

Redrawing Wallace's Line based on the fauna of Christmas Island, eastern Indian Ocean

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Based on a comprehensive literature survey, we determined the sources of the terrestrial vertebrate species on Christmas Island, asking where they originated relative to Wallace's Line (the southern end of the divide lies 1100 km to the east, where the Lombok Strait adjoins the eastern Indian Ocean). The two bats, *Pipistrellus murrayi* and *Pteropus natalis*, are from the west. Concerning the endemic and 'resident' bird species, one is from the west (*Collocalia natalis*), four are from the east (*Accipiter fasciatus*, *Egretta novaehollandiae*, *Falco cenchroides* and *Ninox natalis*) and the other 15 are ambiguous or indeterminate. Most of the land-locked species are also from the east: rodents *Rattus macleari* and *Rattus nativitatis*, and squamates *Cryptoblepharus egeriae*, *Emoia nativitatis* and *Lepidodactylus listeria*. Additionally, two have westerly origins (*Crociodura trichura* and *Cyrtodactylus sadleiri*), one is ambiguous (*Emoia atrocostata*) and another is unknown (*Ramphotyphlops exocoeti*). West-directed surface currents that flow across the eastern Indian Ocean towards Christmas Island would have facilitated most of the land-animal colonizations. We therefore suggest that Wallace's Line be redrawn such that the landmass is placed on the Australasian side of this fundamental biogeographical boundary.

ADDITIONAL KEYWORDS: biogeographical realms – Huxley's Line – Indo-Australian Archipelago – Indonesian throughflow – Lydekker's Line – over-water dispersal – Sahul – Sundaland – Wallacea – Weber's Line.

INTRODUCTION

The Indo-Australian Archipelago (Fig. 1) is one of Earth's key biogeographical regions. It separates the Oriental faunal realm to the west from the Australasian one to the east (e.g. Wallace, 1876; Procheş & Ramdhani, 2012; Holt *et al.*, 2013; Rueda *et al.*, 2013). In an attempt to delineate a boundary between the two, Müller (1846) bisected the island chain with an ecology-based line (see also Sarasin & Sarasin, 1901). Starting off to the SSW of Sumba, he looped it around eastern Sumbawa (Fig. 1; Supporting Information, Fig. S1). After crossing the eastern Java Sea, it bisects the Makassar Strait, then cuts through the Sulu Archipelago before heading ENE to the north of Mindanao. Having made such a bold declaration, it was only a matter of time before others proffered their views using additional data or alternative criteria (e.g.

Sclater, 1858; Wallace, 1859, 1860, 1863; Murray, 1866; Huxley, 1868; Sclater, 1894; Lydekker, 1896; Weber, 1902; Pelseneer, 1904; also see Mayr, 1944; Simpson, 1977).

Today, the line proposed by Wallace (1863) is the most recognized and forms what is generally accepted as the western limit of the Australasian derived land-locked vertebrates within the island belt (e.g. Lohman *et al.*, 2011; Brown *et al.*, 2013; Tsang *et al.* 2020). "Starting in the strait between Bali and Lombok, the boundary tracks north through the Makassar Sea and then to the NE between Mindanao and Talaud" (Fig. 1; Supporting Information, Fig. S1). Wallace's divide also provides the western boundary to Wallacea, a transitional region that extends east and south to the edge of the Australasian continental shelf (Fig. 2). The eastern side of Wallacea matches closely, but not exactly, the line of Lydekker (1896). The discrepancy is caused by the shelf island of Misool off western New Guinea, which is conventionally considered part of the Australian realm; Lydekker ran his boundary around its eastern side, thus separating it

