Skinks of Oceania, New Guinea, and Eastern Wallacea: an underexplored biodiversity hotspot

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ABSTRACT

Context. Skinks comprise the dominant component of the terrestrial vertebrate fauna in Oceania, New Guinea, and Eastern Wallacea (ONGEW). However, knowledge of their diversity is incomplete, and their conservation needs are poorly understood. **Aims.** To explore the diversity and threat status of the skinks of ONGEW and identify knowledge gaps and conservation needs. **Methods.** We compiled a list of all skink species occurring in the region and their threat categories designated by the International Union for Conservation of Nature. We used available genetic sequences deposited in the National Center for Biotechnology Information's GenBank to generate a phylogeny of the region's skinks. We then assessed their diversity within geographical sub-divisions and compared to other reptile taxa in the region. **Key results.** Approximately 300 species of skinks occur in ONGEW, making it the second largest global hotspot of skink diversity following Australia. Many phylogenetic relationships remain unresolved, and many species and genera are in need of taxonomic revision. One in five species are threatened with extinction, a higher proportion than almost all reptile families in the region. **Conclusions.** ONGEW contain a large proportion of global skink diversity on <1% of the Earth's landmass. Many are endemic and face risks such as habitat loss and invasive predators. Yet, little is known about them, and many species require taxonomic revision and threat level re-assessment. **Implications.** The skinks of ONGEW are a diverse yet underexplored group of terrestrial vertebrates, with many species likely facing extreme risks in the near future. Further research is needed to understand the threats they face and how to protect them.

Keywords: islands, knowledge gaps, Melanesia, molecular phylogenetics, Oceania, regional threat assessment, Scincidae, Wallacea.

Introduction

The global biodiversity crisis is among the chief challenges facing humanity in the 21st Century (Pereira et al. 2012). To ensure the long-term survival of the Earth's biodiversity, we need a strong knowledge base to identify threatened taxa, evaluate biodiversity hotspots and inform conservation planning and action (Soulé 1985; Primack 2014). With this goal in mind, it has been a priority of conservation biologists to identify which species are most at risk, where, and why. The International Union for Conservation of Nature (IUCN) has been collecting and curating data on species distribution, demographics, population trends, and threats since 1964 to assess the extinction risk of the world's biota (IUCN 2021). Global initiatives such as the IUCN Red List represent crucial datasets for use in identifying priority areas for conservation, including the recognition of global conservation hotspots – areas of exceptional biodiversity at high risk (Myers et al. 2000; Mittermeier et al. 2004; Brooks et al. 2006; IUCN 2016). However, it is becoming increasingly evident that conservation efforts should also include regional and

local assessments to identify scale-dependent processes and threats requiring targeted management measures (Ferrier 2002; Knight *et al.* 2007; McDonald *et al.* 2022).

The region of Oceania and New Guinea encompasses Melanesia, Micronesia, and Polynesia (see exact definition below; Fig. 1). The region of Wallacea includes additional small and medium-sized Indonesian islands west of New Guinea, and the sovereign state of Timor-Leste. Despite containing less than 1% of the world's landmass, this region is extremely biodiverse. Oceania and especially New Guinea are well recognised for their importance in global diversity for birds (Stattersfield *et al.* 1998), vertebrates in general (Myers *et al.* 2000), insects (Toussaint *et al.* 2014), vascular plants (Cámara-Leret *et al.* 2020), and human cultural diversity (Loh and Harmon 2005). However, Oceania also holds the infamous distinction of being one of the Earth's extinction hotspots – with a particularly poor record of extinctions for terrestrial vertebrates, especially birds (Steadman 1995; Blackburn *et al.* 2004). It is perhaps no surprise that an area comprising many islands, with high levels of endemism, would be prone to high levels of extinction, because insular taxa are particularly vulnerable to human-induced threats (Fisher and Ineich 2012; Slavenko *et al.* 2016; Fromm and Meiri 2021). Indeed, available evidence suggests that colonisation of the area by humans has been associated with proportionally elevated (above ambient or background levels) rates of extinction, principally as a function of evolutionarily novel human predation and alien species introduction (Duncan *et al.* 2013).

One of the dominant features of Oceania, New Guinea, and Eastern Wallacea's terrestrial vertebrate fauna are lizards and particularly those of the family Scincidae, generally referred to as 'skinks' (Squamata: Scincomorpha: Scincidae). Skinks make up almost one-quarter of the world's lizard diversity

and have a prominent richness hotspot in New Guinea (Chapple *et al.* 2021) which is second only to the global hotspot in Australia (Rabosky *et al.* 2007; Powney *et al.* 2010; Chapple *et al.* 2021). In addition to their high diversity in New Guinea, they are also the most diverse terrestrial vertebrates throughout the Pacific Ocean. New Caledonia is home to a particularly notable and large radiation of endemic skinks (Smith *et al.* 2007), many of which are endangered or vulnerable (Chapple *et al.* 2021). Some species and species complexes are extremely widespread, either due to variable microhabitat preferences (Richmond *et al.* 2021) or commensal habits, which facilitated human-mediated dispersal (Bruna *et al.* 1996; Austin 1999; Hamilton *et al.* 2010; Linkem *et al.* 2013; Klein *et al.* 2016; Tan 2016). However, the majority of species are more restricted: many species are habitat specialists (Greer and Simon 1982; Blom *et al.* 2019; Richmond *et al.* 2021; Slavenko *et al.* 2022), and their levels of endemism are high throughout the region (Smith *et al.* 2007; Meiri *et al.* 2018; Kraus 2021).

Despite the prominence of skinks among the terrestrial faunas of Oceania, New Guinea, and Eastern Wallacea, knowledge of their true diversity is incomplete. Little is known of their natural history, and relatively few species have so far been included in molecular phylogenetic analyses. Since the early years of herpetological research in Oceania and New Guinea (Lesson 1830; Duméril and Bibron 1839; Bavay 1869), many new species have been discovered and formally described. However, only relatively recently have studies begun to incorporate molecular markers to infer phylogenetic relationships and revise species boundaries – and many of these studies suggest that true diversity in the region is greatly underestimated, even as recognised species numbers are increasing at a rapid rate (Austin *et al.* 2010; Rodriguez *et al.* 2018; Slavenko *et al.* 2020, 2022;
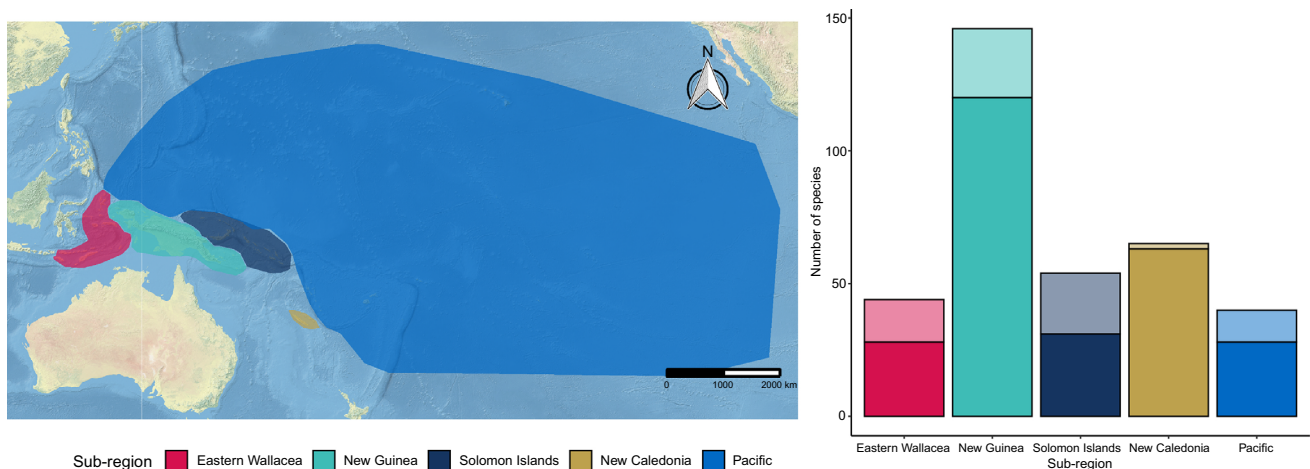
Fig. 1. Map of the Oceania and New Guinea region, with coloured polygons representing the five different sub-regions, and bar plots representing species richness of skinks in each sub-region. The bars are divided based on endemism – the bottom stack (darker colours) are species endemic to the sub-region, and the top stack (lighter colours) are native species that occur elsewhere in the region. Basemap made with Natural Earth. Free vector and raster map data @ naturalearthdata.com.

