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Geographical and temporal origins of terrestrial vertebrates endemic to Taiwan

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Abstract

Aim: Phylogeographical studies of Taiwan have advanced our knowledge of the origins of its fauna, but the discrepancies raise issues related to the interpretation of single-taxon studies. Here, we provide a synthesis of the biogeographical histories of multiple terrestrial vertebrates endemic to Taiwan and infer the colonization processes within the context of geological and climatic events.

Location: Taiwan and neighbouring land masses.

Taxon: Terrestrial vertebrates.

Methods: We conducted a meta-analysis of 28 phylogenetic studies of 33 endemic Taiwanese terrestrial vertebrates to summarize the insights into their source regions and divergence times. We used dispersal–extinction–cladogenesis models to reconstruct the ancestral ranges of 54 endemic species based on a recently published time-calibrated phylogenetic tree. By constructing a frequency histogram that quantified the number and timing of divergence events within 1 Myr bins, we inferred the spatiotemporal colonization patterns of endemic Taiwanese species.

Results: The results from 28 phylogenetic studies revealed that South China is the main source region of endemic Taiwanese species. However, based on a more comprehensive time tree, the ancestral area reconstruction analyses indicated that endemic species are predominately of Eastern Himalayan origin. Both datasets highlighted a temporal pattern that the majority of colonization events of terrestrial vertebrates endemic to Taiwan occurred from the early Pliocene (*c.* 5 Ma) onwards, and these events were temporally congruent with the geological estimates of the emergence of Taiwan Island.

Main conclusions: Terrestrial vertebrates endemic to Taiwan reached the island over the last 5 Myr from a variety of zoogeographical regions. In contrast to the traditional notion, the Eastern Himalayas is the most important source region of endemic Taiwanese species, followed by South China and Indochina. In addition to the land bridge, transoceanic dispersal provided another potential mode for species to colonize Taiwan.

KEYWORDS
colonization, DEC model, endemic species, meta-analysis, origin, phylogeography, Taiwan

1 | INTRODUCTION

The origin of modern communities is a fundamental question in evolutionary biology and biogeography (Crisp, Trewick, & Cook, 2011; Ricklefs, 2004). Islands with well-defined boundaries and high endemism (Ali, 2017) provide ideal models for understanding species origin, adaptive radiation and extinction (Parent, Caccone, & Petren, 2008; Weigelt, Steinbauer, Cabral, & Kreft, 2016). Recently, the spatial and temporal origins of insular communities on several tropical islands have been thoroughly addressed using molecular data (e.g. Brown et al., 2013; Crottini et al., 2012; de Bruyn et al., 2014; Stelbrink, Albrecht, Hall, & von Rintelen, 2012). Nevertheless, studies on East Asian islands are comparatively limited, and due to the distinct geological contexts, the biogeographical patterns on East Asian islands are rather distinct (Li, Fu, & Lei, 2011; Komaki et al., 2017; Su, Brown, Chang, Lin, & Tso, 2016; Yang, Komaki, Brown, & Lin, 2018).

Taiwan Island (hereafter Taiwan) is a continental island located *c.* 130 km from the Asian mainland (Figure 1a) and is well-known for high biodiversity and endemism (Feng, Mao, Sandel, Swenson, & Svenning, 2016; Lei, Qu, Lu, Liu, & Yin, 2003). Taiwan did not emerge above sea level until the Mio-Pliocene boundary (*c.* 5 Ma) owing to the collision of the Philippine Sea plate and the Eurasian plate (Sibuet & Hsu, 2004; Teng, 1990). Accordingly, like newly formed oceanic islands, the present-day biota of Taiwan is expected to have originated from the Asian continent or surrounding islands (Ali, 2017). Taiwan provides varied habitats for species from diverse biomes (Chou, Thomas, Ge, LePage, & Wang, 2011) as it is geographically located at the interface of the Palaearctic and Oriental faunal zones (Päckert, Martens, & Severinghaus, 2009) and exhibits large elevational heterogeneity (Figure 1b; Ito et al., 2017). Furthermore, the periodic emergence of a land bridge that connected Taiwan to the Asian mainland during Quaternary glacial cycling contributed to intermittent biotic interchanges or geographical isolations (Qu et al., 2015). Due to the specific geographical context, Taiwan has served as a natural laboratory for studying the roles of dispersal–vicariance in shaping the present insular biodiversity (Ito et al., 2017; Su et al., 2016). However, temporal and geographical origins of the fauna of Taiwan are still debatable (Ali, 2018; Chen, Chang, et al., 2015).

Recently, five hypothetical source regions of endemic Taiwanese species were proposed (Table 1): South China, North China, the Eastern Himalayas, Japan and Indochina (Figure 1a). Traditionally, South China is considered the most likely source region given its geographical position, and the Pleistocene land bridge that resulted from successive glacial events favours this theory (Jing, Yu, Wu, Wang, & Zheng, 2007; Li et al., 2006; Qu et al., 2015). However, the glaciation maxima not only formed the land bridge but also cooled northeast Asia. Under these scenarios, Taiwan served as a refuge for temperate species contracted from North China during the Quaternary glaciations (Chou et al., 2011), as indicated by the extant species (e.g. *Regulus goodfellowi*, Päckert et al., 2009), as well as the extinct species (e.g. *Mammuthus trogontherii* and *Equus* spp., Kawamura, Chang, & Kawamura, 2016). In addition, some studies noticed that several Taiwanese species originated from distant regions, such as Indochina (Chen, Chang, et al., 2015; Jiang, Wang, Peng, Peng, & Zou, 2014) and the Eastern Himalayas (Mays et al., 2015), which was facilitated by either an exposed continental shelf of the South China Sea or a suitable dispersal corridor from South China during the glacial periods. Furthermore, several lineages were believed to colonize from Japan via a 1,200-km-long stepping stone island chain—the Ryukyu Islands (Li et al., 2011).