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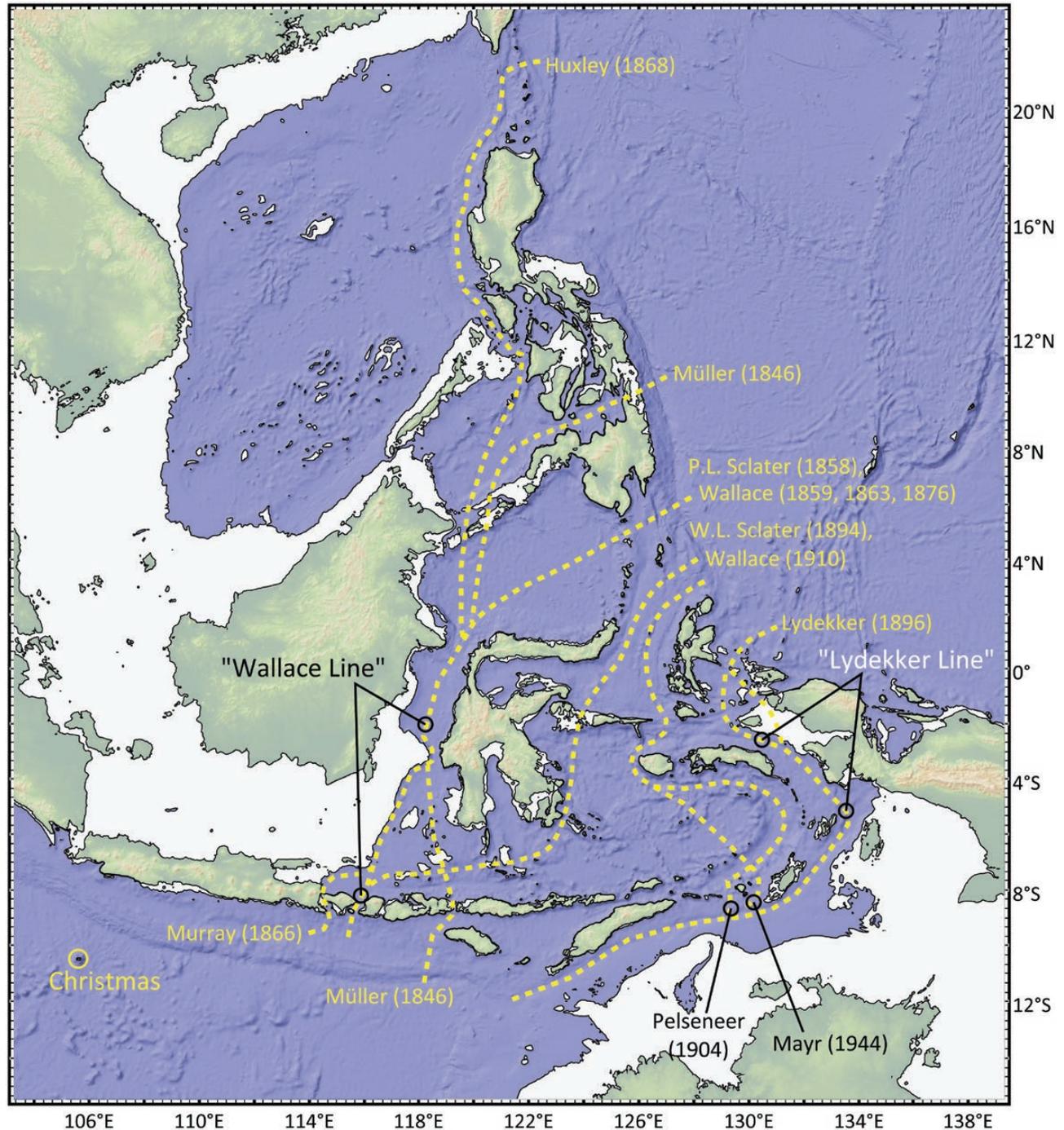


Figure 1. Map of the Indo-Australian Archipelago and adjacent areas, showing the key biogeographical divides that have been proposed by various workers (Christmas Island, 135 km², is circled); Mayr (1944) and Simpson (1977) provide useful reviews. Wallacea is the region between the Wallace (1863) and Lydekker (1896) lines. Weber (1902) proposed that bisections of the archipelago should be based on 'faunal balance'; the lines of Pelseneer (1904) and Mayr (1944) are associated attempts. The white patches next to the landmasses indicate those areas of seabed that are ≤ 120 m deep; these would have been exposed during the lowest global sea-level lows that affected Earth over the last 630 000 years (Bintanja *et al.*, 2005). The base image was generated using GeoMapApp (Ryan *et al.*, 2009). As a scale guide, 10° of latitude is ~1111 km.