Richmond *et al.* 2021; Bernstein *et al.* 2022; Reilly *et al.* 2022). Thus, existing threat assessments (Cox *et al.* 2022) may be outdated or misleading if they apply to inaccurately understood species boundaries and limited species knowledge (Mace 2004; Pimm *et al.* 2014). A clear understanding of knowledge gaps and research priorities in the region is therefore crucial to provide the foundation for effective regional conservation planning.

We assess the composition, threat status, and state of knowledge for the skink biota of Oceania, New Guinea, and Eastern Wallacea as part of the larger framework of the IUCN Species Survival Commission (SSC) Skink Specialist Group: a global network of biologists and wildlife managers that study and conserve the world's skinks (Chapple *et al.* 2021). We highlight the uniqueness of this region's skink fauna in a global context, as well as some of the unique conservation challenges these species face, and we identify knowledge gaps that hinder the continued persistence of this unique fauna. We hope our work will inspire further research into this global biodiversity hotspot, particularly involving understudied, micro-endemic, less conspicuous, smaller, and difficult-to-study components of the terrestrial fauna.

Materials and methods

The focal study region is comprised of all Pacific island nations (excluding Japan, Taiwan, the Philippines, New Zealand, and Australia's Overseas Territories, but including the UK and US Overseas Territories and Hawaii), all islands in the Indonesian provinces of Papua, Highland Papua, Central Papua, South Papua, West Papua, North Maluku, Maluku, and East Nusa Tenggara, and the sovereign state of Timor-Leste (Fig. 1). The Western boundary of the region roughly aligns with the boundary between the Oriental and Australasian biogeographic realms; however, it is somewhat arbitrary due to the complex geological history of the area and differs from other traditionally recognised turnover points, most notably Wallace's Line (Wallace 1860; Mayr 1944; Simpson 1977; Ali and Heaney 2021). For our purposes we view our definition of the Western boundary as an appropriate, biologically defensible definition, because it corresponds with the western extent of multiple prominent skink clades (e.g. tribe Tiliquini, genus *Carlia* with the exception of *Carlia nigrauris*).

We further divided the region into five sub-regions based on their geological histories and skink assemblages. These include:

1. Eastern Wallacea: Timor-Leste and all Indonesian islands in the region, excluding New Guinea and its satellite islands that occur on the Australian continental plate (e.g. Aru Islands, Raja Ampat Islands).
2. New Guinea: the island of New Guinea and all of its satellite islands that occur on the Sahul shelf (e.g. Aru

Islands, Raja Ampat Islands) and the islands of the Woodlark Basin (e.g. Trobriand Islands, D'Entrecasteaux Archipelago, Woodlark Island, and Louisiade Archipelago), but excluding Australian territories (Torres Strait Islands).
3. Solomon Islands: all islands on the Solomon Islands arc and the New Britain arc, comprising the islands of the Bismarck Archipelago (e.g. New Britain, New Ireland, Admiralty Islands), the entire nation of the Solomon Islands, and the islands of Bougainville and Buka in Papua New Guinea's Autonomous Region of Bougainville.
4. New Caledonia: all islands on the French territory of New Caledonia, occurring on the mostly submerged continent of Zealandia.
5. Pacific: all remaining islands in the region, comprising most of the islands in the Western and Southern Pacific Ocean, including American Samoa, Caroline Islands, Clipperton Island (in the North-eastern Pacific Ocean), Cook Islands, Easter Island, Federated States of Micronesia, Fiji, French Polynesia, Guam, Hawaii, Kiribati, Marshall Islands, Nauru, Niue, Northern Mariana Islands, Palau, Pitcairn Islands, Samoa, Tokelau, Tonga, Tuvalu, US Overseas Territories in the Pacific, Vanuatu, and Wallis and Futuna.

We compiled a list of all species of skinks that occur in our focal region (Supplementary Table S1). The list was based on the most up-to-date list of global skink diversity (Chapple *et al.* 2021). We used global distribution maps of the world's reptiles from an updated version of Roll *et al.* (2017; i.e. Caetano *et al.* 2022) and overlaid these maps with polygons defining our region of interest (Fig. 1). We included all species with ranges overlapping these polygons. We also included three skink species (*Papuascincus buergersi*, *Papuascincus phaeodes*, *Prasinohaema parkeri*) whose localities are not specific enough to be mapped but nonetheless occur in our region (namely, in New Guinea) based on verbal description of their ranges in their original description papers. We then assessed which sub-regions overlapped each species' range, tallied species-richness values for each sub-region, and determined the number of species occurring over multiple sub-regions. We repeated this procedure for all mapped terrestrial reptile species to compare richness patterns of skinks in the region to patterns exhibited by other reptilian taxa.

To assess patterns of diversity and taxonomic knowledge, we recorded the description year for each skink species in the region. We then plotted cumulative species richness by year of description to compare rates of species description in the different sub-regions. Additionally, all authors (members of the IUCN SSC Skink Specialist Group specialising on the region) assessed for each species whether, to the best of their knowledge, it is in need of taxonomic revision either at the species (i.e. undescribed diversity likely exists in the species) or genus (i.e. genus likely in need of splitting or species likely needing reassignment to a different genus) level.

To explore patterns in threat status in the region, we compared IUCN threat categories. For each species we recorded its tribe, taxonomic authority, and year of description (Chapple *et al.* 2021; Shea 2021; Uetz *et al.* 2021). We then used the 'iucn_summary' and 'iucn_status' functions from the *taxize* package (Chamberlain and Szöcs 2013; Chamberlain *et al.* 2020) within the R data analysis platform v4.1.0 (R Core Team 2021) to query the IUCN Red List for the Red List status of all species in our list. We classified each species as being either Least Concern (LC), Near Threatened (NT), Threatened (VU, EN, or CR), or Unknown (DD or not evaluated [NE]). One species, *Tachygia microlepis*, is classified as Extinct (EX).

To assess knowledge gaps in molecular sequencing, we used the 'entrez_search' and 'entrez_fetch' functions from the *rentrez* package (Winter 2017) to query the National Center for Biotechnology Information (NCBI) GenBank nucleotide database for sequence data for all species of skinks in our list, and tallied for each species how many unique sequences, and how many loci, are available. We then selected the following genetic markers for downstream phylogenetic analyses to reconstruct a phylogeny of all sampled skinks in the region (although some sequences represent populations outside the region), and explore their phylogenetic relationships: the mitochondrial (mtDNA) markers ribosomal 12S rRNA (*12S*; 61 spp; 398 base pairs [bp]), ribosomal 16S rRNA (*16S*; 42 spp; 468 bp), ribosomal 18S rRNA (*18S*; 8 spp; 1770 bp), cytochrome *c* oxidase subunit I (*COI*; 103 spp; 645 bp), cytochrome *b* (*CYTB*; 42 spp; 270 bp), NADH dehydrogenase subunit 2 (*ND2*; 128 spp; 514 bp), NADH dehydrogenase subunit 4 (*ND4*; 66 spp; 706 bp), and the nuclear (nDNA) markers brain-derived neurotrophic factor (*BDNF*; 15 spp; 712 bp), breast cancer type 2 susceptibility protein (*BRCA2*; 19 spp; 1248 bp), proto-oncogene serine/threonine-protein kinase mos (*c-mos*; 69 spp; 547 bp), exophilin 5 (*EXPH5*; 21 spp; 697 bp), kinesin family member 24 (*KIF24*; 19 spp; 567 bp), nerve growth factor *β* polypeptide (*NGFB*; 34 spp; 582 bp), prolactin receptor (*PRLR*; 13 spp; 564 bp), protein tyrosine phosphatase non-receptor type 12 (*PTPN12*; 14 spp; 609 bp), RNA fingerprint protein 35 (*R35*; 33 spp; 636 bp), and recombination activating gene 1 (*RAG1*; 61 spp; 828 bp). These markers were selected because they were well represented (present for >5 species of multiple genera and tribes). We selected one sequence per-species per-marker to use in phylogenetic analyses, preferring when possible to use sequences from the same individual or geographic locality within species (Supplementary Table S2). In addition, we downloaded sequences of *16S*, *BDNF*, *c-mos*, *CYTB*, *EXPH5*, *ND4*, *NGFB*, *PRLR*, *PTPN12*, and *RAG1* for *Acontias meleagris* (of the skink subfamily Acontiinae, sister to all other skinks; Pyron *et al.* 2013) to use as an outgroup.