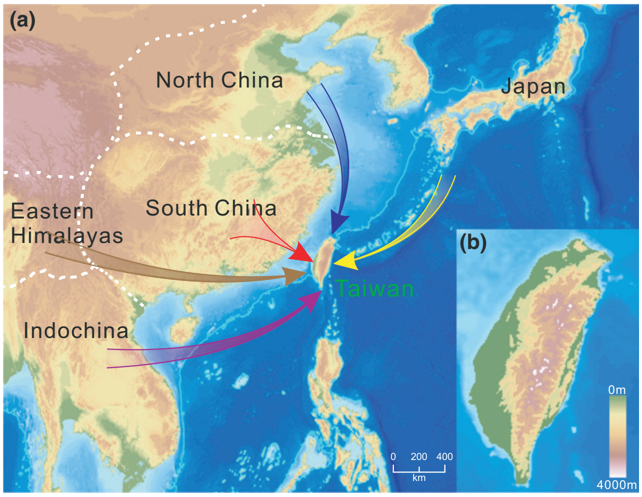

FIGURE 1 Map of Taiwan Island and neighbouring land masses. (a) The map shows five hypothetical colonization routes of species endemic to Taiwan from Indochina (purple), South China (red), the Eastern Himalayas (brown), North China (blue) and Japan (yellow). (b) The map shows the topography of Taiwan Island. The maps were reconstructed from ETOPO1 one arc-minute global relief models, with land topography indicating current land mass surrounded by a −120 m isobath (light blue, indicating sea shores during the Last Glacial Maximum)

Although debates continue regarding the geographical origins of endemic Taiwanese species, evidence that the timing of colonization events is highly related to the land bridges during the Pleistocene is accumulating (e.g. Chen, Chang, et al., 2015; Jing et al., 2007; Li et al., 2006; Qu et al., 2015; Wang et al., 2013). That is, the periodic emergences of a land bridge have facilitated the colonization of mainland-derived species in Taiwan, which was followed by vicariant speciation. Most recently, however, the temporal origins of endemic Taiwanese species have received revived interest (Ali, 2018), owing to the discrepancy between molecular dating of endemic species (Lv, He, Klaus, Brown, & Li, 2018) and geological histories of Taiwan (Sibuet & Hsu, 2004; Teng, 1990). For instance, some species endemic to Taiwan diverged from mainland relatives before the Pliocene-Pleistocene boundary (*c.* 2.6 Ma) when the land bridge was not present (e.g. Päckert et al., 2009; Shinohara et al., 2014); more unexpectedly, some cases even occurred prior to *c.* 5 Ma (e.g. Li et al., 2011; Lv et al., 2018; Nishizawa et al., 2011) when Taiwan had not yet emerged above sea level (Teng, 1990).

TABLE 1 List of 28 previous studies representing 33 taxa endemic to Taiwan used for the phylogeographical meta-analysis

			Divergence time (Ma)			
No	**Taxa**	**Origin**	**Mean**	**95% CI**	**Taxonomic coverage**	**Reference**
Mammal						
1	*Capricornis swinhoei*	SC	0.53	0.41–0.65	3/6	Liu et al. (2013)
2	*Rhinolophus monoceros*	SC	4.8	1.8–7.8	30/77	Stoffberg, Jacobs, Mackie, and Matthee (2010)
3	*Anourosorex yamashinai*	EH	0.66	0.18–1.35	2/4	He et al. (2010)
4	*Chodsigoa sodalis*	EH	2.15	1.32–3.17	4/8	He et al. (2010)
5	*Episoriculus fumidus*	EH	5.57	4.0–7.34	4/4[a]	He et al. (2010)
6	*Mogera kanoana*	SC	4.5	3–6.2	6/8[a]	Shinohara et al. (2014)
7	*Macaca cyclopis*	INC	1.2	0.8–1.6	22/22[a]	Disotell and Tosi (2007)
8	*Microtus kikuchii*	PA	0.79	0.63–0.95	23/62	Bannikova et al. (2010)
9	*Apodemus semotus*	SC	1	—	15/20	Suzuki et al. (2003)
10	*Niviventer coninga*	SC	2.5	1.8–3.6	15/17	He and Jiang (2015)
11	*Niviventer culturatus*	SC	4.88	*c.* 3.5–6.35	15/17	He and Jiang (2015)
Bird						
12	*Arborophila crudigularis*	EH & INC	3.8	2.8–4.8	10/18[a]	Chen, Chang et al. (2015)
13	*Lophura swinhoii*	INC	2.71	1.31–4.22	9/11	Jiang et al. (2014)
14	*Syrmaticus mikado*	SC	2.8	1.0–4.6	5/5[a]	Zhan and Zhang (2005)
15	*Garrulax poecilorhynchus*	SC	0.75	0.62–0.83	23/50[a]	Luo, Qu, Han, Li, and Lei (2009)
16	*Garrulax taewanus*	SC	1.5	1.25–1.75	7/63	Li et al. (2006)
17	*Garrulax ruficeps*	EH	0.96	0.79–1.05	23/50[a]	Luo et al. (2009)
18	*Garrulax morrisonianus*	SC	2.57	2.04–2.77	23/50[a]	Luo et al. (2009)
19	*Liocichla steerii*	EH	8.94	5.55–12.87	5/5[a]	Mays et al. (2015)
20	*Pycnonotus taivanus*	SC	*c.* 0.1	—	35/42[a]	Dejtaradol et al. (2016)
21	*Regulus goodfellowi*	PA	3.48	3.45–3.52	6/6[a]	Päckert et al. (2009)
22	*Pomatorhinus erythrocnemis*	EH	4.67	*c.* 3.5–5.84	8/9[a]	Dong, Li, and Yang (2010)
23	*Pomatorhinus musicus*	SC	*c.* 0.8	*c.* 0.5–1.1	6/11[a]	Reddy et al. (2015)
24	*Megalaima nuchalis*	SC	*c.* 1.2	*c.* 0.8–1.6	30/30[a]	den Tex and Leonard (2013)
Reptile						
25	*Takydromus* spp.	SC & NCK	4.06	2.07–6.55	16/22[a]	Tseng et al. (2015)
26	*Trimeresurus gracilis*	JP	11.06	—	263/332[a]	Alencar et al. (2016)
Amphibian						
27	*Odorrana swinhoana*	SC	6.84	4.86–9.1	43/53[a]	Chen et al. (2013)
28	*Rana longicrus*	SC	1.6	1.0–2.6	15/?	Zhou et al. (2017)
29	*Rana sauteri*	JP	18.33	13.49–22.06	82/?	Yuan et al. (2016)
30	*Buergeria robusta*	JP	26.3	17.8–36.7	3/4[a]	Nishizawa et al. (2011)
31	*Kurixalus idiootocus*	INC	32.8	25.6–39.9	10/14[a]	Lv et al. (2018)
32	*Rhacophorus moltrechti*	SC	*c.* 8.6	—	57/88[a]	Pan et al. (2017)
33	*Hynobius* spp.	JP	32.79	25.94–40.04	32/32[a]	Li et al. (2011)

