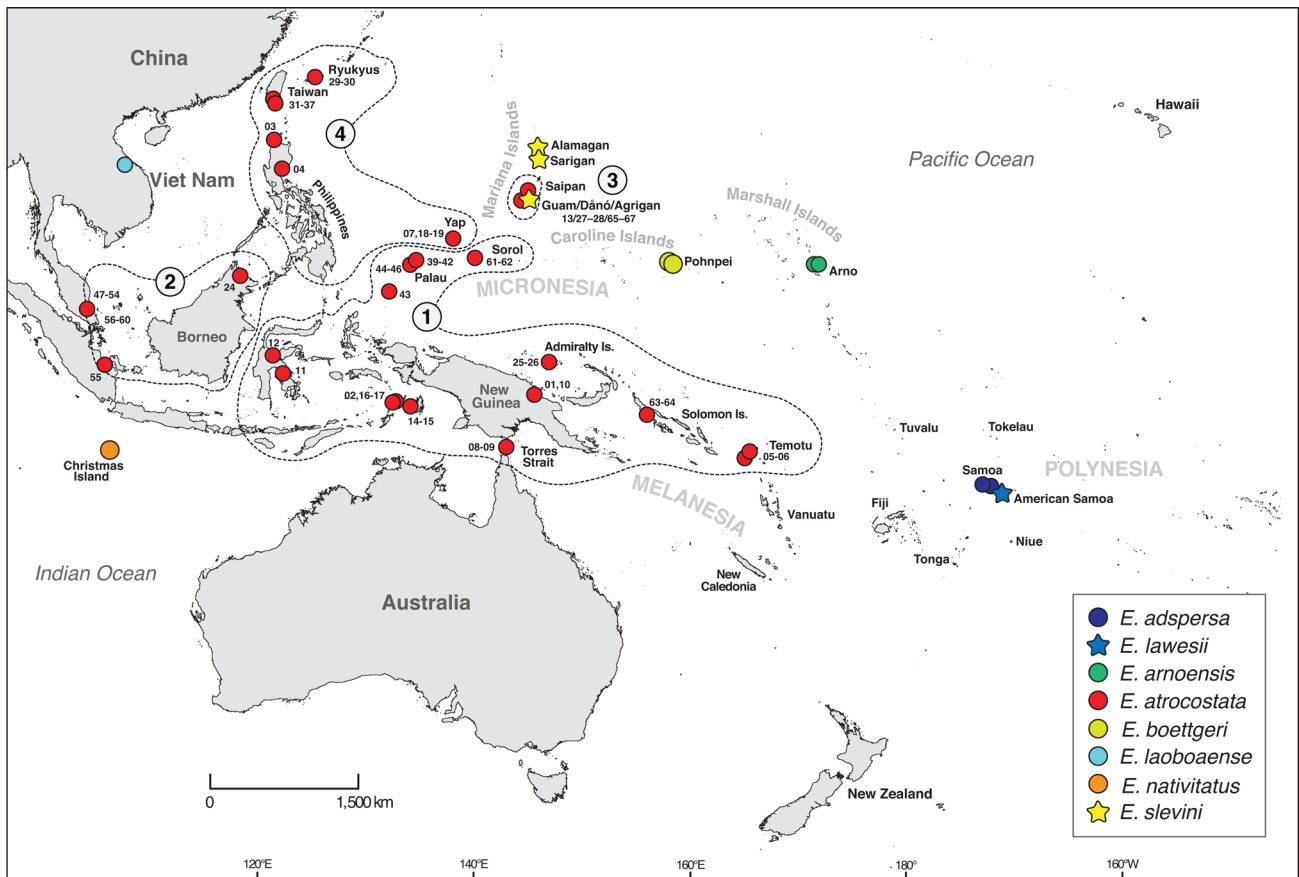


FIG. 2 Sampling map for the phylogenetic analysis of the *atrocostata* group. Numbered polygons indicate the major regional lineages of *E. atrocostata* (figure modified from Richmond et al., 2021; Fig. 3); numbered sampling sites indicate *E. atrocostata* included in the phylogenetic analyses (numbers correspond to branches on the mitochondrial genealogy; Fig. 3).

Windsor, USA; see also Rodda et al., 1993). Lizards were removed from the traps using vegetable oil, which degrades the adhesive, and released on site after taking photographic voucher records. We removed c. 10–15 mm of tail and stored the tissue samples in 95% ethanol until the DNA could be extracted. Locality data for all samples are in Supplementary Table 1.

DNA sequencing

We extracted DNA from tail clips using a Qiagen DNeasy Blood and Tissue Kit (Qiagen, Germantown, USA) and sequenced the following genes: mitochondrial NADH₂ gene (*ND2*) and adjacent tRNAs (*tRNA-trp* and *-ala*) and three nuclear genes: *RAG1*, *Cmos*, and *R35*. We sequenced these genes for consistency with a larger, more comprehensive dataset that includes nearly all species of *Emoia* (authors, unpubl. data). Primer sequences, PCR reagents, and cycling conditions are detailed in Supplementary Material 1. PCR products were subjected to Sanger dideoxy sequencing using an ABI PRISM 3730 Analyzer (Applied Biosystems, Waltham, USA) at Genewiz, Inc. (La Jolla, USA). We edited

the raw sequences using *Sequencher 5.0* (Gene Codes Corp., Ann Arbor, USA) and manually aligned them by eye.