We aligned sequences using MUSCLE multiple-sequence alignment as implemented in MEGA 11 (Tamura *et al.* 2021). We partitioned the multiple-sequence alignment for phylogenetic analyses and selected substitution models by running ModelFinder (Kalyaanamoorthy *et al.* 2017) as implemented in IQ-TREE 2 (Minh *et al.* 2020) using a relaxed hierarchical clustering algorithm (Lanfear *et al.* 2014), and with initial partitions set to single partition for *12S*, *16S*, and *18S*, and by codon for all protein-coding genes (all others). Partitions and models can be found in Supplementary Table S3.

We performed phylogenetic inference using three methods:

1. Maximum Likelihood (ML) analyses in IQ-TREE 2 (Minh *et al.* 2020), as implemented in the IQ-TREE web server (Trifinopoulos *et al.* 2016). We set the partitions to be edge-linked (same set of branch lengths among partitions, but with partition-specific rates). We assessed nodal support with 1000 ultrafast bootstrap (UFBoot) alignments with up to 1000 iterations as a stopping rule (Hoang *et al.* 2018). We considered nodes well-supported if they received UFBoot values ≥ 95%.

2. Maximum Likelihood (ML) analyses in RAxML v8 (Stamatakis 2014), as implemented in raxmlGUI v2.0.9 (Edler *et al.* 2021). We performed model selection using ModelTest-NG (Darriba *et al.* 2020) and used the selected GTR+G+I model of sequence evolution for all partitions. We assessed nodal support with 500 rapid bootstrap (BS) replicates, and considered nodes well-supported if they received BS values ≥ 80%.

3. Bayesian Inference (BI) analyses in MrBayes v3.2.7a (Ronquist *et al.* 2012) as implemented in CIPRES Science Gateway (Miller *et al.* 2010), using the BEAGLE library (Ayres *et al.* 2012). Since ModelFinder has more possible models than are accepted in MrBayes, we assigned the GTR model to all partitions where the best-fit model was K3P, TPM2, TPM, TIM, or TVM. In partitions where the best-fit models included the FreeRate model, we instead assigned the more restrictive (but still variable) gamma model for among-site rate variation. Nucleotide-substitution-model parameters were unlinked across partitions, and we allowed the different partitions to evolve at different rates. We performed two simultaneous parallel runs (Altekar *et al.* 2004) with four chains per run (three heated, one cold) for 10^7 generations, sampling every 1000 generations. We examined the standard deviation of the split frequencies between the two runs and the Potential Scale Reduction Factor (PSRF) diagnostic, and discarded the first 25% of trees as burn-in.

We then repeated the above analyses, from partitioning to phylogenetic inference, for concatenated mtDNA (seven markers; 173 spp; 4771 bp) and nDNA (10 markers;

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112 spp; 6990 bp) alignments separately to assess agreement in topology between the different markers. Partitions and models for the mtDNA and nDNA datasets can be found in Supplementary Table S3.

Results

Skink diversity

We identified 303 species of skinks that occur in our target region, one of which is introduced from Australia (*Lampropholis delicata*), and one of which is possibly native to New Guinea but its presence is unverified (*Carlia quinquecarinata*). Of the remaining 301 species, 18 are native but also occur elsewhere (mostly Australia), and 283 are endemic to the region. Together these 301 species constitute roughly 17% of the ~1740 species of skinks currently known worldwide. Almost half (146 species) occur in New Guinea alone (Fig. 1). Skink species vastly outnumber all other reptilian families in the region, particularly in New Guinea, but this pattern is also evident in all sub-regions (Fig. 2*a*).

All skinks in the region belong to the subfamily Lygosominae, and within this, most belong to the tribes Eugongylini and Sphenomorphini (Fig. 3), the two largest tribes in the subfamily (Chapple *et al.* 2021; Shea 2021). There are also several species from the tribe Tiliquini (most prominently crocodile skinks of the genus *Tribolonotus*, endemic to the region), two species of the tribe Mabuyini (one of which, *Eutropis palauensis*, is endemic), and a single species from the tribe Lygosomini (*Lamprolepis smaragdina*). Species from the tribe Eugongylini are widespread throughout the region and it is the dominant tribe in Eastern Wallacea, New Caledonia, the Solomon Islands, and the Pacific, with a prominent hotspot in New Caledonia where all skinks are eugongylins (Fig. 3). Conversely, the dominant tribe in New Guinea is Sphenomorphini – and indeed most sphenomorphin skinks in the region occur in New Guinea.

Extinction risk

Among the skinks of Oceania, New Guinea, and Eastern Wallacea, 56 species (18.7%) are evaluated by the IUCN as threatened with extinction, and one Tongan endemic (*Tachygia microlepis*) is extinct. Slightly over half (173 species) are listed as Least Concern, an additional eight are Near Threatened. Another 66 (22.0%) are either listed as Data Deficient or have not been assessed. When weighted by their species richness, the mean proportion of species in the Threatened categories across families in the region is 14.5%. Thus, skinks have a relatively high proportion of species threatened with extinction, higher than other speciose families such as Gekkonidae (121 spp., 9.9% Threatened),

Colubridae (54 spp., 3.7% Threatened), Elapidae (42 spp., 7.1% Threatened), and Agamidae (36 spp., 2.8% Threatened).

Most New Caledonian skinks are classified as Threatened (63.1%; Fig. 3), followed by the Pacific (32.5%), and Eastern Wallacea (4.5%) sub-regions. New Guinea and the Solomon Islands both have no known Threatened species. New Guinea and Eastern Wallacea have the highest proportion of species with an unknown conservation status (26.0% and 18.2%, respectively).

Phylogenetic relationships

Despite the high absolute species richness, skinks are poorly sampled relative to other families: 174 species of skinks (57.1%) have sequences in NCBI genbank (Fig. 2*c*), lower than the mean proportion among reptile families in the region (66.3%). Our final dataset comprised 17 genetic markers (7 mtDNA, 10 nDNA) with a total length of 11 761 bp. Coverage averaged only 2.6 mtDNA markers and 1.7 nDNA markers per species (range 0–7, mean 36.8% and 15.6%, respectively). Coverage also varied between tribes and markers (Supplementary Table S4): eugongylin skinks had the lowest coverage for mitochondrial markers (range 1–7, mean 2.3 [33.3%] markers per species), followed by sphenomorphin skinks (range 0–5, mean 2.9 [41.2%] markers per species) and tiliquin skinks (range 2–6, mean 3.3 [46.4%] markers per species). Eugongylin skinks also had the lowest coverage for nDNA markers (range 0–7, mean 1.5 [14.0%] markers per species), followed by tiliquin skinks (range 0–6, mean 1.6 [14.4%] markers per species) and sphenomorphin skinks (range 0–6, mean 1.9 [17.5%] markers per species).