Note. "Origin" is used for cases where Taiwanese taxa are merely sister groups to lineages inhabiting adjacent regions: SC, South China; INC, Indochina; EH, the Eastern Himalayas; PA, Palaearctic; JP, Japan; NCK, North China & Korea. "Taxonomic coverage" refers to the fraction of species used in original studies out of the total number of species currently described in the genus-level clade, with "a" indicating that the species numbers are extracted from the original studies.

As a result, the temporal biogeographical patterns of Taiwanese fauna need to be addressed to reconcile the patterns with geological and climatic events.

Recently, the development of molecular time trees and phylogeographical studies have greatly contributed to our knowledge of the origins of Taiwanese species, but most of these studies are on a case by case basis. Fragmented knowledge of the routes and timings of colonization events limits our understanding of the spatiotemporal biogeographical patterns. In this study, we aimed to investigate the geographical and temporal origins of Taiwanese fauna based on a synthesis of multiple terrestrial vertebrates endemic to this island. Using a meta-analysis of phylogeographical studies and ancestral range estimates, we specifically asked three primary questions: (a) From where did the endemic Taiwanese species originate? (b) When did these species colonize Taiwan? (c) Did all species colonize Taiwan via a land bridge during glaciation maxima?

2 | MATERIALS AND METHODS

2.1 | Species distribution data

A checklist of Taiwanese terrestrial vertebrates was built using Lin (2008) for mammals, Ding et al. (2017) for birds, and Hsiang, Lee, and Yang (2009) for reptiles and amphibians. The geographical ranges of birds were obtained from Birdlife International and NatureServe (http://www.birdlife.org). The species distribution maps for mammals and amphibians were downloaded from the IUCN Red List website (http://www.iucnredlist.org). Distributional information for reptiles was based on the Reptile Database (http://reptile-database.reptarium.cz/). We excluded 611 introduced, marine and migratory species according to the species distribution databases. The final database had a total of 272 species (including 80 endemic species), which were used in the analysis (see Supporting Information Appendix S1).

2.2 | Analysed studies

A literature search was performed for published time-calibrated phylogenies that contained at least one tip representing terrestrial vertebrates endemic to Taiwan. To investigate the spatial and temporal colonization events of Taiwanese fauna, we selected the phylogenies based on three criteria: (a) taxa were analysed at the species level, (b) the source regions of sister taxa could be identified, and (c) a quantitative divergence time was available. For those lineages that were investigated by several studies, we used only the phylogenies from the latest published studies. This method resulted in 28 phylogenetic studies covering 33 endemic Taiwanese taxa for further analysis (Table 1; see also Supporting Information Appendix S2: Table S2.1 for a full list of previous phylogenetic studies). The geographical ranges of crown groups and divergence times between Taiwanese clades and their closest non-Taiwanese sister groups are the main evidence for inferring the spatial and temporal arrival patterns of endemic Taiwanese taxa. For each divergence event, we extracted the most likely source region of the Taiwanese clade (i.e. where the closest non-Taiwanese relative inhabits) as well as the mean age estimates of the stem-based node (separation of the Taiwanese clades from their relatives) with 95% confidence intervals of the ages if available.

2.3 | Phylogenetic information

To estimate the ancestral ranges of the clades of endemic Taiwanese species, we used a nearly complete and highly resolved (nodes-to-tips ratio: 75%) time tree of extant terrestrial vertebrates (Hedges, Marin, Suleski, Paymer, & Kumar, 2015). This phylogenetic tree was built based on published time trees from 2,274 molecular studies and provides a framework to study the origin and diversity of life (Hedges et al., 2015). Because incomplete taxon sampling strongly affects the quality of the topology and age estimates of phylogenies (Stelbrink et al., 2012), as well as the sources and ages of specific colonization events, we used only phylogenies with relatively complete species sampling ($\geq$80%). In addition, to enhance the taxonomic coverage, we extracted the smoothed mammal and bird phylogenies from Hedges et al. (2015); however, *c.* 30% of species were interpolated without molecular data, and the precise placements and divergence times of these species remain uncertain to some degree. Accordingly, after combining species distributions and phylogenetic information, we extracted 41 individual phylogenies covering 54 endemic Taiwanese species for further analysis. To validate our inferences, we repeated the analyses based on four independent dated phylogenies (Kuhn, Mooers, & Thomas, 2011 for mammals; Jetz, Thomas, Joy, Hartmann, & Mooers, 2012 for birds; Zheng & Wiens, 2016 for reptiles; and Pyron, 2014 for amphibians). Phylogenetic data for birds (Jetz et al., 2012) and mammals (Kuhn et al., 2011) were available as resampled sets of posterior distributions of trees (n = 100), and we built maximum clade credibility phylogenies using the ‘phangorn’ package (Schliep, 2011) in R version 3.2.3 (R Development Core Team, 2015). For the reptiles (Zheng & Wiens, 2016) and amphibians (Pyron, 2014), we used only the single trees provided by the authors.