Phylogenetic analysis

We first compared the patristic (*p*) distances among mtDNA haplotypes from separate island populations of *E. slevini* and among different species in the *atrocostata* group using *DNA_{sp} 6* (Rozas et al., 2017). We did not compare the *p*-distances based on nuclear alleles because of their high sequence similarity, and instead report only the number of substitutions by which the alleles differed.

To place *E. slevini* within the broader evolutionary history of the *atrocostata* group and contextualize the relationships among different island populations, we estimated both a mitochondrial genealogy and the most probable species tree from the set of genealogies inferred for each nuclear and mitochondrial locus (Maddison, 1997; Knowles & Carstens, 2007). A detailed description of the phylogenetic methods can be found in Richmond et al. (2021). Data partitions and respective substitution models are provided in Supplementary Table 3. We inferred the mitochondrial

TABLE 1 Uncorrected pairwise p -distances for *ND2* haplotypes of *Emoia slevini* collected in the Mariana Islands. A zero value indicates identical sequences. Species codes are the first two letters of the genus and species, respectively¹. Numerical identifiers following the species code indicate localities (Supplementary Table 1).

Location		EMAT 13	EMAT 27	EMAT 66	EMAT 68	EMSL 01	EMSL 02	EMSL 03	EMSL 07	EMCY 05	EMCA 09
Dãno'	EMAT 13	–									
Guam	EMAT 27	0.0000	–								
Agrigan	EMAT 66	0.0106	0.0106	–							
Saipan	EMAT 68	0.0048	0.0048	0.0097	–						
Sarigan	EMSL 01	0.0077	0.0077	0.0048	0.0068	–					
Sarigan	EMSL 02	0.0087	0.0087	0.0058	0.0077	0.0029	–				
Dãno'	EMSL 03	0.0106	0.0106	0.0039	0.0097	0.0048	0.0058	–			
Alamagan	EMSL 07	0.0087	0.0087	0.0058	0.0077	0.0029	0.0000	0.0058	–		
Dãno'	EMCY 05	0.2203	0.2203	0.2251	0.2203	0.2261	0.2261	0.2261	0.2261	–	
Guam	EMCA 09	0.2406	0.2406	0.2425	0.2416	0.2425	0.2454	0.2435	0.2454	0.2106	–
Dãno'	EMCA 19	0.2416	0.2416	0.2435	0.2425	0.2435	0.2464	0.2444	0.2464	0.2116	0.0010

¹EMAT, *Emoia atrocostata*; EMSL, *Emoia slevini*; EMCY, *Emoia cyanura*; EMCA, *Emoia caeruleocauda*.

genealogy using *MrBayes 2.3* (Ronquist et al., 2012) and estimated divergence times and the species tree using *BEAST 2* (Bouckaert et al., 2014). To calculate divergence times, we allowed the substitution rate to vary independently on each tree branch according to a log-normally distributed rate prior for the *ND2* gene (median = 0.0235 substitutions/site/MY, 95% highest posterior density 0.0134–0.0336), which was estimated using an island-age calibration (Richmond et al., 2021). The species tree analysis required that the sequences from all samples be assigned to a particular species; we followed Richmond et al. (2021) in treating four regional clades recovered within *E. atrocostata* as candidate species and considered the remaining nominal species as valid.

Results

Haplotype and allelic diversity

All *ND2* sequences of *E. slevini* from Dãno' were identical to each other but had unique substitutions compared to two haplotypes from Sarigan, one of which was identical to the single haplotype from Alamagan. These three *E. slevini* haplotypes differed from each other by only three substitutions and were most similar to haplotypes of *E. atrocostata* from Agrigan, from which they differed at only six sites. In contrast, haplotypes of *E. slevini* differ markedly from the two other co-occurring and more ecologically similar species of skink on Dãno' (*E. caeruleocauda* and *E. cyanura*) and Guam (*E. caeruleocauda* only). Uncorrected pairwise p -distances for *ND2* haplotypes collected in the Marianas are shown in Table 1, and a list of haplotypes by name and location are provided in Supplementary Table 2.

As expected, based on the limited mtDNA sequence divergence, there was little variation at the three nuclear loci among samples of *E. slevini* from Dãno' and Sarigan,

and none could distinguish individuals between the two islands. Because of this lack of variation, and added cost, we did not sequence the nuclear loci for the Alamagan samples as mtDNA were sufficient for our purposes. For those samples with nuclear sequence data, we detected (1) three alleles for *Cmos*, one of which was unique to Sarigan, (2) two alleles for *RAG-1*, with one unique to Sarigan, and (3) two alleles for *R35*, both occurring on Dãno' and only one on Sarigan. The number of polymorphic sites was three, two and two for *Cmos*, *RAG-1* and *R35*, respectively.

Phylogenetics

The mtDNA genealogy suggests a close relationship between the Dãno', Sarigan and Alamagan populations of *E. slevini* and that they diverged from a common ancestor c. 0.27 MYA (range 0.14–0.40; Fig. 3 inset). We also found strong posterior support for a close relationship between *E. slevini* and the Mariana lineage of *E. atrocostata*, such that the haplotypes belonging to either species were paraphyletic with respect to each other. Divergence estimates indicate that the two species separated from a common ancestor c. 0.48 MYA (range 0.29–0.68). Together, these two species are the sibling to *E. arnoensis*, an endemic to the Marshall and Caroline Islands, with all three diverging from a shared ancestor c. 2.78 MYA (range 2.07–3.49; see also Supplementary Fig. 1 for an ultrametric tree with branch lengths scaled according to time).