The higher-order relationships of skinks in our phylogeny were only moderately resolved (Fig. 4), with the monophyly of Tiliquini and Sphenomorphini receiving low support. In most regions, several different lineages of skinks are represented. However, most skink species on New Caledonia belong to a single, moderately supported eugongylin radiation (Fig. 4). Deeper relationships within the Sphenomorphini and Eugongylini are not well resolved (Fig. 4), particularly in the speciose genus *Sphenomorphus* and in the large radiation of New Caledonian eugongylin skinks. Most genera were supported as monophyletic, except *Lipinia*, *Emoia* (both with at least two distinct clades), *Prasinohaema*, and *Sphenomorphus* (both with at least three distinct clades).

With all three methods of phylogenetic inference, the full concatenated gene trees were mostly concordant with the concatenated mtDNA trees, and less so with the nDNA trees (Figs S1–S3). In general, concatenated nDNA trees had poorly supported topology, especially in the Eugongylini.

Among the full concatenated gene trees, the ML IQ-TREE phylogeny generally had better supported topology than the ML RAxML phylogeny (Fig. 4). However, the topology was similar between the two methods (Fig. S4), with major differences only in deeper nodes between genera within the Eugongylini (*Carlia*, *Lygisaurus*, *Caesoris*, *Phasmasaurus*,
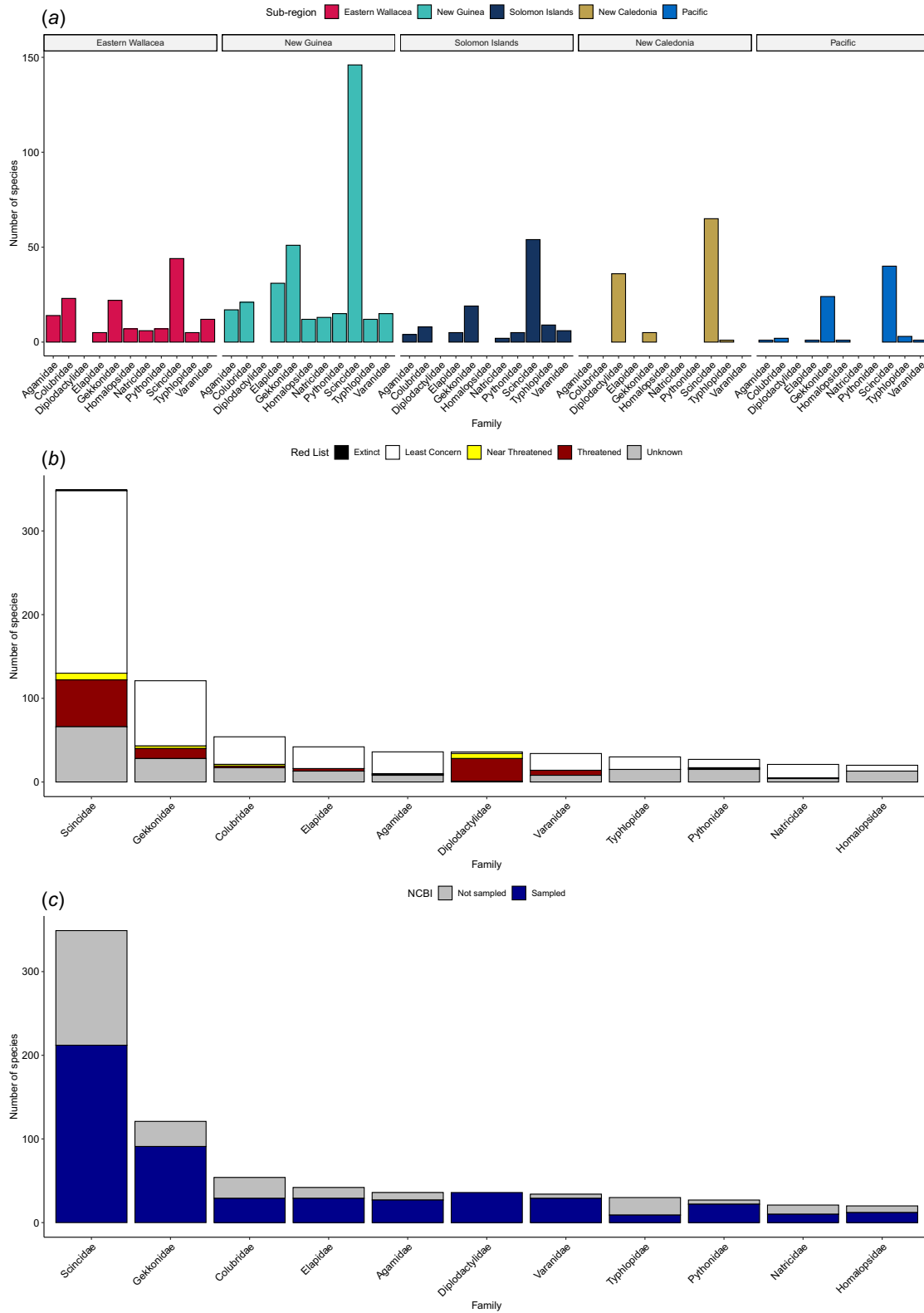
Fig. 2. Comparison of skinks to other reptilian families in Oceania, New Guinea, and Eastern Wallacea. (*a*) Species richness per family in each of the five sub-regions. (*b*) Red List assessments of species per family, divided into Least Concern (LC), Near Threatened (NT), Threatened (VU, EN, or CR), Extinct (EW or EX), or Unknown (NE or DD). (*c*) Numbers of species per family with sequences available in NCBI genbank (blue) vs not available (grey). For clearer visualisation, in all panels only families with 20 or more species are shown.
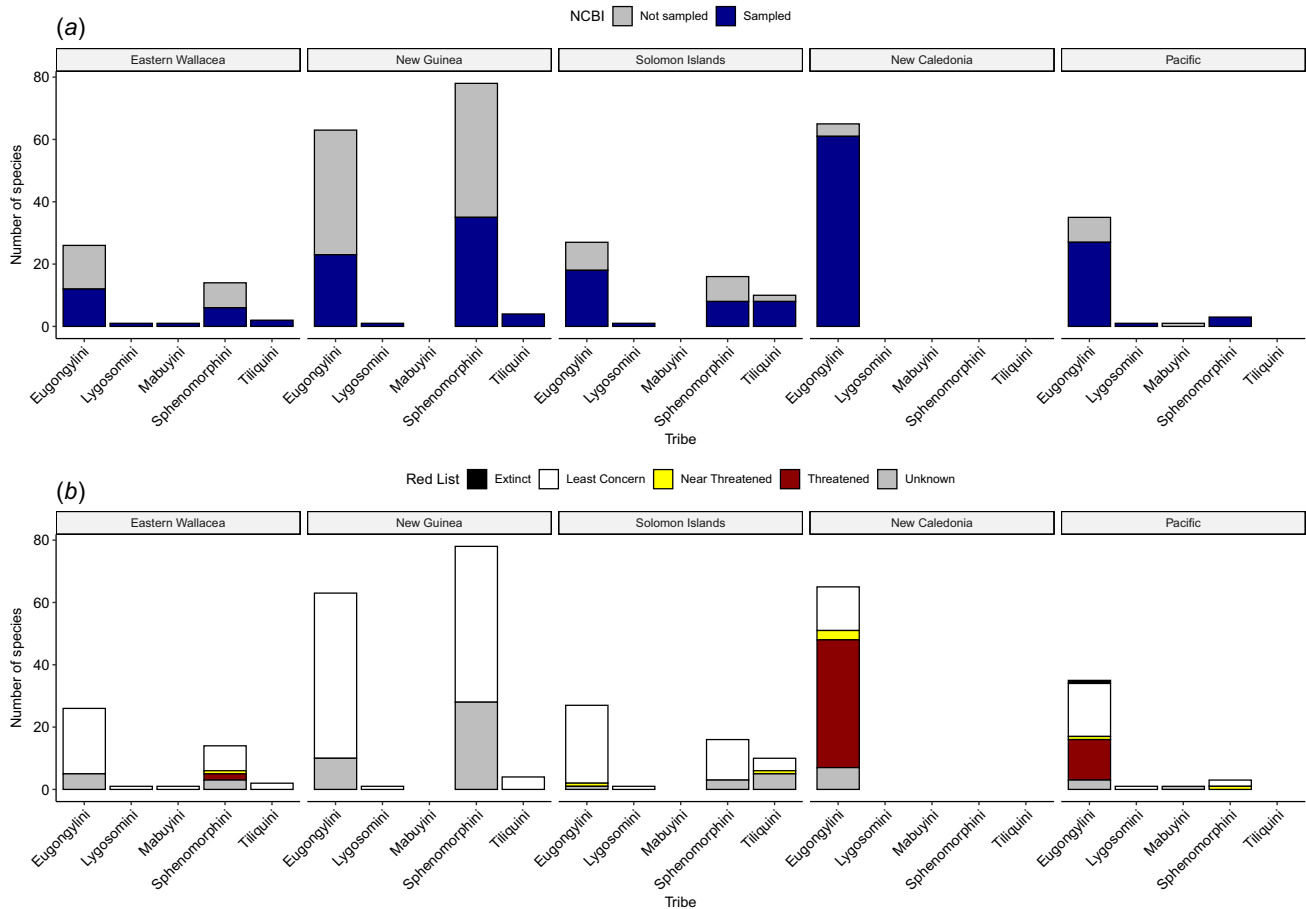
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Fig. 3. Comparison between skink tribes in Oceania, New Guinea, and Eastern Wallacea. (*a*) Numbers of species per tribe with sequences available in NCBI genbank (blue) vs not available (grey). (*b*) Red List assessments of species per tribe, divided into Least Concern (LC), Near Threatened (NT), Threatened (VU, EN, or CR), Extinct (EW or EX), or Unknown (NE or DD). In both panels, data are faceted by the five sub-regions.