2.4 | Ancestral range estimates

To reconstruct the biogeographical history of endemic Taiwanese species, we used the ‘BioGeoBEARS’ package (Matzke, 2014) to perform ancestral area estimations across 41 individual phylogenies extracted from Hedges et al. (2015) (Supporting Information Appendix S3). We applied the dispersal–extinction–cladogenesis model (DEC; Ree & Smith, 2008), and the modified dispersal–extinction–cladogenesis+j (DEC+j) model, which incorporates a parameter known as founder-event speciation (long-distance or oversea dispersal, Matzke, 2014). We compared models with two parameters (d: dispersal and e: extinction) against models with three parameters (d, e, and j: founder-event speciation) and used Akaike's information criterion (AIC) to select the best biogeographical model (Matzke, 2014). The geographical distributions of species were coded as presence/absence in 12 biogeographical regions (He, Kreft, Gao, Wang, & Jiang, 2017; Kreft & Jetz, 2010), namely, Taiwan (TW), South China (SC), North China & Korea (NCK), Japan (JP), the Eastern Himalayas (EH), the Malay Archipelago (ML), Indochina (INC), India & Sri Lanka (INL), Australian (AU), Americas (AM), Africa (AF) and the Palaearctic (PA) (Supporting Information Appendix S2: Figure S2.1). To confirm our findings, we repeated the ancestral range estimates using four independent time trees.

2.5 | Biogeographical event estimates

To investigate the biogeographical histories of endemic Taiwanese species, we compiled the ancestral ranges and age estimates of divergence events between Taiwanese taxa and non-Taiwanese sister clades based on two datasets: (a) 28 individual phylogenies from previous studies and (b) 41 phylogenies extracted from Hedges et al. (2015). We assume that the geographical and temporal congruence of divergence events across multiple and independent lineages indicates major colonization events, where species colonized Taiwan (Klaus, Morley, Plath, Zhang, & Li, 2016). Furthermore, to explore whether the temporal frequency of divergence events changed in space, three predominant colonization routes were categorized as follows: northern route (Palaearctic + North China & Korea + Japan), western route (South China + the Eastern Himalayas + India & Sri Lanka) and southern route (Indochina + the Malay Archipelago). Subsequently, we quantified the number and timing of divergence events within each 1 Myr bin and constructed a cumulative frequency histogram. In addition to the absolute number of divergence events, which is potentially biased towards the present by accelerated speciation rates (Jetz et al., 2012), we assessed the temporal shifts in divergence events following the methods in Klaus et al. (2016) using change point analysis in the 'ecp' package (James & Matteson, 2014) in R. Finally, we compared the timeframe-specific divergence events to palaeogeographic contexts for those periods.

3 | RESULTS

Our database resulted in a total of 272 species in Taiwan for analysis (Table 2). Among them, 80 species are endemic, including 18 mammals, 23 birds, 22 reptiles and 17 amphibians. Thus, 192 non-endemic species that shared geographical ranges with adjacent land masses, such as South China (84.4%) and Indochina (60.4%), remained (Table 2).

Our meta-analysis of 28 published molecular datasets yielded divergence events of 33 endemic taxa, indicating that most (17 taxa) originated from South China (Table 1). The Eastern Himalayas emerged as the second-most important source region with 7 taxa originating from that region, followed by Japan (4 taxa), Indochina (3 taxa) and Palaearctic (2 taxa). Based on the results of the biogeographical models, the DEC+j models generally received the highest support for all but four phylogenies: *Arielulus*, *Episoriculus*, *Yuhina* and *Kurixalus* (Supporting Information Appendix S2: Table S2.2). The topology of the time-calibrated tree combined with the DEC+j models yielded 48 divergence events between endemic Taiwanese species and their sister clades, including an Eastern Himalayan origins for 17 taxa, a South China origins for 11 taxa, an Indochinese origins for nine taxa, a Japanese origins for four taxa, a Palaearctic origins for four taxa, a Malay Archipelago origins for two taxa and an India & Sri Lanka origin for one taxa (Figure 2). In addition, repeated analyses based on four independent phylogenetic trees provided similar results. According to the best models selected by the AICs (Supporting Information Appendix S2: Table S2.3), 15 taxa (out of 45 taxa) originated from the Eastern Himalayas, followed by eight taxa from Indochina and seven taxa from South China (Supporting Information Appendix S2: Table S2.4).

The meta-analysis of 28 published phylogenetic studies revealed that a majority of divergence events across multiple endemic Taiwanese species (24 of 33 taxa; 72.7% cases) were temporally congruent, dating back to the early Pliocene period (*c.* 5 Ma; Figure 3a). The result from the single time-calibrated molecular phylogeny also revealed a consistent pattern wherein the largest divergence wave (33 of 48 taxa; 68.8% cases) emerged from *c.* 5–6 Ma onwards (Figure 3b). In addition, the change point analyses indicated that the sudden change points of two approaches coincidently occurred *c.* 5–6 Ma (Figure 3), supporting the importance of this time window. Considering the geographical and temporal divergence events, there was a trend that the divergence ages of clades originating from the northern routes (Palaearctic + North China & Korea + Japan) are older than those from the western routes (South China + the Eastern Himalayas + India & Sri Lanka) or the southern routes (Indochina + the Malay Archipelago) (Mann–Whitney U test, $p < 0.05$; Figure 3; Supporting Information Appendix S2: Figure S2.2a).

Among the 54 species endemic to Taiwan, 45 species are single-species endemic (Figure 2), indicating that adaptive radiation is rather rare and multiple successful colonizations primarily shaped the present-day vertebrate fauna of Taiwan. However, the remaining

TABLE 2 Number of resident and endemic terrestrial vertebrates of Taiwan and their relationships with nearby regions. Introduced, marine and migratory species were excluded

	Number of species in Taiwan (*n*)			Percentage of non-endemic species to Taiwan shared with nearby regions (%)						
Class	Total	Endemic	Non-endemic	North China & Korea	Japan	South China	Indochina	Eastern Himalayas	Malay Archipelago	India and Sri Lanka
Mammal	68	18	50	40.0	20.0	90.0	58.0	66.0	28.0	24.0
Bird	85	23	62	17.7	14.5	80.6	77.4	75.8	51.6	51.6
Reptile	83	22	61	19.7	8.2	86.9	47.5	37.7	18.0	21.3
Amphibian	36	17	19	10.5	21.1	73.7	52.6	31.6	26.3	15.8
Total	272	80	192	23.4	14.6	84.4	60.4	56.8	32.3	31.3