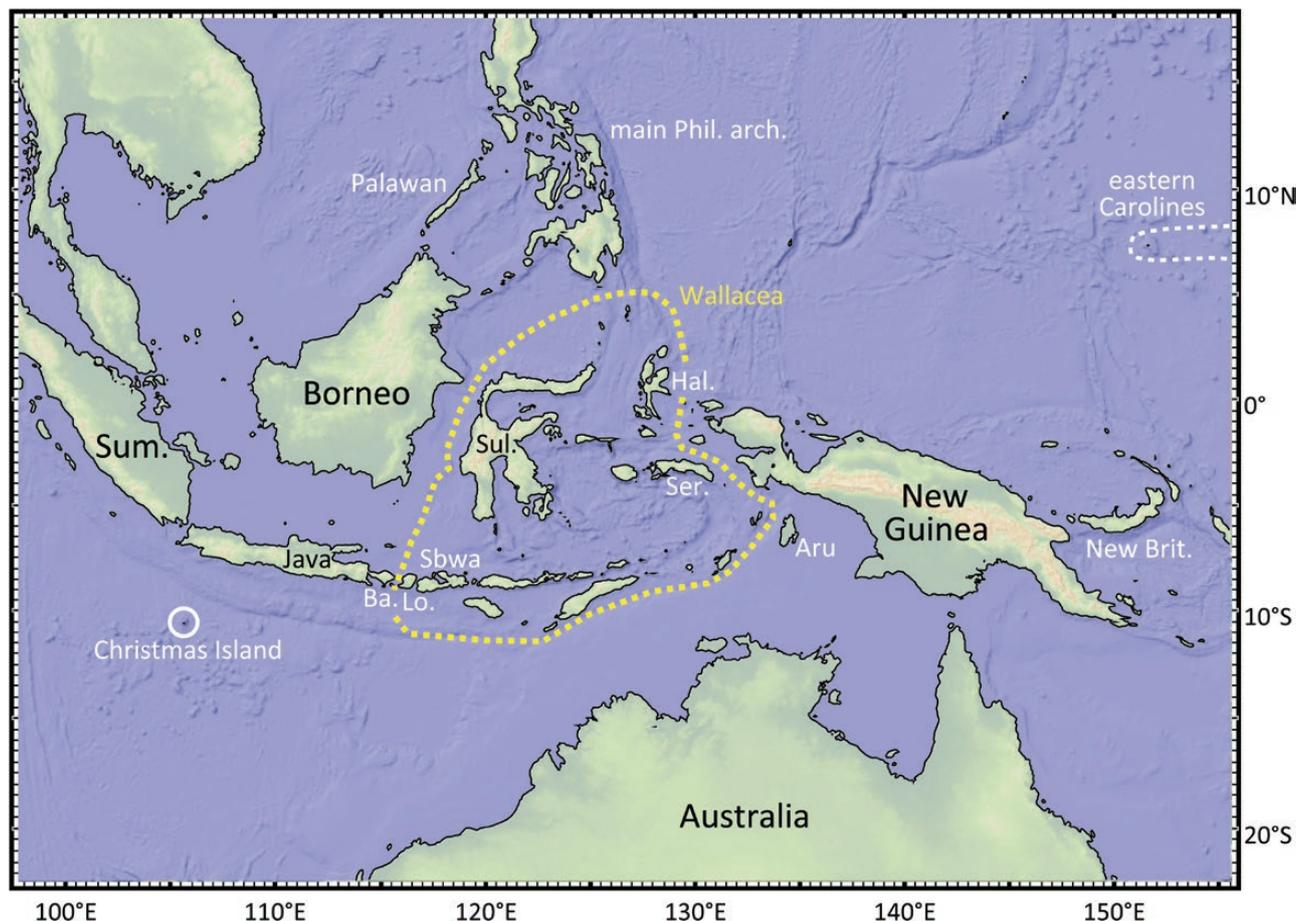


Figure 2. Map showing the islands and areas mentioned in the Results and Discussion (Christmas Island is circled). Also depicted is Wallacea. Abbreviations: Ba., Bali; Hal., Halmahera; Lo., Lombok; Sbw., Sumbawa; Sul., Sulawesi; Sum., Sumatra. The base image was generated using GeoMapApp (Ryan *et al.*, 2009).

from its larger neighbour (Supporting Information, Fig. S1). Additionally, it should be noted that some of the landmasses in Wallacea, particularly Sulawesi and its neighbours, host a number of deep-time endemic faunal components (see Stelbrink *et al.*, 2012). These are on top of many recent arrivées that have washed in or flown over from both the Oriental and Australasian realms.

The fauna of Christmas Island, in the eastern Indian Ocean, has not really featured in biogeographical discussions of the Indo-Australian Archipelago. This is probably because of the location of the island, ~1100 km west of Wallace's Line (Fig. 1; 10.49°S, 105.64°E; 350 km south of the western end of Java), and its diminutive size, only 135 km² and with a peak elevation of 361 m. However, during a recent palaeogeographical study of the island (Ali & Aitchison, 2020), we became aware that several of the native terrestrial vertebrates on the island belong to clades that are regarded as occupants of lands east of the Wallace Line (Wyatt *et al.*, 2008; Oliver *et al.*, 2018). The objectives of this study stem from that, namely to determine the sources of each of

resident land vertebrate species (land mammals, land reptiles, bats and birds) of Christmas Island and to consider the biogeographical implications.

BACKGROUND ISSUES

Before proceeding to the biological/biogeographical core of this investigation, it is necessary for a number of background issues to be considered.

Wallace's Line: 'problems' created by Sulawesi's fauna; Huxley's 'modification'

Two issues related to the Wallace Line need to be explained. Firstly, the fauna on Sulawesi (Celebes) created considerable problems for Wallace, and in several publications he pondered whether his divide should run to the west or east of the island. In some he chose the former: Wallace (1859, 1863, 1876). In others he was less committal: Wallace [1860, 1880, 1892; on this issue, the 1860 paper is a challenging read;

compare the interpretations of [George \(1981\)](#) with [Camerini \(1993\)](#). Notably, a few years before his death, he settled on running the boundary to the east of the island ([Wallace, 1910](#)). It should be stated, however, that during all of his deliberations he consistently positioned the south-west termination of the divide between Bali and Lombok. This is important because we will later consider how this part of his line might be changed to accommodate the Christmas Island fauna.

The second matter concerns the line proposal of [Huxley \(1868\)](#). Like [Wallace \(1863\)](#), Huxley started his bird-based divide of the Australian and Oriental faunas between Bali and Lombok and continued it through the Makassar Straits. However, upon entering the Celebes Sea, he then tracked his line north along the western side of the basin before threading it first past the south-west end of the Sula Archipelago, then the north-east tip of the Palawan Group ([Fig. 1; Supporting Information, Fig. S1](#)). Finally, it was hooked east around the northern Philippines. Huxley named the boundary the ‘Wallace Line’, but, famously, Wallace never accepted the attribution. Instead, in a series of later publications spanning four decades, he continued to place the Philippines in the Oriental realm ([Wallace, 1869, 1876, 1880, 1910](#)).

Earliest studies of the Christmas Island fauna post-dated the main phase of biogeographical divide drawing

An obvious question that leads from the title of the manuscript is, why has the Christmas Island fauna never really featured in discussions of the biogeography of the Indo-Australian Archipelago? A significant factor concerns the timing of the line drawing relative to the earliest scientific publications on the flora and fauna of Christmas Island. Although the former spanned the mid-1800s and early 1900s [i.e. from [Müller \(1846\)](#) to [Pelseneer \(1904\)](#)], the key ones for the western part of the region date from the first third of that period ([Müller, 1846; Wallace, 1863; Murray, 1866; Huxley, 1868](#)). Thus, they appeared a considerable time before the first studies of the Christmas Island biota, which started in the 1880s ([Günther *et al.*, 1887; Wharton, 1887; Lister, 1888; Andrews, 1900](#)). Later proponents of other associated boundaries (e.g. [Lydekker, 1896; Weber, 1902; Pelseneer, 1904](#)) were possibly unaware of the emerging information about Christmas Island. Also, their efforts were focused on the zoogeographical patterns > 2000 km to the east.