Kanakysaurus). Both the IQ-TREE and RAxML phylogenies showed much larger differences to the MrBayes phylogeny, although again most differences were in the relationships between genera within Eugongylini (Fig. S4).

Trends in species discoveries

The earliest described skink species from the region are widespread large species that would have been noticeable to early naturalists, some of which occur outside the region, including *Tiliqua scincoides* (Hunter 1790), *Tiliqua gigas* (Schneider 1801) and *Eugongylus rufescens* (Shaw 1802). Descriptions of species endemic to the region began accumulating throughout the 19th Century, with prominent spikes in descriptions of New Guinean and New Caledonian species towards the end of the century (Fig. 5). Throughout the 20th Century, descriptions of species from Eastern Wallacea, New Caledonia, the Pacific, and the Solomon Islands were published at a steady rate of ~0.19–0.33 species per year on average, whereas descriptions from New Guinea have been published at a much higher rate (~0.75 species per year on

average). A pronounced upwards shift in these dynamics occurred at the start of the 21st Century. While rates of description in Eastern Wallacea, the Pacific, and the Solomon Islands remained static, average rates of description in New Caledonia and New Guinea increased dramatically to 1.4 and 1.7 species per year, respectively (Fig. 5).

Discussion

We identified Oceania, New Guinea, and Eastern Wallacea as a global hotspot of skink diversity, especially in the context of available land area – less than 1% of the world's landmass. Despite its relatively small area, this region is home to almost a fifth of all skink species, making it second only to Australia in terms of absolute species richness (Rabosky *et al.* 2007; Powney *et al.* 2010; Chapple *et al.* 2021). The skink diversity of the region is impressive not only in its numbers, but also in terms of the range and magnitude of phenotypic and ecological variability including trophic

spectra. Skinks in the region possess adaptations for extremely high elevations (Greer *et al.* 2005; Slavenko *et al.* 2021, 2022) and tolerance of highly saline conditions (Richmond *et al.* 2021). Some possess unique morphologies associated with aquatic (Greer and Simon 1982) or arboreal (Zippel *et al.* 1999) lifestyles. Others exhibit rare attributes among squamates in general, such as green blood pigmentation (Greer and Raizes 1969; Rodriguez *et al.* 2018), adhesive toe pads (Williams and Peterson 1982; Irschick *et al.* 1996), vocalisation (Hartdegen *et al.* 2001; Bauer *et al.* 2004), carcinophagy (Jowers *et al.* 2022), living inside 'ant plants' of the genus *Hydnophytum* (Brown and Gibbons 1986),
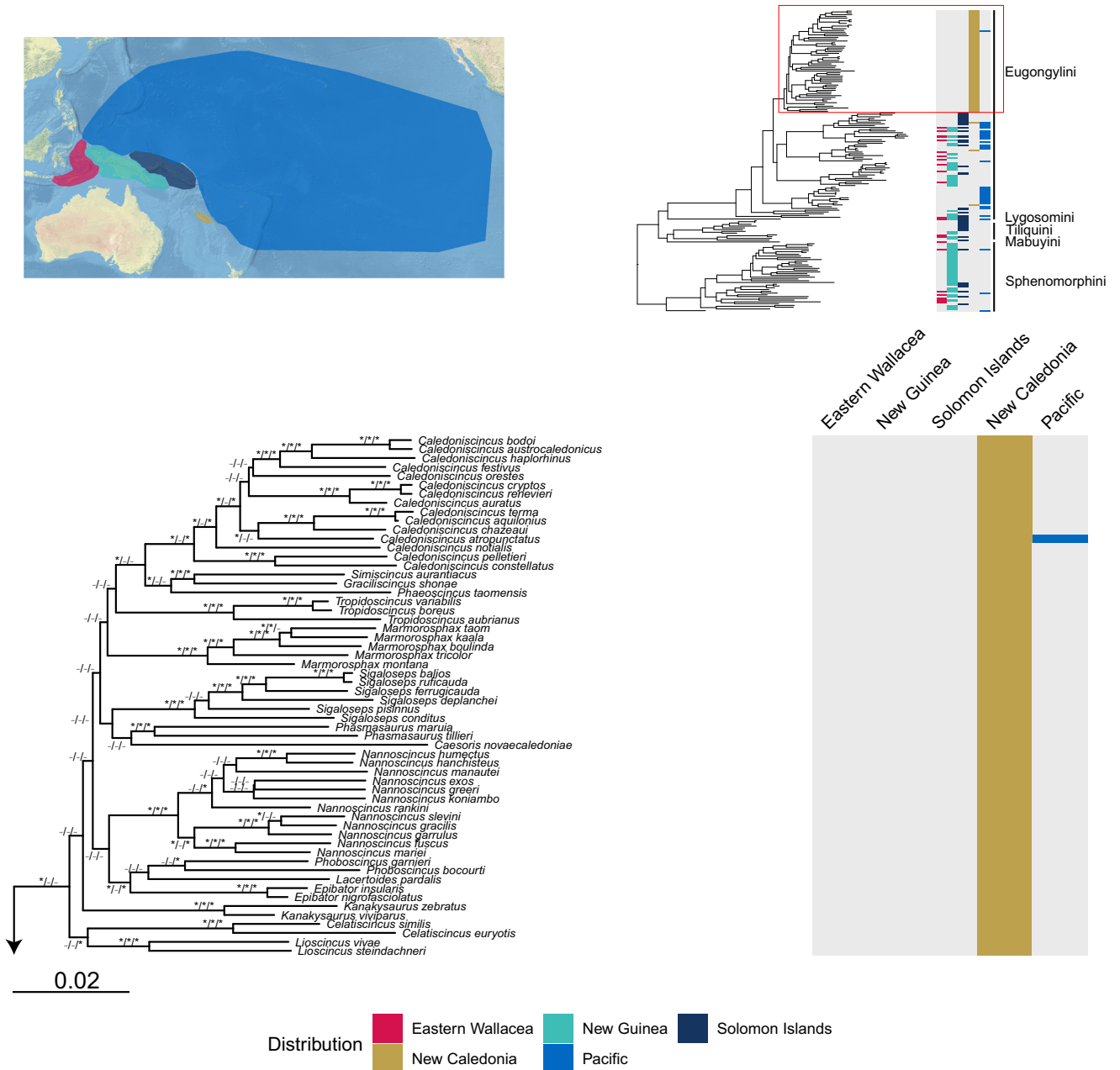