Topologies of the nuclear gene genealogies were predictably less resolved than the mtDNA genealogy because of the many fewer phylogenetically informative sites (not shown), with each genealogy showing close relatedness between *E. slevini* and the Mariana lineage of *E. atrocostata*. The most probable species tree based on the multispecies coalescent model from this set of genealogies places *E. slevini* as the sibling to the Mariana lineage of *E. atrocostata*, with high posterior support (Fig. 4).

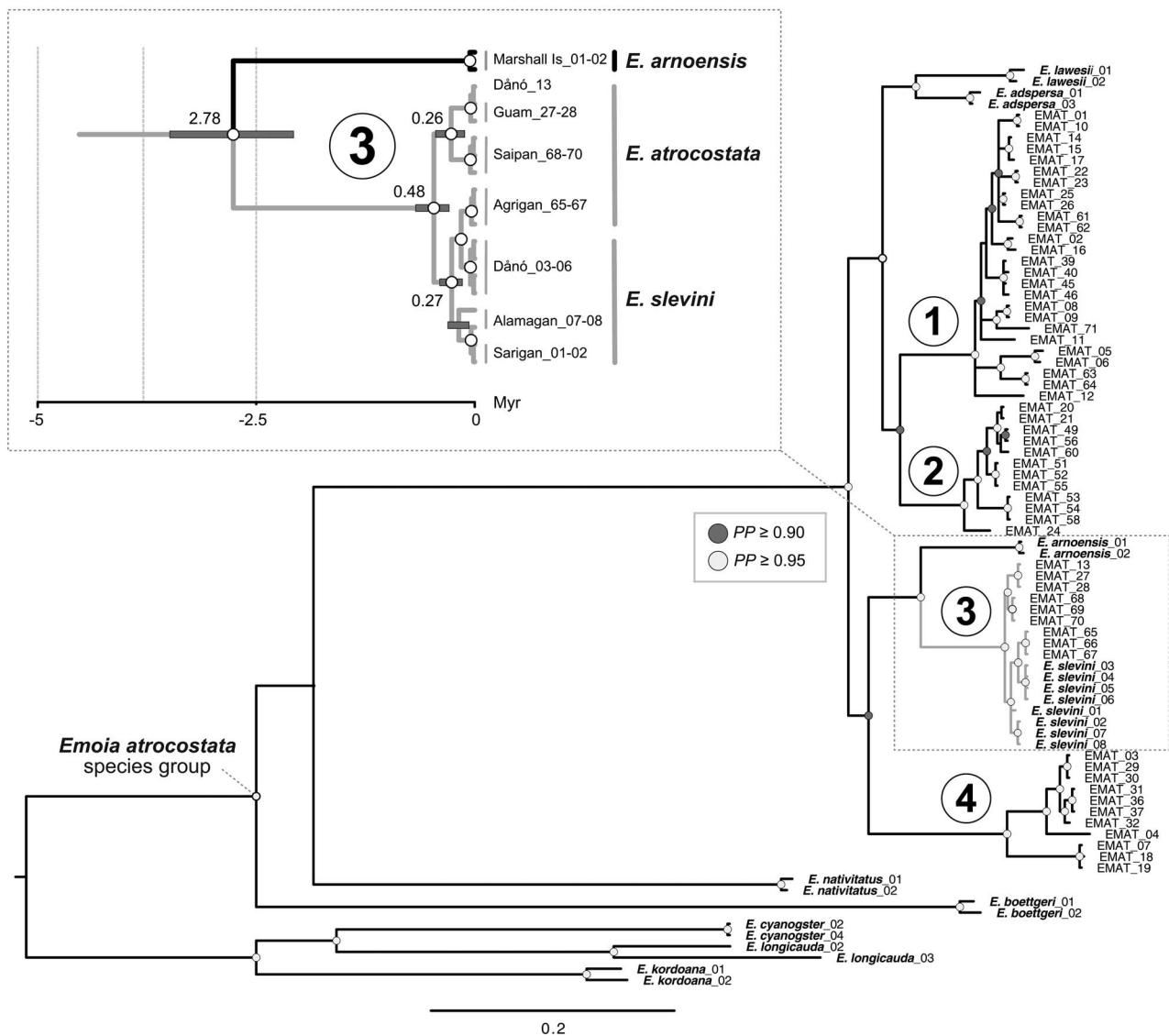


FIG. 3 Mitochondrial genealogy (50% majority consensus tree, branch lengths scaled according to substitutions; PP = posterior probability). The major regional lineages (1–4) of *E. atrocostata* (EMAT) correspond to the following biogeographical regions: (1) Wallacea, Sahul Shelf, and western Caroline Basin, (2) Sunda Shelf, (3) Mariana Islands, and (4) Philippines, Taiwan, Ryukyu Islands and western Caroline Basin (Fig. 2). Inset shows a close-up of the Mariana lineage, described in the text, with branch lengths scaled according to time in millions of years (grey bars indicate the 95% highest posterior density for the age estimates; numbers on the branches indicate the median of the 95% highest posterior density in millions of years).