Geo-physical considerations

Offshore, Southeast Asia is tectonically complex and dynamic, and many of its constituent elements have experienced significant horizontal and vertical movements since the mid-Cenozoic (e.g. [Hall, 2009,](#)

[2013](#)) and even since the start of the Pliocene slightly > 5 Mya. This is attributable to the Eurasia, Indo-Australia, Pacific and Philippine plates all converging upon the region (e.g. [Argus *et al.*, 2011; Supporting Information, Fig. S2](#)). Critically, many of the landmasses within Wallacea have emerged only in the last 5 Myr ([Hall, 2013](#)). Sulawesi is an exception, because there appears to have been exposure of the parts of the composite-terrane island (see [Ali, 2017](#)) since the beginning of the Neogene (23 Mya; [Nugraha & Hall, 2018](#)) and probably throughout the Cenozoic ([Hall, 2013](#); the era started 66 Mya). Notably, [Wallace \(1860\)](#) formed a similar view after attempting to place the Sulawesi fauna in its regional context: ‘...this island of Celebes is more ancient than most of the islands now surrounding it, and obtained some part of its fauna before they came into existence’. Therefore, assemblages on individual surfaces within Wallacea have resulted from a combination of land-bridge colonizations during lowered sea levels and over-water dispersal events. The latter would have involved relatively short journeys that can probably be best described as ‘island hopping’. Specifically, the animals did not traverse wide expanses of ocean (see [Ali & Vences, 2019a](#)).

A further complication results from the many different island types that occupy the Indo-Australian Archipelago. As explained recently, the three categories of marine islands that Darwin and Wallace established, i.e. recent continental, ancient continental and oceanic, are overly simplistic ([Ali, 2017, 2018](#)). Based on geotectonic setting, Earth has more than two dozen different sorts. The Indo-Australian Archipelago has a sizeable number of these, including continental shelf (e.g. Borneo, Sumatra, Java), orogenic margin (New Guinea), composite terrane (Sulawesi, Mindanao, Palawan), micro-continental terrane (Sumba, Buru, Timor, Seram), intra-oceanic arc (Sangihe) and uplifted intra-oceanic fore-arc (Talaud). As a consequence, each will have its own ontogenetic development.

Christmas Island is geotectonically remarkable because it is one of a handful of seamounts, alongside New Caledonia’s Loyalty Islands and Niue Island ([Woodroffe, 1988; Nunn & Britton, 2004; Dickinson, 2013](#)), that have re-emerged above sea level having spent many millions of years as ‘drowned atolls’ ([Flood, 2001](#)). In all such cases, the parts of the oceanic plate the edifices are constructed upon are being locally up-warped before their descent into a subduction zone trench (see [Turcotte *et al.*, 1978](#)). In a recent palaeogeographical study of Christmas Island, which sits slightly outboard of the Sunda Trench south of Java ([Supporting Information, Fig. S2](#)), the ocean-surface breaching was estimated to have occurred between 5.66 and 4.49 Mya (5.03 + 0.63/–0.54 Mya; latest Miocene–mid Early Pliocene; [Ali & Aitchison, 2020](#)). The Christmas Island seamount sits upon the

Indo-Australia Plate and is moving north-northeast at ~68 mm/year (Argus *et al.*, 2011). Assuming a constant velocity, at the time of its re-emergence it would have been 385–305 km south-southwest of its present location (and also further away from the south-west end of the Wallace Line).

The surface currents around Christmas Island (Supporting Information, Fig. S3) are largely controlled by the sizeable flux of water, known as the 'Indonesian Throughflow', that spills over from the western Pacific Ocean into the eastern Indian Ocean (e.g. Hu *et al.*, 2015; Wijeratne *et al.*, 2018). Therefore, any terrestrial vertebrates that washed over to the island on vegetation mats/large trees ('rafts') would have a high probability of being from lands to the east of the Wallace Line. This is supported by Green (1999), who looked at the sources of plant material that were transported to the island. Sumatra and Borneo supplied some, but the lands to the east of the Wallace Line dominate (Green, 1999: 937): '... most disseminules probably arriving via the Timor and Arafura seas'. Likewise, the cave-dwelling trochanteriid spider on Christmas Island, *Olin platnicki* Deeleman-Reinhold, 2001, appears to be most closely related to those on the Togian Islands, off north-east Sulawesi, again east of the Wallace Line (Platnick, 2002). On the contrary, it should be noted that the regional currents make it difficult for land vertebrates washing off Java to beach on Christmas Island (Supporting Information, Fig. S3).

Regional air flows, which presumably influence bat and the bird colonizations, show strong seasonality (e.g. Cheng *et al.*, 2012; Han *et al.*, 2014). In January, the intertropical convergence zone is slightly south of the equator, hence the winds over the Christmas Island region are weak. In contrast, during July the low-pressure climatic belt shifts northwards over South and East Asia to ~25–35°N, resulting in the 'Southeast Trades' blowing west-north-west across the low-latitude eastern Indian Ocean (Han *et al.*, 2014: fig. 3b; Supporting Information, Fig. S3).

MATERIAL AND METHODS

Drawing upon an extensive literature survey, we determined which native bat, bird, mammal and reptile species (there are no amphibians) are present on Christmas Island (extant, extinct in the wild and extinct; the formal conservation status of each is listed in Fig. 3). We then identified, for each species, the phylogenetically nearest off-island relatives and the geographical ranges they occupy.