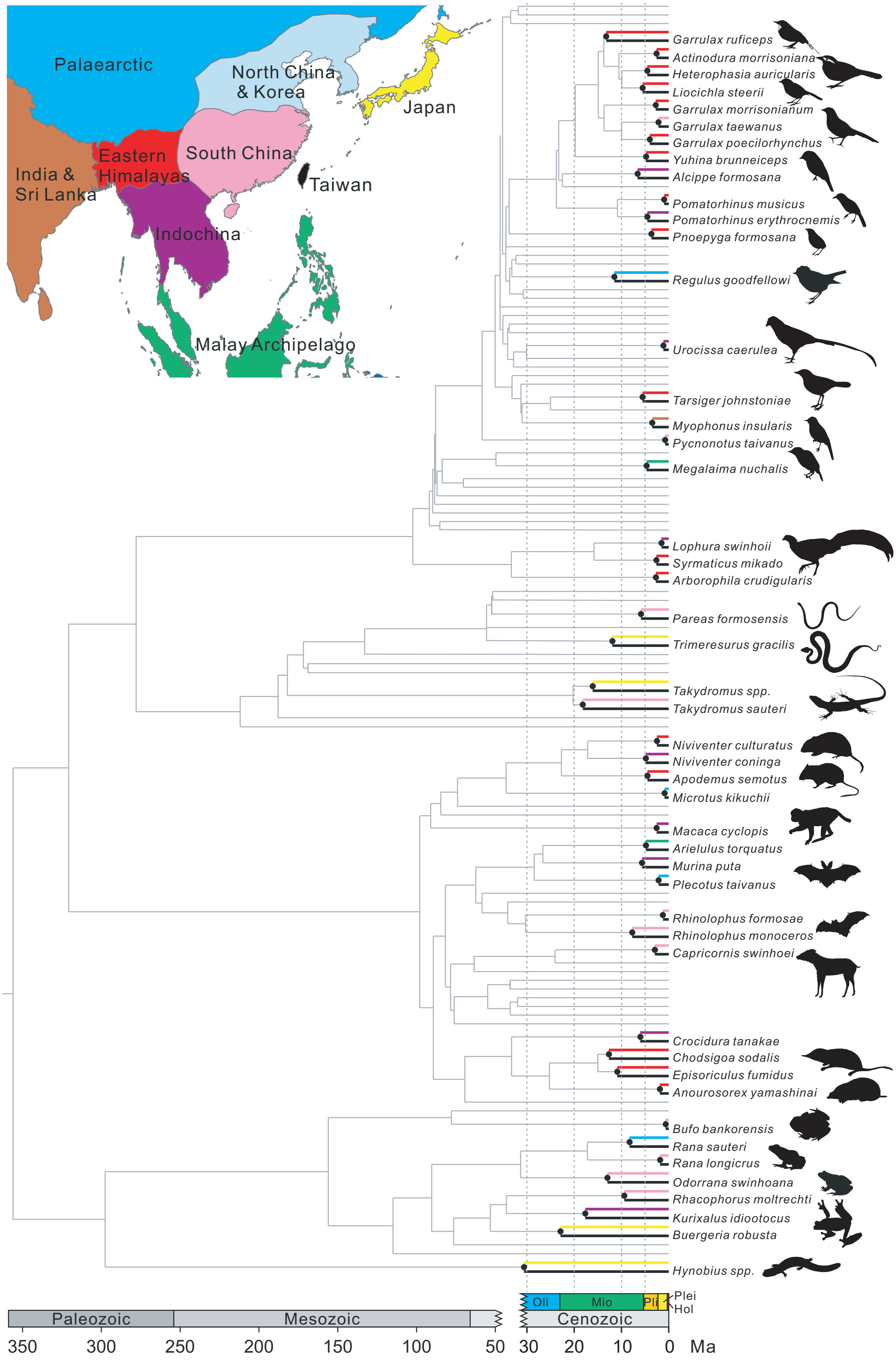
Palaearctic
North China & Korea
Japan
Eastern Himalayas
South China
India & Sri Lanka
Taiwan
Indochina
Malay Archipelago
Garrulax ruficeps
Actinodura morrisoniana
Heterophasia auricularis
Liocichla steerii
Garrulax morrisonianum
Garrulax taewanus
Garrulax poecilorhynchus
Yuhina brunneiceps
Alcippe formosana
Pomatorhinus musicus
Pomatorhinus erythrocnemis
Pnoepyga formosana
Regulus goodfellowi
Urocissa caerulea
Tarsiger johnstoniae
Myophonus insularis
Pycnonotus taivanus
Megalaima nuchalis
Lophura swinhoii
Syrmaticus mikado
Arborophila crudigularis
Pareas formosensis
Trimeresurus gracilis
Takydromus spp.
Takydromus sauteri
Niviventer culturatus
Niviventer coninga
Apodemus semotus
Microtus kikuchii
Macaca cyclopis
Arielulus torquatus
Murina puta
Plecotus taivanus
Rhinolophus formosae
Rhinolophus monoceros
Capricornis swinhoei
Crocidura tanakae
Chodsigoa sodalis
Episoriculus fumidus
Anourosorex yamashinai
Bufo bankorensis
Rana sauteri
Rana longicrus
Odorrana swinhoana
Rhacophorus moltrechti
Kurixalus idiootocus
Buergeria robusta
Hynobius spp.
Oli
Mio
Pli
Plei
Hol
Paleozoic
Mesozoic
Cenozoic
350
300
250
200
150
100
50
30
20
10
0
Ma

FIGURE 2 Phylogenetic tree of terrestrial vertebrates endemic to Taiwan and their sister clades. The black branches with species names are taxa endemic to Taiwan, and the coloured branches indicate their closest relatives that were recorded in nearby regions with colours consistent with the inset map (see Supporting Information Appendix S3 for all detailed DEC results)

nine species belonging to two groups (*Hynobius* spp. and *Takydromus* spp.) exhibited exceptional biogeographical patterns (Figure 2). The ancestor of the Taiwanese *Hynobius* salamanders split from the Japanese relatives *c.* 30 Ma, and this split was followed by successive divergence events in this clade (see Supporting Information Appendix S3). The biogeographical history of the Taiwanese glass lizards (*Takydromus*) is more complicated. At least two independent divergence events have occurred, with one splitting from the South China lineage (*c.* 20.8 Ma) and another splitting from the Japanese lineage (*c.* 15.9 Ma). Subsequently, lineages within the Asian mainland, Taiwan and Japan have experienced multiple divergence events from *c.* 10 Ma onwards (Supporting Information Appendix S3).