Discussion

Samples of the recently detected *Emoia* from Dãno' are close genetic matches to *E. slevini* from Sarigan and Alamagan, confirming they are *E. slevini* and that the species has apparently persisted at low density on Dãno' for > 2 decades. The population may be recovering, with individuals now dispersed after being confined to an area of < 300 m² at the time of the 2011 rediscovery. Rodent eradication appears to be the most likely cause of the recovery of the Mariana skink, but suppression of *V. tsukamotoi* and/or other as yet unquantified factors may have also contributed. These

findings suggest that *E. slevini* could potentially be surviving on other islands in the northern Marianas where the species is currently considered extirpated or where a lack of records has been accepted as a true gap in its distribution (Rodda et al., 1991; McCoid et al., 1995; Reed et al., 2010).

The mitochondrial haplotypes and nuclear alleles belonging to *E. slevini* and *E. atrocostata* display a bush-like rather than a tree-like phylogenetic structure as a result of their recent shared ancestry. Speciation is a protracted process such that diverging populations will share a high proportion of the same or similar alleles for extended periods of time until genetic drift and mutations sort the alleles by species (referred to as lineage

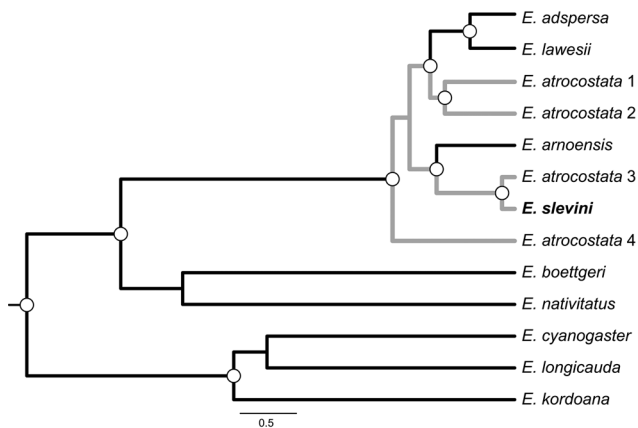


FIG. 4 Species tree inference based on the multi-species coalescent of all gene genealogies. Nodes with circles indicate posterior branch support of ≥ 0.90 . Numbers 1–4 indicate the major regional lineages of *E. atrocostata* (Figs 2 & 3).

sorting; Hudson & Coyne, 2002; Knowles & Carstens, 2007). For slower evolving, bi-parentally inherited nuclear genes, the process is often considerably slower than for rapidly evolving and maternally inherited mitochondrial genes. In these two closely related species, speciation is so recent that the sorting of genetic variation at the targeted loci is incomplete, leading to interdigitating branches in the phylogenetic tree.

Factors determining the distribution of *E. slevini*

The patchy distribution and decline of *E. slevini* in the Mariana Islands remain enigmatic, as no obvious pattern exists with respect to underlying causes (McCoid et al., 1995; Fig. 1). The species has shown a positive response to the removal of invasive ungulates (pigs *Sus scrofa* and goats *Capra hircus*) on Sarigan, which has the highest detection rates for *E. slevini* of any island reported to date (Kessler, 2002, 2011). Recovery of the species on Sarigan may be primarily a result of forest regeneration following ungulate removal. Our observations on Dãno' suggest that an even greater response could occur if *R. exulans* were eradicated from Sarigan.

In New Zealand, negative effects of invasive rodents on the lizard fauna are well documented, with data indicating that severity is dependent on island size, degree of habitat modification, accessibility to refuge habitat, and length of time since the introduction (Whitaker, 1973; Towns, 1991, 1994, 1996; Newman, 1994). In Fiji, endemic iguanas had increased recruitment after eradication of rats and goats (Fisher et al., 2019). Predation by introduced rodents also appears to be an important issue for lizard conservation in New Caledonia, as some threatened species have been shown to be regular prey items of the ship rat *Rattus rattus* and *R. exulans* (Thibault et al., 2017).

Emoia slevini and *V. tsukamotoi* are currently the only endemic species of reptile in the Mariana Islands (Brown & Falanruw, 1972; Rodda et al., 1991; Weijola et al., 2019). However, data from this study and Richmond et al. (2021) suggest that *E. cf. atrocostata* in the Marianas is a probable third endemic species that merits further attention. Little is known about its distribution and status on other islands (Fig. 1); currently it is known from Dãno', Guam, Rota, Tinian and Saipan. On Guam, populations persist on small barrier islets (e.g. Agrigan, Fig. 1) at the outer margins of lagoons along the southern edge of the island (Perry et al., 1998; Reed et al., 2007; this study) where they may not be subject to predation by the brown treesnake or other predators.

Other pertinent rediscoveries involving introduced species

Several species of *Emoia* have been rediscovered on other Pacific islands in recent years, suggesting that at least some can survive at low abundance in the presence of invasive species and/or are capable of finding refugia that insulate them from predation and/or competition. Both phenomena helped explain the 10-fold increase in capture rates for the shore skink *Oligosoma smithi* in the third year following rat eradications on Korapuki Island, New Zealand, and why other species that coexisted with rats showed changes in both range and productivity once rats were eradicated (Towns, 1991).