Fig. 4. Concatenated gene tree (17 loci, 11 761 bp) showing the phylogenetic relationships between skinks in the Oceania and New Guinea region. The plotted phylogeny was generated using IQ-TREE. Support values are shown at the nodes for bootstrap values (BS; RAxML)/ ultrafast bootstrap (UFBoot; IQ-TREE)/posterior probability (PP; MrBayes). Supported nodes (BS ≥ 80%, UFBoot ≥ 95%, PP ≥ 0.95) are denoted by black asterisks, unsupported nodes are denoted by grey hyphens. Scale bar at the bottom for branch lengths represents the average number of substitutions per site. The grid on the right shows presence/absence of each species in the five different sub-regions, represented in the inset map (top left). On the top right is the full phylogeny, with labels indicating the five tribes (Eugongylini, Mabuyini, Lygosomini, Sphenomorphini, and Tiliquini). The blown up section of the phylogeny in each page is marked with a red rectangle.
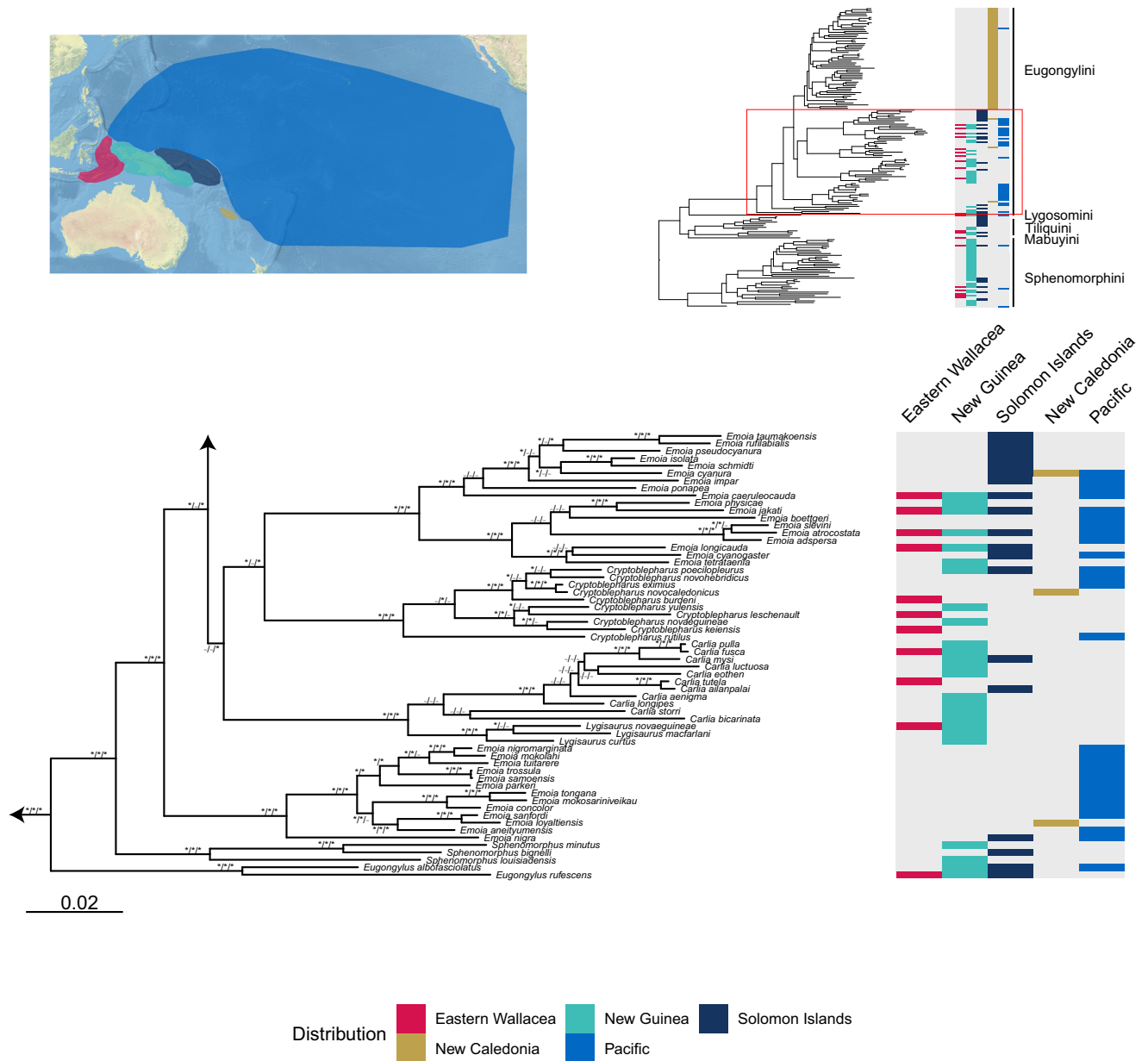
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Fig. 4. (*Continued*).

herbivory, low reproductive rates, sociality, and colonial aggregations (Iverson 1982).

Knowledge gaps are still evident. Skinks are similar to other squamates (Tingley *et al.* 2016) in having a high proportion of species whose conservation status is unknown, with roughly a fifth of species in the region either not yet assessed by the IUCN, or assessed as Data Deficient (Tingley *et al.* 2016; Chapple *et al.* 2021; Cox *et al.* 2022). This assessment gap is particularly evident in New Guinea and Eastern Wallacea (Fig. 3). Data Deficient species are likely to be at least as threatened (Bland and Böhm 2016), or even more so (Gumbs *et al.* 2020; Caetano *et al.* 2022),

than the general threat level for other reptiles. Species that have not yet been assessed are likely to be even more threatened due to their smaller geographic range sizes (Meiri 2016). Thus, the actual threat level of skinks presented here for Oceania and New Guinea is likely to be a conservative estimate (Chapple *et al.* 2021).