Constructing an inventory for the Christmas Island land mammals, squamates and bats (Fig. 3) was relatively straightforward because there are few species (three, eight and two, respectively), and these are recorded in publications that are either focused

(e.g. Eldridge *et al.*, 2014; Oliver *et al.*, 2018; James *et al.*, 2019) or general (e.g. IUCN Red List, 2020). In contrast, different categories of birds have been recorded on the island: breeding visitors, endemics, extirpated, indeterminates, introduced, passage migrants, residents, vagrants and visitors. Each of those may be considered common, uncommon or rare. For this study, we used only the breeding birds, i.e. the six endemic and 14 non-endemic 'resident' species that are listed by Johnstone & Darnell (2017) and James *et al.* (2019). Of the latter, we treated separately the ten species that were present at the time of the settlement of Christmas Island in the 1890s from the four that colonized it naturally in the 20th century. Based on the work of James & McAllan (2014), we excluded from the compilation two introduced species, the Java finch *Lonchura oryzivora* (Linnaeus, 1758) and the Palearctic sparrow *Passer montanus* Linnaeus, 1758.

The nearest off-island relatives for each of the Christmas Island species can, except for two instances, be deduced from phylogenetic studies (Fig. 3). In several cases, divergence dates are also available. The geographical ranges of most Christmas Island-linked species can be established using specialist publications and validated using Roll *et al.* (2017) and the IUCN Red List (2020).

To summarize succinctly each of the vertebrate assemblage groups (terrestrial mammals, squamates, bats and a subset of birds) for Christmas Island, we make use of the recently proposed assemblage lineage taxonomy spectrum (ALTS; Ali & Vences, 2019b). The coding system encapsulates quantitatively the 'evolutionary maturity' of an isolated biological suite. Notably, for those in marine settings the ALTS strongly reflects the geological developments and geo-physical settings of the islands, for instance age, area, isolation, regional ocean currents and prevailing winds. The first part of the analysis involves determining, for each of the native lineages within each of the vertebrate groups on an island/shallow-platform archipelago, its type, where LT1 is a non-endemic species, LT2 is a single endemic species from a non-endemic genus, LT3 comprises multiple endemic species from a non-endemic genus, LT4 is a sole member of a genus that arose on the island, LT5 is multiple species from a single endemic genus, and LT6 is multiple endemic genera. There are, however, three related issues to consider. First, if a non-endemic genus is represented by two or more clades, only one of the highest types is counted, with all of the others being excluded. Second, molecular phylogenetic data overrule taxonomic data; therefore, say, a supposed endemic genus is nested within an off-island genus, it is categorized as an LT2 or LT3 rather than an LT4 or LT5. Third, to avoid confusion with the term 'endemic', LT4 and higher types allow for derived species to have colonized a mainland or another island. Once the lineages have been categorized, an insular assemblage can, in a