4 | DISCUSSION

4.1 | Geographical origin of Taiwanese fauna

Based on the results of 28 phylogenetic studies, species endemic to Taiwan are predominately of South China origin (Table 1). However, the results of the DEC models revealed that a majority of endemic Taiwanese species colonized from the Eastern Himalayas (Figure 2; Supporting Information Appendix S2: Table S2.4). These discrepancies may be attributed to three reasons. First, phylogenetic information of endemic Taiwanese species was not available for all taxa. The published studies were generally biased towards the species that colonized from nearby South China (Supporting Information Appendix S2: Table S2.4), leaving large gaps in those potentially originating from other distant regions (Chen, Chang, et al., 2015), and thus, hindering the comparison to some degree. Second, owing to the different objectives of the previous studies, some phylogenetic analyses that did not include all possible mainland relatives could have biased the results (e.g. He et al., 2010; Liu et al., 2013). Third, most studies used the term “origin” in a loose sense for cases where Taiwanese taxa shared an immediate common ancestor with a mainland clade, rather than incorporating more convincing methods such as ancestral range estimates. Under these circumstances, potential mistakes could arise. Thus, taking advantage of the most comprehensive taxon sampling and ancestral range reconstruction, we advocate that the Eastern Himalayas are the main source region of species endemic to Taiwan.

Although recent phylogeographical studies have noted that several endemic Taiwanese taxa originated from the Eastern Himalayas rather than nearby South China, either at the species level (Mays et al., 2015; Päckert et al., 2012) or the population level (Tietze, Päckert, Martens, Lehmann, & Sun, 2013; Wang et al., 2013; Wu et al., 2011), few of these studies considered it a common pattern (Päckert et al., 2012). One possible reason is that Quaternary glaciations not only formed a land bridge but also prompted the dispersal of montane species from the Eastern Himalayas to lowland South China and Taiwan (Tietze et al., 2013; Wu et al., 2011). Once the glaciations ended, the rising sea levels resulted in vicariant isolation, and the relict populations might have retreated to the montane habitat of Taiwan and the Eastern Himalayas and caused disjunctive distributions (Päckert et al., 2012; Wang et al., 2013). Similarly, high floristic similarity between Taiwan and the Eastern Himalayas has been reported before (Liao & Chen, 2017), and disjunctive

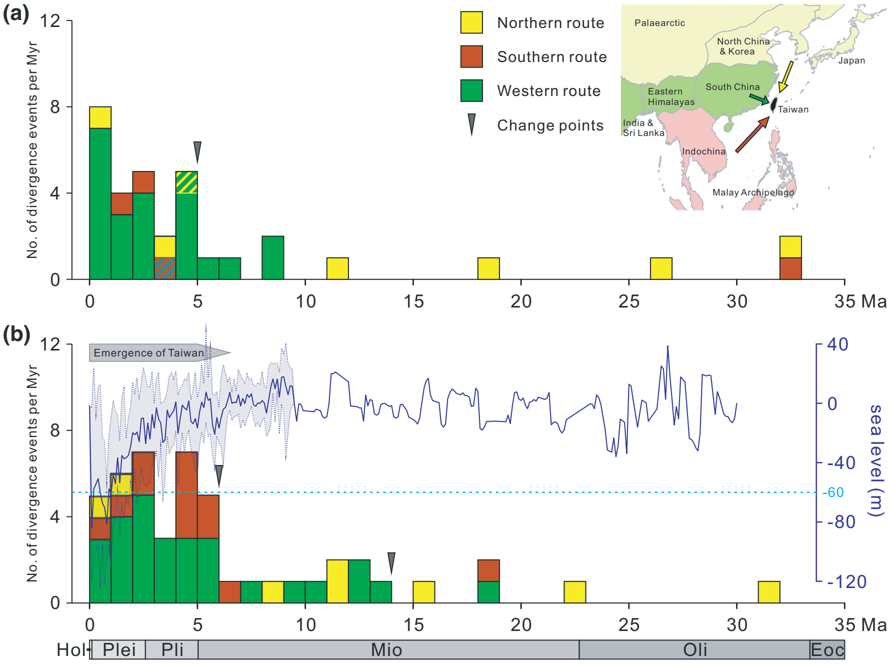

FIGURE 3 Histograms of stem divergence ages of taxa endemic to Taiwan within 1 Myr time bins. Divergence events were derived from (a) 28 individual studies (based on Table 1), and (b) 41 phylogenetic trees extracted from Hedges et al. (2015) (based on Figure 2). Sea level fluctuations are redrawn from Miller et al. (2005), with the solid blue line indicating the mean sea level and dotted lines (from 9.5 Ma onwards) indicating the maximum and minimum sea level within 0.1 Myr time bins. The land bridge connecting Taiwan with the Asian mainland was submerged unless the sea level dropped more than 60 m (light blue line). The emergence of Taiwan was dated back to *c.* 5 Ma (Teng, 1990)

distributions between these two regions have also been recently noted in multiple plants (e.g. Matuszak, Muellner-Riehl, Sun, & Favre, 2016; Niu et al., 2018), supporting the Eastern Himalayas as an important source of endemic Taiwanese species.

Compared with the Eastern Himalayas, South China served as the secondary source of species endemic to Taiwan (Figure 2; Supporting Information Appendix S2: Table S2.5), even though this area shares the highest proportion of non-endemic Taiwanese species (Table 2). This finding is reasonable because the close geographical setting between South China and Taiwan provides more opportunities for biotic interchange, thus lowering the genetic endemism of the Taiwanese populations (Qu et al., 2015). In addition, in agreement with previous studies, we recognized Indochina (Chen, Chang, et al., 2015; Jiang et al., 2014; Lv et al., 2018), Japan (Li et al., 2011; Nishizawa et al., 2011) and the Palaearctic (Päckert et al., 2009) as source regions of endemic Taiwanese species (Figure 2). Nevertheless, our result revealed that three endemic species (*Myophonus insularis*, *Megalaima nuchalis*, and *Arielulus torquatus*) originated from India & Sri Lanka and the Malay Archipelago, which were rarely considered possible source regions (Figure 2). These species with strong flight abilities might occasionally disperse the long-distance to Taiwan (Chen, Chang, et al., 2015), and the disjunctive distributions are presumably attributed to the long geographical isolation (Qu et al., 2015) or the legacy of historical climate change (Wang et al., 2013).