The introduced big-headed ant *Pheidole megacephala* was implicated in the decline and presumed extirpation of *Emoia impar* in the Hawaiian Islands in the early 1900s (Fisher & Ineich, 2012). However, in 2000 *E. impar* was recorded on the offshore islet of Mōkapu, Moloka'i, where an apparently stable and presumably native population now persists, possibly because the islet lacks *P. megacephala* (Wood et al., 2013). Similarly, the Fiji barred tree skink *Emoia trossula* was thought to be extirpated from Vanua Levu, where invasive mammals have been implicated as the primary culprit, but a single individual was observed (and possibly a second one) in 2015 in old growth lowland rain forest (Clause et al., 2018). This suggests that tracts of interior forest may in some cases shelter native species against exposure to invasive rats and mongooses (Olson et al., 2006; Clause et al., 2018).

Rediscoveries of *Emoia* in various parts of the Pacific also offer hope for survival of *E. atrocostata* (described as *E. sinus*) and the endemic *E. nativitatis* on Christmas Island in the Indian Ocean (Fig. 2); both are presumed to have recently gone extinct. Smith et al. (2012) speculated that increased abundance of the yellow crazy ant *Anoplolepis gracilipes* and giant centipede *Scolopendra subspinipes* since the 1990s, combined with the introduction and spread of the

Asian wolf snake *Lycodon capucinus* during a period of unusually dry weather, caused the disappearance of the two *Emoia*. If these skinks are persisting at low densities, then local eradication of invasive predators may facilitate their recovery. Eradication campaigns targeting the yellow crazy ant *A. gracilipes* and big-headed ant *P. megacephala* have had some success, with the highest proportion of successes worldwide occurring for *P. megacephala* (78% of all documented attempts; see reviews in Hoffman et al., 2016). Whether these or other invasive ants pose severe problems in the Marianas is unknown, as the ant communities are poorly characterized for most islands.

Refugia as safeguard against extinction

On biogeographical grounds, a reasonable assumption is that the reptile populations on Dãno' originated from Guam, because of its proximity and larger size (Rodda et al., 1991). This displacement of taxa away from Guam and the recent resurfacing of *E. slevini* are consistent with the range eclipse hypothesis, which predicts that rediscoveries will occur at the edges of a species' pre-decline range if threats emanate from the interior and force populations into more secure, peripheral habitats (Channell & Lomolino, 2000; Hemerik et al., 2006; Fisher, 2011). A similar pattern exists for New Zealand biota, where losses in biodiversity would be even higher if relict populations were unable to survive on offshore islands that are beyond the dispersal reach of invasive species (Daugherty et al., 1990; Towns, 2002).

Dãno' has become a valuable refuge for endemic biodiversity that either has been lost or is declining in the Marianas, particularly on Guam. There are nine indigenous species of reptiles that historically occurred on both islands (Rodda et al., 1991); four are now extirpated on Guam, but all persist on Dãno'. In addition to *E. slevini*, the extirpated species on Guam include *E. cyanura*, the snake-eyed skink *Cryptoblepharus poecilopleurus*, and the Micronesia saw-tailed gecko *Perochirus ateles* (Rodda et al., 1991). Dãno' also supports the Micronesian starling *Aplonis opaca* (rare on Guam but abundant elsewhere in the Marianas) and a reintroduced population of the Critically Endangered flightless Guam rail *H. owstoni*.

Success in the restoration and enhancement of the Dãno' ecosystem provides new inspiration for efforts to conserve and restore Guam's biodiversity. It also emphasizes a need for caution in declaring a species extinct or extirpated, as this could detract from surveys that lead to rediscoveries. Alternatively, the rediscovery of a species believed to be extirpated or extinct could spur unsupported optimism for future survival, or perhaps draw the attention of unscrupulous collectors once the rediscoveries are made public (Scheffers et al., 2011; Meijaard & Nijman, 2014; Caviedes-Solis et al., 2015). Although the short-term suitability of Dãno' as a biodiversity refuge has been proven, its long-term status is tenuous. The

total island area is 37 ha, with a maximum elevation of 2 m, and only c. 33% of the island is native atoll forest (McCoid, 1996). This small size and low topographic relief make it susceptible to overwash during typhoons. When combined with the persistent threat of non-indigenous species on Guam, these populations of *Emoia* probably remain at high risk of extirpation. Translocating individuals to managed assurance colonies and/or other offshore islets, parts of Guam, or even other islands in the Marianas merits consideration.

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Conflicts of interest None.

Ethical standards This study complies with the *Oryx* guidelines on ethical standards and those outlined in *Animal Behaviour* (2001) 61, 271–275. Non-lethal tissue sampling was conducted under scientific collecting permits issued to JQR and RNR by the Guam Department of Agriculture/Division of Aquatic and Wildlife Resources and the Commonwealth of the Northern Mariana Islands Division of Fish and Wildlife. Lizards were released at the point of capture and tissue samples from *E. slevini* were collected prior its listing under the U.S. Endangered Species Act of 1973.

References

- ALLISON, A., FISHER, R.N., HAMILTON, A. & TALLOWIN, O. (2013) *Emoia slevini*. In *The IUCN Red List of Threatened Species* 2013. [dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T196621A2467313.en](https://doi.org/10.2305/IUCN.UK.2013-1.RLTS.T196621A2467313.en) [accessed 19 May 2021].
- ANDREW, P., COGGER, H., DRISCOLL, D., FLAKUS, S., HARLOW, P., MAPLE, D. et al. (2018) Somewhat saved: a captive breeding program for two endemic Christmas Island lizard species, now extinct in the wild. *Oryx*, 52, 171–174.
- AYERS, J.F. & VACHER, H.L. (1986) Hydrogeology of an atoll island: a conceptual model from detailed study of a Micronesian example. *Groundwater*, 24, 185–198.
- BIRDLIFE INTERNATIONAL (2019) *Hypotaenidia owstoni*. The IUCN Red List of Threatened Species 2019. [dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T22692441A156506469.en](https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T22692441A156506469.en) [accessed 15 July 2021].
- BOUCKAERT, R., HELED, J., KÜHNERT, D., VAUGHAN, T., WU, C.-H. et al. (2014) BEAST 2: a software platform for Bayesian evolutionary analysis. *PLOS Computational Biology*, 10, e1003537.
- BOURRETT, R. (1937) Notes herpetologiques sur L'Indochine Française, XII. Les lézards dela collection du laboratoire des sciences naturelles de l'université. *Annexe au Bulletin Général de l'Instruction Publique*, 1937, 1–25.