Another large knowledge gap involves species-level diversity. Although species richness of skinks in the region is high, this diversity is likely still underestimated. During the past decade alone, the rate of description for skinks in Oceania, New Guinea, and Eastern Wallacea has more than tripled to ~3 species per year (Fig. 5). This amounts to
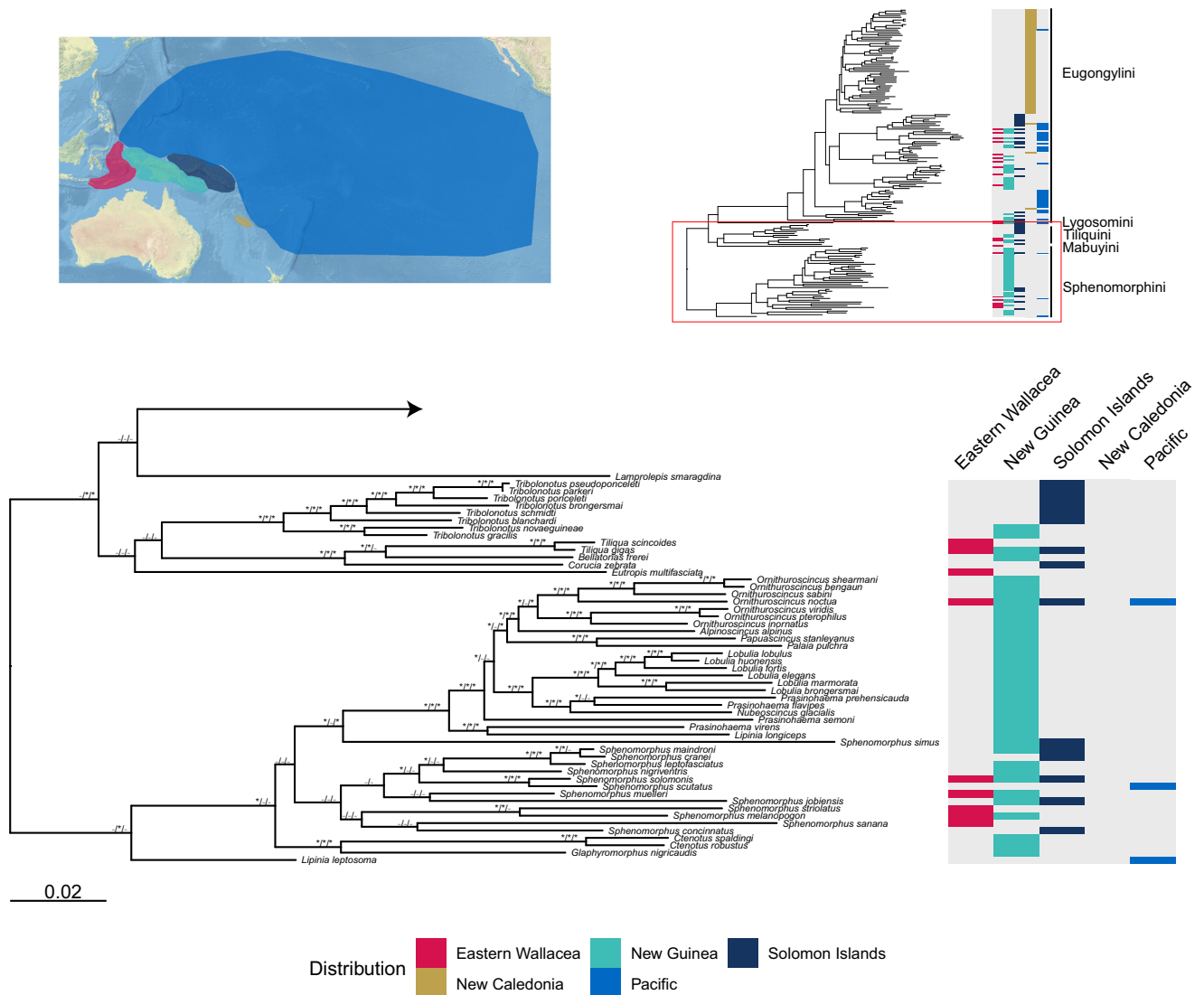
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Fig. 4. (*Continued*).

15% of the ~20 species of skinks per year that have been described worldwide over the past decade (Chapple *et al.* 2021) in an area that takes up less than 1% of the Earth's total landmass.

The foundations for our understanding of skink diversity of the region were set during the first half of the 19th Century mostly through the work of prominent French naturalists (Lescure 2002) such as René-Primevère Lesson (Lesson 1830), Auguste Duméril, and Gabriel Bibron (Duméril and Bibron 1839). However, the true process of exploration and description of the skink fauna of the region began in the latter half of the 19th Century and the beginning of the 20th Century (Fig. 5), starting with Arthur Bavay's original description of the fauna of New Caledonia (Bavay 1869)

and several monographs describing fauna collected in British, Italian, and German expeditions into the interior of New Guinea (Meyer 1874; Macleay 1877; Peters and Doria 1878; Boulenger 1887, 1897, 1903, 1914). The 20th Century saw a continuation of this trend, as species descriptions accumulated at a more or less steady rate (Fig. 5), with foundational treatises on the widespread eugongylin genera *Cryptoblepharus* (Mertens 1928, 1931, 1933, 1934, 1964) and *Emoia* (Brown 1953, 1954, 1983, 1991; Brown and Parker 1985; Brown and Allison 1986; Brown and Gibbons 1986), on New Guinea's sphenomorphin skinks (Vogt 1932; Parker 1936; Loveridge 1945; Greer and Parker 1967*a*, 1967*b*, 1971, 1974; Greer 1973, 1974), on the eugongylin skinks of New Caledonia (Sadlier 1987), and on the tiliquin
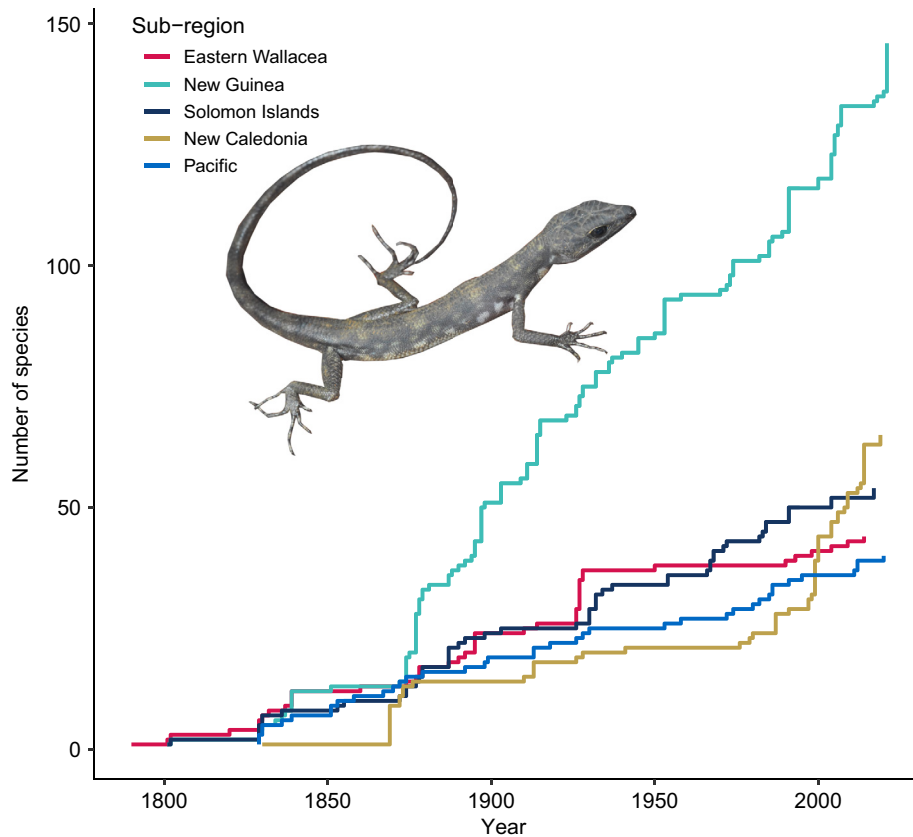
Fig. 5. Cumulative number of species described vs the year of original description in each sub-region in Oceania and New Guinea. Photo of *Fojia bumui*, endemic to New Guinea, by Allen Allison.

genus *Tribolonotus* (Zweifel 1966; Greer and Parker 1968; Cogger 1972). A revolution in taxonomic research in the region began towards the end of the 20th and into the 21st Century, with the advent of technological advancements that made molecular phylogenetic inference cheaper and easier than before. This revolution was most prominent in New Caledonia, which experienced a four-fold increase in species description rate in the 21st Century (Fig. 5), as its fauna was thoroughly researched and described (Sadlier *et al.* 1999; Bauer and Sadlier 2000; Sadlier *et al.* 2006, 2009a, 2009b, 2014a, 2014b, 2014c, 2019). New Guinea also experienced a more than two-fold increase in its skink species description rate, but many of these new descriptions were based on morphology alone (Günther 2000; Greer and Shea 2004; Zug 2004; Greer *et al.* 2005; Shea 2017; Kraus 2018, 2020; Shea and Allison 2021). Only relatively recently have the skinks of New Guinea and the Solomon Islands begun to be explored using molecular phylogenetic methods (Austin 1995; Austin *et al.* 2010; Rittmeyer and Austin 2017; Rodriguez *et al.* 2018; Slavenko *et al.* 2020, 2022), and the potential exists for New Guinea to experience a similar if not more spectacular taxonomic revolution as New Caledonia before it.