Notably, some differences emerged when contrasting the source regions of different lineages (Figure 2; Supporting Information Appendix S2: Table S2.5). For instance, 12 birds and five mammals originated from the Eastern Himalayas, whereas a majority of ectotherms colonized from the nearby regions such as South China and Japan. This incongruence among lineages is consistent with previous studies that focused on the pairwise similarities of species composition (He et al., 2017; Holt et al., 2013). It has been reported that different lineages showed varied biogeographical patterns in response to the geological and climatic history (Wang et al., 2013), which is partly due to different dispersal capabilities and thermal tolerances. Alternatively, compared with ectotherms that have relatively limited dispersal abilities, the periodic land bridge might have provided greater opportunities for gene flow between the Taiwanese avian species and their sister clades in South China (Hung et al., 2014; Qu et al., 2015). Together, either of these scenarios might result in this low cross-taxon congruence. Nevertheless, different lineages have shared significant geological, evolutionary and climatic histories, which are revealed by the consistent biogeographical patterns (Crottini et al., 2012; Klaus et al., 2016). Thus, synthesizing multiple lineages to infer the spatiotemporal colonization processes of insular fauna proved to be informative (Brown et al., 2013; de Bruyn et al., 2014; Stelbrink et al., 2012).

4.2 | Temporal origin of Taiwanese fauna

The temporal patterns of these colonization events based on the meta-analysis were strikingly consistent with those resulting from the DEC models (compare Figure 3a to b), indicating that the major colonization wave into Taiwan may have occurred *c.* 5–6 Ma. Further evidence supporting this important timing of colonization events can be found in other lineages, such as invertebrates (Shih, Hung, Schubart, Chen, & Chang, 2006; Su et al., 2016), freshwater fish (Chiang, Lin, Shao, & Hsu, 2010) and plants (Chou et al., 2011; Ito et al., 2017; Matuszak et al., 2016). Collectively, the highly supported congruency provided robust biogeographical evidence that extant Taiwanese species have colonized from neighbouring land masses since the early Pliocene (*c.* 5 Ma), which is highly coincident with the estimated geological age of Taiwan (Sibuet & Hsu, 2004; Teng, 1990).

Although the emergence of Taiwan offered new habitat for potential colonization, the colonization events that occurred during different time windows were likely via different modes. Traditionally, the most proposed colonization mode of Taiwanese species has been the land bridge hypothesis (Jing et al., 2007; Li et al., 2006; Qu et al., 2015). However, this land bridge did not emerge before *c.* 2.6 Ma when the sea level was frequently below −60 m (Figure 3b; Miller et al., 2005). This finding implies that the colonization events into Taiwan cannot be entirely explained by the land bridge hypothesis, and divergence events that occurred before 2.6 Ma might be the results of transoceanic dispersal. Despite the lack of empirical evidence, several Taiwanese reptiles have been posited to colonize from the Malay Archipelago by oversea dispersal (Hsiang et al., 2009). Evidence from the Taiwan-Ryukyu Islands (Komaki et al., 2017; Yang et al., 2018) and the Taiwan-Luzon Islands (Esselstyn & Oliveros, 2010) has also supported oversea dispersal as a potential mechanism for the geographical origin of insular vertebrates. Accordingly, we suggest that prior to the emergence of the Pleistocene land bridge; Taiwan might have provided virgin habitat such as newly formed oceanic islands for the pioneers derived from the mainland via oversea dispersal.

We also identified that some of the endemic taxa of Taiwan diverged from their mainland relatives prior to *c.* 5 Ma (Figures 2 and 3), when Taiwan had not yet emerged above sea level (Teng, 1990). Recent studies on animals (Li et al., 2011; Lv et al., 2018; Nishizawa et al., 2011) and plants (Wang et al., 2017) have noted a similar pattern. In other regions of the world, it has been reported that the ages of island endemic taxa significantly pre-date the ages of islands (Parent et al., 2008; Renner, Strijk, Strasberg, & Thébaud, 2010). Hawlitschek et al. (2017) provided two potential explanations: (a) the sister clades of island lineages have recently gone extinct, or the historical stepping-stone dispersal routes have submerged; (b) the geological ages of the islands were largely underestimated. With respect to Taiwan, a much earlier emergence of this island has been suggested to reconcile with the earlier timing of colonization (Li et al., 2011). However, unlike oceanic islands whose geological ages are easily underestimated due to irregular volcanic activities (Hawlitschek et al., 2017; Parent et al., 2008), palaeogeological studies (Sibuet & Hsu, 2004; Teng, 1990) and palaeontological information (i.e. fossils; Kawamura et al., 2016) have provided strong and widely accepted evidence regarding the timing of the emergence of Taiwan.

In addition, although *in situ* speciation events of terrestrial Taiwanese vertebrates have been reported (Lai & Lue, 2008; Li et al., 2011; Tseng, Li, Hsieh, Wang, & Lin, 2014; Tseng, Wang, Li, & Lin, 2015), few of these events pre-date the early Pliocene (*c.* 5 Ma; but see Li et al., 2011 for *Hynobius* spp.). Therefore, we advocate for the first explanation of Hawlitschek et al. (2017) that the divergence events of extant species occurred before their colonization into Taiwan, and extinctions within the ancestral taxa resulted in relict populations in Taiwan (Mays et al., 2015; Wang et al., 2013). This reconciliation does not necessarily oppose the time window of colonization events occurring from *c.* 5 Ma onwards.