- BROWN, W.C. (1991) Lizards of the genus *Emoia* (Scincidae) with observations on their evolution and biogeography. *Memoirs of the California Academy of Sciences*, 15, 1–94.
- BROWN, W.C. & FALANRUW, M.V.C. (1972) A new lizard of the genus *Emoia* (Scincidae) from the Marianas Islands. *Proceedings of the California Academy of Sciences*, 39, 105–110.
- BROWN, W.C. & MARSHALL, J. (1953) New scincoid lizards from the Marshall Islands, with notes on their distribution. *Copeia*, 1953, 201–207.
- BUTCHART, S.H.M., LOWE, S., MARTIN, R.W., SYMES, A., WESTRIP, J.R.S. & WHEATLEY, H. (2018) Which bird species have gone extinct? A novel quantitative classification approach. *Biological Conservation*, 227, 9–18.
- CAVIEDES-SOLIS, I.W., VÁZQUEZ-VEGA, L.F., SOLANO-ZAVALA, I., PÉREZ-RAMOS, E., ROVITO, S.M., DEVITT, T.J. et al. (2015) Everything is not lost: recent records, rediscoveries, and range extensions of Mexican hylid frogs. *Mesoamerican Herpetology*, 2, 230–241.
- CHANNELL, R. & LOMOLINO, M.V. (2000) Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. *Journal of Biogeography*, 27, 169–179.
- CHRISTY, M.T., SAVIDGE, J.A. & RODDA, G.H. (2007) Multiple pathways for invasion of anurans on a Pacific island. *Diversity and Distributions*, 13, 598–607.
- CLAUDE, A.G., THOMAS-MOKO, N., RASALATO, S. & FISHER, R.N. (2018) All is not lost: herpetofaunal ‘extinctions’ in the Fiji Islands. *Pacific Science*, 72, 321–328.
- DAUGHERTY, C.H., TOWNS, D.R., ATKINSON, I.A.E. & GIBBS, G.W. (1990) The significance of the biological resources of New Zealand islands for ecological restoration. In *Ecological Restoration of New Zealand Islands* (eds D.R. Towns, C.H. Daugherty & I.A.E. Atkinson), pp. 9–21. Conservation Sciences Publication 2, Wellington, New Zealand.
- DURSO, A.M., WILLSON, J.D. & WINNE, C.T. (2011) Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. *Biological Conservation*, 144, 1508–1515.
- EHRHARD, S.P. (2016) *Dietary behavior of the mangrove monitor lizard (Varanus indicus) on Cocos Island, Guam, and strategies for Varanus indicus eradication*. MSc thesis. University of Hawaii at Hilo, Hawaii, USA.
- FISHER, D.O. (2011) Trajectories from extinction: where are missing mammals rediscovered? *Global Ecology and Biogeography*, 20, 415–425.
- FISHER, D.O. & BLOMBERG, S.P. (2011) Correlates of rediscovery and the detectability of extinction in mammals. *Proceedings of the Royal Society B: Biological Sciences*, 278, 1090–1097.
- FISHER, R.N. & INEICH, I. (2012) Cryptic extinction of a common Pacific lizard *Emoia impar* (Squamata, Scincidae) from the Hawaiian Islands. *Oryx*, 46, 187–195.
- FISHER, R.N., NIUKULA, J., HARLOW, P., RASALATO, S., CHAND, R., THAMAN, B. et al. (2019) Community-based conservation and recovery of native species on Monuriki Island, Fiji. In *Island Invasives: Scaling Up to Meet the Challenge* (eds C.R. Veitch, M.N. Clout, A.R. Martin, J.C. Russell & C.J. West), pp. 552–557. Occasional Paper of the IUCN Species Survival Commission No. 62, Gland, Switzerland, IUCN.
- FRITTS, T.H. & RODDA, G.H. (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annual Review of Ecology and Systematics*, 29, 113–140.
- HEMERIK, L., HENGEVELD, R. & LIPPE, E. (2006) The eclipse of species ranges. *Acta Biotheoretica*, 54, 255–266.
- HOFFMAN, B.D., LUQUE, G.M., BELLARD, C., HOLMES, N.D. & DONLAN, C.J. (2016) Improving invasive ant eradication as a conservation tool: a review. *Biological Conservation*, 198, 37–49.
- HUDSON, R.R. & COYNE, J.A. (2002) Mathematical consequences of the genealogical species concept. *Evolution*, 56, 1557–1565.