Christmas Island species	Order	Family	Conserv. Stat.	LT code	Closest off-island relative(s)	Loc. closest relative	Age of split (Ma)	Where rel. Wallace line	References (phylogeny)
Land Mammals									
<i>Crocridura trichura</i>	Eulipotyphla	Soricidae	Crit. endangered	LT2	<i>Crocridura orientalis</i>	western Java	ND	Sundaland	Eldridge <i>et al.</i> (2014)
<i>Rattus macleari</i>	Rodentia	Muridae	Extinct	LT2	<i>Rattus leucopus</i> , <i>Rattus villosissimus</i>	northern Aust.	ND	NG-Aust.	Wyatt <i>et al.</i> (2008)
<i>Rattus nativitatis</i>	Rodentia	Muridae	Extinct	LT2	<i>Bunomys andrewsi</i>	Sulawesi	ND	Wallacea	Wyatt <i>et al.</i> (2008); Musser (2014)
Squamates									
<i>Cyrtodactylus sadleiri</i>	Squamata	Gekkonidae	Endangered	LT2	<i>Cyrtodactylus</i> sp.	Bali	2 (1–3)	Sundaland	Oliver <i>et al.</i> (2018)
<i>Lepidodactylus listeri</i>	Squamata	Gekkonidae	Ext. in the wild	LT2	<i>Lepidodactylus</i> spp.	Phil. + Moluc.	26 (21–31)	Wallacea	Oliver <i>et al.</i> (2018)
<i>Cryptoblepharus egeriae</i>	Squamata	Scincidae	Ext. in the wild	LT2	<i>Cryptoblepharus metallicus</i>	northern Aust.	7 (5–10)	NG-Aust.	Oliver <i>et al.</i> (2018)
<i>Emoia atrocostata</i>	Squamata	Scincidae	Ext. on the island	LT1	<i>Emoia atrocostata</i>	Java	NA	E and W	Oliver <i>et al.</i> (2018)
<i>Emoia nativitatis</i>	Squamata	Scincidae	Extinct	LT2	<i>Emoia boettgeri</i>	Micronesia	13 (9–18)	Eastern Carol.	Oliver <i>et al.</i> (2018)
<i>Ramphotyphlops exocoeti</i>	Squamata	Typhlopidae	Vulnerable	LT2	Not known (no phylo. data)	?	ND	?	Pyron & Wallach (2014)
Bats									
<i>Pipistrellus murrayi</i>	Chiroptera	Vespertilionidae	Extinct	LT2	<i>Pipistrellus tenuis</i>	Java	ND	mainly W, but E	Helgen <i>et al.</i> (2009)
<i>Pteropus natalis</i>	Chiroptera	Pteropodidae	Crit. endangered	LT2	<i>Pteropus</i> sp. on P. Panjang (N of Java)	"Java"	ND	Sundaland	Phalen <i>et al.</i> (2017)
Endemic birds									
<i>Collocalia natalis</i>	Charadriiformes	Apodidae	Not assessed	LT2	<i>Collocalia linchi linchi</i>	Java	0.5–0.7	Sundaland	Rheindt <i>et al.</i> (2017); James <i>et al.</i> (2019)
<i>Ducula whartoni</i>	Charadriiformes	Columbidae	Near threatened	LT2	<i>Ducula rosacea</i>	Java Sea isles	ND	E and W	James <i>et al.</i> (2019)
<i>Zosterops natalis</i>	Passeriformes	Zosteropidae	Near threatened	LT2	Not known (no phylo. data)	?	ND	?	
<i>Ninox natalis</i>	Strigiformes	Strigidae	Vulnerable	LT2	<i>Ninox squamipila</i> , <i>Ninox hypogramma</i>	Moluccas	4	Wallacea	Norman <i>et al.</i> (1998); Kumar <i>et al.</i> (2017)
<i>Fregata andrewsi</i>	Suliformes	Fregatidae	Crit. endangered	LT2	<i>Fregata minor</i>	Java	0.9	widespread	Kennedy & Spencer (2004)
<i>Papasula abbotti</i>	Suliformes	Sulidae	Endangered	LT4	c. 22 Ma diverg. nearest fam. rel.	?	21.8 (17.1–27.4)	?	Patterson <i>et al.</i> (2011)
Non-Endem. Resid. Birds									
<i>Accipiter fasciatus</i>	Accipitriformes	Accipitridae	Least concern	LT1	<i>Accipiter fasciatus</i>	Lombok	NA	Wall.+NG+Aust.	
<i>Chalcophaps indica</i>	Charadriiformes	Columbidae	Least concern	LT1	<i>Chalcophaps indica</i>	Java	NA	E and W	
<i>Anous stolidus</i>	Charadriiformes	Laridae	Least concern	LT1	<i>Anous stolidus</i>	Java	NA	widespread	
<i>Turdus poliocephalus</i>	Passeriformes	Turdidae	Least concern	LT1	<i>Turdus poliocephalus</i>	Java	NA	widespread	Peterson (2007)
<i>Egretta sacra</i>	Pelecaniformes	Ardeidae	Least concern	LT1	<i>Egretta sacra</i>	Java	NA	E and W	
<i>Phaethon lepturus</i>	Phaethontiformes	Phaethontidae	Least concern	LT1	<i>Phaethon lepturus</i>	Java	NA	widespread	
<i>Phaethon rubricauda</i>	Phaethontiformes	Phaethontidae	Least concern	LT1	<i>Phaethon rubricauda</i>	Java	NA	widespread	
<i>Fregata minor</i>	Suliformes	Fregatidae	Least concern	LT1	<i>Fregata minor</i>	Java	NA	widespread	
<i>Sula leucogaster</i>	Suliformes	Sulidae	Least concern	LT1	<i>Sula leucogaster</i>	Java	NA	widespread	
<i>Sula sula</i>	Suliformes	Sulidae	Least concern	LT1	<i>Sula sula</i>	Java	NA	widespread	
Recently Resident Birds									
<i>Falco cenchroides</i>	Falconiformes	Falconidae	Least concern	LT1	<i>Falco cenchroides</i>	northern Aust.	NA	Aust.	
<i>Amaurornis phoenicurus</i>	Gruiformes	Rallidae	Least concern	LT1	<i>Amaurornis phoenicurus</i>	Java	NA	E and W	
<i>Egretta novaehollandiae</i>	Pelecaniformes	Ardeidae	Least concern	LT1	<i>Egretta novaehollandiae</i>	northern Aust.	NA	Wall.+NG+Aust.	
<i>Fregata ariel</i>	Suliformes	Fregatidae	Least concern	LT1	<i>Fregata ariel</i>	Java	NA	widespread	

Figure 3. Summary of the native land-locked mammals, reptiles, bats and endemic and resident birds of Christmas Island. Within each group, the species are listed alphabetically by order, then family, then species. Geographical ranges of the nearest off-island relatives are from the IUCN Red List (2020) and the various specialist articles. For each Christmas Island species, the Ali & Vences (2019b) assemblage lineage taxonomy spectrum (ALTS) type is listed (see Material and Methods for details). To guide the reader, the colours for the cell fillers in the column 'Where relative to the Wallace Line' match those in Figure 4. Abbreviations: NA, not applicable; ND, no data; NG, New Guinea; Wall., Wallacea, which is the area between the Wallace (1863) and Lydekker (1896) lines.

large majority of cases, be represented using a six-plus-one figure code, e.g. 05:20:30:25:20:00[40]. Here, the first digit indicates the percentage of LT1s (5%), the second the percentage of LT2s (20%), the third the percentage of LT3s (30%) etc., whilst the bold number in square brackets is the number of processed lineages (40). If LT7 or LT8 lineages are present, then the coding is extended to either a seven-plus-one or an eight-plus-one number sequence.