Interestingly, the divergence ages of endemic species colonizing Taiwan from the northern routes are older than those from the western and southern routes (Figure 3; Supporting Information Appendix S2: Figure S2.2a). Of the eight divergence events from the northern route, six cases occurred before the formation of Taiwan (Figure 3b), and most of these cases are ectotherms (five out of six taxa; Figure 2) with higher sensitivities to climatic conditions. Furthermore, the elevation ranges of endemic species from the northern routes are significantly higher than those from the western and southern routes (Mann–Whitney *U* test, $p < 0.05$; Supporting Information Appendix S2: Figure S2.2b). Together, these findings could lend support to the hypothesis that during the glacial maxima, a land bridge facilitated the contraction of the geographical ranges of some ancient species southwards into Taiwan (Kawamura et al., 2016). Moreover, during interglacial periods, these temperate species were locked by rising sea levels and might have migrated to higher elevations and eventually survived in Taiwan. In contrast, species from the western and southern routes predominately colonized Taiwan after *c.* 5 Ma, and these colonizations were followed by subsequent vicariance events, thus resulting in relatively young divergence ages (Figures 2 and 3).

4.3 | Unsolved biogeographical patterns

The biogeographical history of Taiwanese *Hynobius* salamanders and *Takydromus* could not be unambiguously resolved (Figure 2; Supporting Information Appendix S3). Although previous studies have also explored the spatiotemporal origins of these lineages (Li et al., 2011; Lin, Chen, & Lue, 2002; Tseng et al., 2015), some discrepancies have emerged between the molecular dating and geological context. For example, the first divergence of the Taiwanese *Hynobius* lineages from the Japanese lineages was estimated to have occurred *c.* 16–32.8 Ma, and the subsequent speciation within the Taiwanese salamanders occurred before *c.* 5 Ma (Hedges et al., 2015; Li et al., 2011; Pyron, 2014), which largely precedes the existence of Taiwan (Teng, 1990). Although the ages of island endemic species do not necessarily post-date the ages of islands as discussed above, it is unlikely that the closest relatives of all five Taiwanese salamanders went extinct after the colonization events. Alternatively, a previous study has blamed this phenomenon on a much earlier emergence of Taiwan as a result of the so-called "Taiwan-Sinzi Folded Zone" (Li et al., 2011). However, we failed to find convincing evidence of such a palaeogeographic event and could not detect similar patterns in other Taiwanese taxa to support this hypothesis. Therefore, this inconsistency implies that a younger stem divergence time of Taiwanese *Hynobius* salamanders should be considered (Chen, Mao, et al., 2015). Similarly, this incongruence also exists in the *Takydromus* group. The estimated divergence events between Taiwanese lineages and other lineages were dated back to *c.* 15.9–20.8 Ma (Hedges et al., 2015) or *c.* 19.1–20.7 Ma (Zheng & Wiens, 2016). However, Lin et al. (2002) proposed a much younger divergence time (<7 Ma) based on two alternate biogeographical models, which was recently supported by Tseng et al. (2015). Consequently, combining phylogenetic data and geologic evidence cannot unambiguously support or refute any of these hypotheses to resolve the biogeographical history of this lineage, and more convincing evidence is necessary for future studies.

4.4 | Reliability of this analysis

Synthesizing different molecular datasets to infer the biogeographical history of species endemic to Taiwan suffers from several potential problems. First, incongruent molecular markers and time constraints used in independent phylogenies might result in incomparable results across clades (Crottini et al., 2012), particularly in the meta-analysis of 28 published phylogenies. For example, the discrepancy of molecular dating between mitochondrial cytochrome *b* gene and nuclear loci could result in different estimated divergence times and thus potentially mislead the explanation (Li et al., 2010). Second, although our study covered 54 out of 80 species endemic to Taiwan (including more than 90% of birds, 83% of mammals and 70% of amphibians), the phylogenetic relationships of *c.* 30% of the mammals and birds were added to the original phylogenies by interpolation methods (Hedges et al., 2015), which reduced the power of the analyses to some degree. However, when comparing the results from different datasets and analyses (compare Figure 3a to b; see also Supporting Information Appendix S2: Table S2.4), large spatial and temporal congruence emerged across multiple, independent lineages, which naturally increases the probability of inferring the biogeographical history shared by different endemic species. Third, most of the endemic reptiles (16 of 22 species) are missing from our analysis. This gap in our dataset is mostly because detailed molecular phylogenetic data are still unavailable. Given that reptiles are one of the best lineages for understanding the colonization processes of island fauna (Hawlitschek et al., 2017), and more importantly, Taiwan harbours a highly distinct assemblage of lizards (Hsiang et al., 2009), the inclusion of only a few endemic Taiwanese reptiles in our analysis limits our knowledge of the colonization history of Taiwanese terrestrial vertebrates. Thus, it is still essential in the future to integrate more comparable, well-resolved phylogenies and advanced palaeogeographic data to reconstruct a more detailed picture of the biogeographical history of biota endemic to Taiwan.

5 | CONCLUSION

Phylogeographical studies, albeit case by case, have improved our understanding of the biogeographical origins of Taiwanese biota in a spatiotemporal framework, but a comprehensive study representing multiple lineages is still lacking. Here, based on a meta-analysis of previous studies and ancestral range estimates of 54 endemic terrestrial vertebrates, we provided new insights into the biogeographical patterns of Taiwanese vertebrate fauna. (a) In contrast with the traditional hypothesis, we found support for the Eastern Himalayas as the main source region of species endemic to Taiwan, although South China shares the largest proportion of resident species with Taiwan. (b) Our results provide a time frame that the majority of colonization events of endemic Taiwanese species occurred from the early Pliocene (*c.* 5 Ma) onwards, which is in line with the emergence of Taiwan. (c) Apart from the land bridge hypothesis, overwater dispersal provides another potential mode for species to colonize from surrounding land masses. (d) Despite the efforts attempting to address the biogeographical histories of Taiwanese *Hynobius* salamanders and *Takydromus*, the discrepancies between the molecular dating of their divergence times and the geological age estimates of Taiwan are still unsolved. Therefore, more convincing evidence is necessary to resolve the biogeographical histories of species endemic to Taiwan.

DATA ACCESSIBILITY

Data are fully accessible as Supporting Information Appendix S1.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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BIOSKETCHE

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SUPPORTING INFORMATION

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