- JONES, H.P., HOLMES, N.D., BUTCHART, S.H., TERSHY, B.R., KAPPES, P.J. et al. (2016) Invasive mammal eradication on islands results in substantial conservation gains. *Proceedings of the National Academy of Sciences*, 113, 4033–4038.
- KESSLER, C.C. (2002) Eradication of feral goats and pigs and consequences for other biota on Sarigan Island, commonwealth of the Northern Mariana Islands. In *Turning the Tide: The Eradication of Invasive Species* (eds C.R. Veitch & M.N. Clout), pp. 132–140. IUCN, Species Survival Commission, Invasive Species Specialist Group, Gland, Switzerland and Cambridge, UK.
- KESSLER, C.C. (2011) Invasive species removal and ecosystem recovery in the Mariana Islands; challenges and outcomes on Sarigan and Anatahan. In *Island Invasives: Eradication and Management* (eds C.R. Veitch, M.N. Clout & D.R. Towns), pp. 320–324. IUCN, Gland, Switzerland.
- KNOWLES, L.L. & CARSTENS, B.C. (2007) Delimiting species without monophyletic gene trees. *Systematic Biology*, 56, 887–895.
- LADLE, R., JEPSON, P., MALHADO, A.C., JENNINGS, S. & BARUA, M. (2011) The causes and biogeographical significance of species’ rediscovery. *Frontiers of Biogeography*, 3, 111–118.
- LEE, T.E., FISHER, D.O., BLOMBERG, S.P. & WINTLE, B.A. (2017) Extinct or still out there? Disentangling influences on extinction and rediscovery helps to clarify the fate of species on the edge. *Global Change Biology*, 23, 621–634.
- LUJAN, D.T., VICE, D.S., GUERRERO, J.P. & CANDASO, C.C. (2010) Rodent eradication on Cocos Island, Guam: integrating wildlife damage management, resort operations, and non-target concerns. *Proceedings of the 24th Vertebrate Pest Conference*, 24, 9–13.
- MADDISON, W.P. (1997) Gene trees in species trees. *Systematic Biology*, 46, 523–536.
- MARSHALL, S.D.G., MOORE, A., VAQALO, M., NOBLE, A. & JACKSON, T.A. (2017). A new haplotype of coconut rhinoceros beetle, *Oryctes rhinoceros*, has escaped biological control by *Oryctes rhinoceros* Nudivirus and is invading Pacific Islands. *Journal of Invertebrate Pathology*, 149, 127–134.
- MCCOID, M.J. (1996) Effect of typhoons on the lizard community of a shelf atoll. *Atoll Research Bulletin*, 439, 1–5.
- MCCOID, M.J., RODDA, G.H. & FRITTS, T.H. (1995) Distribution and abundance of *Emoia slevini* (Scincidae) in the Mariana Islands. *Herpetological Review*, 26, 70–72.
- MEIJAARD, E. & NIJMAN, V. (2014) Secrecy considerations for conserving Lazarus species. *Biological Conservation*, 175, 121–124.
- MORRISON, C., NAIKATINI, A., THOMAS, N., ROUNDS, I. & THAMAN NIUKULA, B. (2004) Rediscovery of an endangered frog *Platymantis vitianus*, on mainland Fiji: implications for conservation and management. *Pacific Conservation Biology*, 10, 237–240.
- NEUBAUER, C.P. & NEUBAUER, D.R. (1981) The vegetation of Cocos Island, Guam. In *Plant Biogeography of Guam* (ed. C.L. Raulerson), pp. 23–39. University of Guam Marine Laboratory Technical Report, 69, Mangilao, Guam.
- NEWMAN, D.G. (1994) Effects of a mouse, *Mus musculus*, eradication programme and habitat change on lizard populations of Mana Island, New Zealand, with species reference to McGregor’s skink, *Cyclodina macgregori*. *New Zealand Journal of Zoology*, 21, 443–456.
- OLSON, D., FARLEY, L., NAILISILILI, W., RAIKABULA, A., PRASAD, O., ATHERTON, J. & MORLEY, C. (2006) Remote forest refugia for Fijian wildlife. *Conservation Biology*, 20, 568–572.
- PERRY, G., RODDA, G.H., FRITTS, T.H. & SHARP, T.R. (1998) The lizard fauna of Guam’s fringing islets: island biogeography, phylogenetic history, and conservation implications. *Global Ecology and Biogeography Letters*, 7, 353–365.