RESULTS

NON-FLYING, NON-AQUATIC VERTEBRATES: LAND MAMMALS

Christmas Island hosts three land mammals (all endemic), which result from three separate colonizations and subsequent anagenesis (Meiri

et al., 2018): the shrew *Crocridura trichura* Dobson, 1889 and the rodents *Rattus macleari* (Thomas, 1887) and *Rattus nativitatis* (Thomas, 1888) (Fig. 3). However, *Rattus nativitatis* is nested within the genus *Bunomys* (Thomas, 1910), which is otherwise exclusive to Sulawesi (Wyatt *et al.* 2007; Musser, 2014); phylogenetically, it is closest to *Bunomys andrewsi* (Allen, 1911). Therefore, for the purpose of calculating the assemblage lineage taxonomy spectrum we treat it as a member of *Bunomys*, hence the coding is 00:100:00:00:00:00[3]. The nearest living phylogenetic relative for the Christmas Island shrew is *Crocridura orientalis* Jentink, 1890 from western Java (Eldridge *et al.*, 2014). *Rattus leucopus* (Gray, 1867) and *Rattus villosissimus* (Waite, 1898), with a combined range spanning Aru Island, southern New Guinea and northern Australia (i.e. all east of Wallace's Line; Wyatt *et al.*, 2008; Fig. 2), are the closest relatives of *Rattus*

macleari on Christmas Island. In summary, *Crocodyrus trichura* has its origins to the west of the Wallace Line, *Rattus nativitatis* is from Wallacea, and *Rattus macleari* is from east of Lydekker's Line (Fig. 4).

NON-FLYING, NON-AQUATIC VERTEBRATES: SQUAMATES

Christmas Island has six native squamate species: the geckos *Cyrtodactylus sadleiri* Wells & Wellington, 1985, and *Lepidodactylus listeri* (Boulenger, 1889); the skinks *Cryptoblepharus egeriae* (Boulenger, 1888), *Emoia atrocostata* (Lesson, 1830) and *Emoia nativitatis* (Boulenger, 1887); and the blind snake *Ramphotyphlops exocoeti* (Boulenger, 1887). However, only the first and the last remain extant on the landmass (Fig. 3). The ALTS is 00:100:00:00:00:00[5]; the presence of *E. nativitatis* (LT2) means that *E. atrocostata* (LT1) is excluded from the coding. The recent paper by Oliver *et al.* (2018) provides key information on the origins of each of the species. The gecko *Cyrtodactylus sadleiri* diverged from an unnamed *Cyrtodactylus* species on Bali ~2 Mya (1–3 Mya) and is thus from the west of Wallace's Line (Fig. 2). The closest relatives to *L. listeri* are some *Lepidodactylus* species in the Moluccas (east of Wallace's Line) and the Philippines (west of the divide), and their split is dated as ~26 Mya (21–31 Mya). The skink *Cryptoblepharus egeriae* is sister to *Cryptoblepharus metallicus* (Boulenger, 1887), which occurs in northern Australia; the separation is estimated to have occurred ~7 Mya (5–10 Mya). *Emoia nativitatis* is sister to *Emoia boettgeri* (Sternfeld, 1918), which is present on the eastern Caroline Islands [split dated to ~13 Mya (9–18 Mya); Fig. 2]. The sources of the other two native squamates are either ambiguous or unknown. *Emoia atrocostata* is a supertramp species that spans a vast region from East Asia to the south-west Pacific. Finally, there is no molecular information for *Ramphotyphlops exocoeti*; the genus *Ramphotyphlops*, to which it is assigned (Hedges *et al.*, 2014), ranges from north-west Sumatra to the Loyalty Islands (Roll *et al.*, 2017).

FLYING VERTEBRATES: BATS

Despite being only a short distance from Southeast Asia, Christmas Island hosts only two bat species: the vesper bat *Pipistrellus murrayi* (Andrews, 1900) and the fruit bat *Pteropus natalis* Thomas, 1887 (Fig. 3). Although both are presently classified as endemics, their genetic divergence with respect to their nearest off-island relatives is not especially great. The closest relative to *Pipistrellus murrayi* is *Pipistrellus tenuis* (Temminck, 1840), which occurs on Java (Helgen *et al.*, 2009); *Pteropus natalis* is sister to an unnamed *Pteropus* sp. on Pulau Panjang (6.58°S, 110.63°E), a 19 ha island 1.7 km off northern central Java (Phalen