Despite these recent advances in taxonomic research in the region, some issues remain. Many phylogenetic relationships among the region's skinks remain unresolved, particularly deeper nodes with short branches (Fig. 4). Parts of the topology in our phylogeny are likely erroneous, such as the low support for monophyly of Tiliquini and Sphenomorphini, two tribes whose monophyly is otherwise widely supported (Pyron *et al.* 2013). However, other nodes are strongly supported and represent cases in need of taxonomic revision – such as the non-monophyly of *Emoia*, *Lipinia*, *Prasinohaema*, and *Sphenomorphus*. We have identified 42 species (all occur in New Guinea and most are sphenomorphin) that likely contain undescribed diversity, and even more dramatically, 143 species in six genera that likely require either generic reassignment or a full revision of their genera and their contents. New Guinea and Eastern Wallacea remain especially poorly sampled genetically compared to the other sub-regions of the area (Fig. 3) – either due to lack of tissue samples, or due to lack of sequencing of available tissues. This is also evident in the weak resolution of deeper phylogenetic relationships among New Guinea's sphenomorphin skinks (Fig. 4), likely a direct result of the patchy genetic coverage,

particularly of nDNA markers, in these species (Supplementary Table S4 and Fig. S5).

New Guinea's western half (Indonesian New Guinea) remains extremely poorly known especially compared to the better-sampled eastern half (Papua New Guinea) (Heads 2002; Slavenko *et al.* 2022), and the island of New Guinea in general has a huge diversity of habitats ranging from tropical rainforests and savannas to alpine vegetation at high elevation (Bryan and Shearman 2015). We thus suspect Eastern Wallacea and New Guinea, where much of our knowledge is based on fragmented, old collections, hold the most undescribed diversity in the entire region. Lack of accessibility to many localities remains a barrier that can only be overcome by political access and sufficient funding for fieldwork, which would be most efficient if done through local research, rather than 'parachute science'. A strong emphasis should thus be placed on collections-based research tied to local capacity building through training of students and establishment of regional collections.

Although extinction risk is high throughout the region, with nearly a fifth of species in one of the IUCN's threatened categories (Fig. 2), the skink fauna of New Caledonia especially emerges as a hotspot not only of biodiversity but also of extinction risk. Over 60% of New Caledonia's skinks are listed as threatened (Fig. 3), with the largest threats to its terrestrial biodiversity being due to mining, particularly of nickel (Pascal *et al.* 2008; L'Huillier and Jaffré 2010). Other sub-regions, while seemingly in better shape in terms of their threat assessments (but note many assessments are lacking or outdated and may change pending taxonomic revisions; Chapple *et al.* 2021), face their own unique challenges. New Guinea is facing increasing development pressures, including from the mining, petroleum, plantation, and logging industries (Shearman *et al.* 2009; Laurance *et al.* 2011; Alamgir *et al.* 2019), threatening some of the largest remaining tracts of pristine primary rainforest on the planet. Many of New Guinea's skinks are micro-endemics and microhabitat specialists (Slavenko *et al.* 2020, 2022; Kraus 2021). This places them at great risk if their habitats are not properly conserved. A clear example of the dangers that might threaten all of New Guinea is exemplified by Woodlark (Muyua) Island – an endemism hotspot that is under severe threat of habitat loss due to mining (Kraus 2021).

Habitat loss is also a major threat to skinks on other Pacific islands (Fisher and Ineich 2012), which on the whole face greater extinction risk than on New Guinea (Fig. 3). Logging, land clearance for palm oil, and nickel mining are key drivers of habitat loss in the Solomon Islands (Kabutaulaka 2000; Morrison *et al.* 2007; Wairiu 2007; Katovai *et al.* 2015; Lavery *et al.* 2021). Additionally, for especially charismatic species such as the Solomon Islands skink (*Corucia zebrata*) or crocodile skinks (*Tribolonotus* spp.), illegal harvesting for the pet trade can be a major threat (Leary 1991; Janssen and Shepherd 2018; Lavery *et al.* 2021). In addition to existing stressors, human-induced climate change is also

likely to negatively affect species in Oceania, New Guinea, and Eastern Wallacea, especially lowland species that may be vulnerable to rising sea levels; or montane endemics, which are at risk of climatic conditions shifting beyond their thermal tolerances (Duffy 2011; Kingsford and Watson 2011).

Invasive species, especially predators, have proven to be one of the greatest threats to endemic insular skinks. Introduced wolf snakes (*Lycodon capucinus*) were a primary cause of the extinction of four or more skinks species on Christmas Island and Mauritius (Smith *et al.* 2012; Michaelides *et al.* 2015; Andrew *et al.* 2018; Oliver *et al.* 2018). In the Pacific, brown tree snakes (*Boiga irregularis*) have led to the local extinction of several lizard species on Guam (Rodda and Fritts 1992; Richmond *et al.* 2022), Indian brown mongooses (*Urva fusca*) prey on skinks in Fiji (Morley and Winder 2015; see also Clause *et al.* 2018), and little fire ants (*Wasmannia auropunctata*) are associated with declines of lizards in New Caledonia (Jourdan *et al.* 2001). Wolf snakes have been spreading eastward and establishing populations on additional islands in Wallacea and New Guinea, and may therefore create an additional threat in this region in particular (Kuch and McGuire 2004; Karin *et al.* 2018; O'Shea *et al.* 2018). Given how poorly known the fauna of these regions is, there is also a real risk that invasive species could (and may have already) eliminated species that have been overlooked before they were even scientifically described (McDonald *et al.* 2022).

A sobering cautionary tale can be found in one of the few documented reptile extinctions of the modern era: the Tonga ground skink (*T. microlepis*). This species has not been seen since the 19th Century when it was originally described based on two syntypes (Duméril and Bibron 1839). It was declared extinct by the IUCN in 1996 (Allison *et al.* 2022), its extinction likely caused by direct exploitation by the original Polynesian settlers, invasive species such as pigs, cats, and rats introduced by later European explorers, and extensive land-use change for pumpkin plantations all over the main island (Ineich and Zug 1996). Although its large body size likely made it especially vulnerable to such stresses (Slavenko *et al.* 2016), it should be seen not as an outlier but rather as a canary in the coal mine – a similar fate might await other skink species in Oceania, New Guinea, and Eastern Wallacea if their conservation needs are not properly met.

In conclusion, our analyses clearly establish the islands of Oceania, New Guinea, and Eastern Wallacea as hotspots of skink diversity, and potentially of large conservation concern not only for skinks but surely other taxa as well. As this fauna is relatively poorly known, it is also likely even richer and more threatened than we are currently aware. Habitat loss, mainly due to logging and agricultural land clearing, and invasive species emerge as the major threats to the skinks of the region (Rodda and Fritts 1992; Kabutaulaka 2000; Jourdan *et al.* 2001; Laurance *et al.* 2011;

Fisher and Ineich 2012; Katovai *et al.* 2015; Morley and Winder 2015; Alamgir *et al.* 2019; McDonald *et al.* 2022). However, the region also faces unique conservation challenges: many skinks have not been assessed by the IUCN (Figs 2 and 3) and few are placed on national threatened species lists. Thus most species receive no official protection and do not attract species management plans. Local government capacity to manage threats or species conservation is often lacking, and greater involvement of local landowning communities is necessary to support conservation action (Keppel *et al.* 2012; Jupiter *et al.* 2017; Morrison *et al.* 2022). It is also likely that a large portion of the biota remains undescribed and unrecognised, suggesting a high risk of cryptic extinction (i.e. the loss of species before they are scientifically documented). Crucially – more data are needed, and local capacity to collect these data is lacking. However, local communities also offer a treasure trove of traditional knowledge approaches to conservation and data collection, which may fill many of the gaps in species ecology and distribution (McMillen *et al.* 2014; Pollard *et al.* 2014; Keppel *et al.* 2015). Oceania, New Guinea, and Eastern Wallacea are thus placed in a unique context even in the larger framework of global skink conservation (Chapple *et al.* 2021), and we encourage similar regional assessments in other regions and on other taxa. The knowledge gaps identified here may seem daunting, but they also present remarkable opportunities for further research in a fascinating, global biodiversity hotspot. However, the need to fill these gaps is urgent, and we must strive to do this before much of this unique diversity is lost.

Supplementary material

Supplementary material is available online.

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