- RAYMUNDO M.L. & MILLER R.H. (2011) Little Fire Ant, *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae), established at several locations on Guam. *Proceedings of the Hawaiian Entomological Society*, 44, 85–87.
- REED, R.M., RODDA, G.H. & HINKLE, T.J. (2007) *Emoia atrocostata* (Littoral skink). *Herpetological Review*, 34, 100.
- REED, R.N., RODDA, G.H., SIERS, S.R., WOSTL, E. & YACKEL ADAMS, A.A. (2010) Terrestrial reptiles of Pagan Island, Commonwealth of the Northern Mariana Islands. In *Marianas Expedition Wildlife Surveys 2010: Terrestrial Resource Surveys of Pagan, Commonwealth of the Northern Mariana Islands*. U.S. Fish & Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, Hawaii, USA.
- RICHMOND, J.Q., OTA, H., GRISMER, L.L. & FISHER, R.N. (2021) Influence of niche breadth and position on the historical biogeography of seafaring scincid lizards. *Biological Journal of the Linnean Society*, 132, 74–92.
- RODDA, G.H. & FRITTS, T.H. (1992) The impact of the introduction of the brown tree snake, *Boiga irregularis*, on Guam's lizards. *Journal of Herpetology*, 26, 166–174.
- RODDA, G.H., FRITTS, T.H. & CHISZAR, D. (1997) The disappearance of Guam's wildlife: new insights for herpetology, evolutionary ecology, and conservation. *BioScience*, 47, 565–574.
- RODDA, G.H., FRITTS, T.H. & REICHEL, J.D. (1991) The distributional patterns of reptiles and amphibians on the Mariana Islands. *Micronesia*, 24, 195–210.
- RODDA, G.H., MCCOY, M.J. & FRITTS, T.H. (1993) Adhesive trapping II. *Herpetological Review*, 24, 99–100.
- ROGERS, H., LAMBERS, J.H.R., MILLER, R. & TEWKSBURY, J.J. (2012) Natural experiment demonstrates top-down control of spiders by birds on a landscape level. *PLOS ONE*, 7, e43446.
- RONQUIST, F., TESLENKO, M., MARK, P.V.D., AYRES, D.L., DARLING, A., HÖHNA, S. et al. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
- ROZAS, J., FERRER-MATA, A., SÁNCHEZ-DELBARRIO, J.C., GUIRAO-RICO, S., LIBRADO, P., RAMOS-ONSINS, S.E. & SÁNCHEZ-GRACIA, A. (2017) DnaSP 6: DNA Sequence Polymorphism Analysis of Large Data Sets. *Molecular Biology and Evolution*, 34, 3299–3302.
- SAVIDGE, J.A. (1987) Extinction of an island forest avifauna by an introduced snake. *Ecology*, 68, 660–668.
- SCHEFFERS, B.R., YONG, D.L., HARRIS, J.B.C., GIAM, X. & SODHI, N.S. (2011) The world's rediscovered species: back from the brink? *PLOS ONE*, 6, e22531.
- SCHWANER, T.D. & BROWN, W.C. (1984) Taxonomic status and distribution of the scincid lizards *Emoia adspersa* Steindachner and *E. lawesi* Günther on islands of the southwestern Pacific. *Herpetologica*, 40, 158–164.
- SIMBERLOFF, D. & VON HOLLE, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, 1, 21–32.
- SMITH, M.J., COGGER, H., TIERNAN, B., MAPLE, D., BOLAND, C., NAPIER, F. et al. (2012) An oceanic island community under threat: the decline of reptiles on Christmas Island, Indian Ocean. *Herpetological Conservation Biology*, 7, 206–218.
- THIBAUT, M., BRESCIA, F., JOURDAN, H. & VIDAL, E. (2017) Invasive rodents, an overlooked threat for skinks in a tropical island hotspot of biodiversity. *New Zealand Journal of Ecology*, 41, 74–83.
- THOMPSON, C.J., KOSHKINA, V., BURGMAN, M.A., BUTCHART, S.H.M. & STONE, L. (2017) Inferring extinctions II: a practical, iterative model based on records and surveys. *Biological Conservation*, 214, 328–335.
- TOWNS, D.R. (1991) Response of lizard assemblages in the Mercury Islands, New Zealand, to removal of an introduced rodent: the kiore (*Rattus exulans*). *Journal of the Royal Society of New Zealand*, 21, 119–136.
- TOWNS, D.R. (1994) The role of ecological restoration in the conservation of Whitaker's skink (*Cyclodina whitakeri*), a rare New Zealand lizard (Lacertilia: Scincidae). *New Zealand Journal of Zoology*, 21, 457–471.
- TOWNS, D.R. (1996) Changes in habitat use by lizards on a New Zealand island following removal of the introduced Pacific rat *Rattus exulans*. *Pacific Conservation Biology*, 2, 286–292.
- TOWNS, D.R. (2002) Korapuki Island as a case study for restoration of insular ecosystems in New Zealand. *Journal of Biogeography*, 29, 593–567.
- TRACEY, JR, J.I., SCHLANGER, S.O., STARK, J.T., DOAN, D.B. & MAY, H.G. (1964) General geology of Guam. *Geological Survey Professional Paper*, 403-A, 1–104.
- U.S. FISH & WILDLIFE SERVICE (1984) Determination of endangered status for seven birds and two bats of Guam and Northern Mariana Islands. *Federal Register*, 49, 33881–33885.
- U.S. FISH & WILDLIFE SERVICE (2015) Endangered and threatened wildlife and plants; endangered status for 16 species and threatened status for 7 species in Micronesia. *Federal Register*, 80, 59424–59497.
- WEIJOLA, V., VAHTERA, V., LINDQVIST, C. & KRAUS, F. (2019) A molecular phylogeny for the Pacific monitor lizards (*Varanus* subgenus *Euprepiosaurus*) reveals a recent and rapid radiation with high levels of cryptic diversity. *Zoological Journal of the Linnean Society*, 186, 1053–1066.
- WHITAKER, A.H. (1973) Lizard populations on islands with and without Polynesian rats, *Rattus exulans* (Peale). *Proceedings of the New Zealand Ecological Society*, 20, 121–130.
- WILES, G.J. (1987) Current research and future management of Marianas fruit bats (Chiroptera: Pteropodidae) on Guam. *Australian Mammalogy*, 10, 93–95.
- WOOD, K.R., BURNEY, D.A., ALLISON, A. & FISHER, R.N. (2013) *Emoia impar* (Squamata, Scincidae): not extinct in the Hawaiian Islands. *Oryx*, 47, 328.