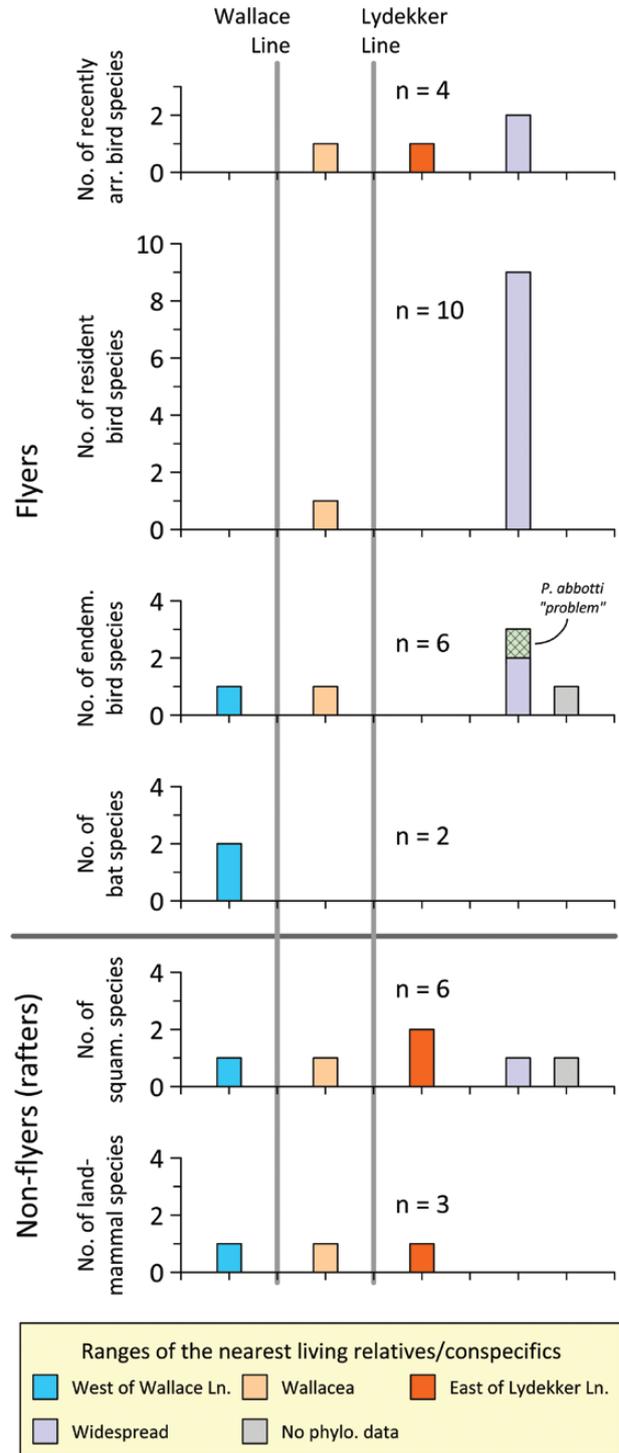


Figure 4. Bar charts summarizing the geographical locations of the nearest living relatives of the Christmas Island landlocked mammals and squamates, bats, and endemic, non-endemic resident and recent non-endemic resident birds.

et al., 2017). Both species are therefore derived from west of Wallace's Line. The ALTS coding is 00:100:00:00:00:00[2].

FLYING VERTEBRATES: ENDEMIC AND NON-ENDEMIC
RESIDENT BIRDS

Christmas Island has six endemic and 14 non-endemic, resident birds (Fig. 3; James & McAllan, 2014; Johnstone & Darnell, 2017; James *et al.*, 2019). The ALTS coding is 60:33:00:07:00:00[15], with Abbot's booby, *Papasula abbotti* (Ridgway, 1893), being the sole LT4 type (endemic monotypic genus) of any vertebrate species on the island. Three genera, *Fregata*, *Phaethon* and *Sula*, are represented by two species each, probably resulting from separate colonizations.

Concerning the endemic species and where they dispersed from relative to Wallace's Line, from the west there is one, the swiftlet *Collocalia natalis* Lister, 1889. According to Rheindt *et al.* (2017), it is sister to *Collocalia linchi linchi* Horsfield & Moore, 1854 (Fig. 3), which occupies Java and some islands in the eastern Java Sea (IUCN Red List, 2020). Norman *et al.* (1998) indicates that the hawk-owl *Ninox natalis* Lister, 1888 came from the east, because it is most closely related to *Ninox squamipila* (Bonaparte, 1850) on Seram and nearby islands, and to *Ninox hypogramma* (Gray, 1861) on Halmahera. Of the four other endemic species, two have sisters that straddle the boundary, the frigatebird *Fregata andrewsi* Mathews, 1914 and the pink-headed pigeon *Ducula whartoni* (Sharpe, 1887) (Fig. 3). Abbot's booby, *Papasula abbotti*, is an oddity because it belongs to a monotypic genus. Patterson *et al.* (2011) and Wang & Clark (2014) indicate that it forms the basal split within the family Sulidae and diverged from its nearest living relatives ~22 Mya (Early Miocene). Given that Christmas Island is no older than between 5.66 and 4.49 Mya (see Geophysical considerations), it is impossible to deduce where the colonizer ancestor might have flown in from. The white-eye passerine *Zosterops natalis* Lister, 1889 has not yet been incorporated into a phylogenetic tree. Members of this genus, one of the most species-rich of all bird genera, are widely distributed across the 'Old World tropics, parts of temperate Asia, and numerous Atlantic, Pacific, and Indian Ocean archipelagos' (Moyle *et al.*, 2009).

Of the ten non-endemic pre-settlement resident bird species, nine could have come from either side of the Wallace Line, because the ranges of the off-island conspecifics straddle the boundary (Figs 3, 4). Only the source of the goshawk *Accipiter fasciatus* (Vigors & Horsfield, 1827) is unequivocal (with respect to the divide evaluation). It is found east of the line, in Wallacea and in New Guinea and Australia, plus New Caledonia.

Of the four species that have colonized since the first settlement, *Amaurornis phoenicurus* Pennant, 1769 (arrived ~1992) and *Fregata ariel* (G.R. Gray, 1845) (arrived before 1980) straddle the Wallace Line (Figs 3, 4). *Egretta novaehollandiae* (Latham,

1790) (arrived between 1965 and 1977) and *Falco cenchroides* Vigors & Horsfield, 1827 (arrived ~1940s) are from the east.

DISCUSSION

Considering its proximity to western Java, it is surprising to learn that many of the native vertebrate species of Christmas Island originated from east of Wallace's Line. This is especially the case with the non-flying animals. Of the seven land mammal and squamate species for which it is possible to determine an origin, two are from west of Wallace's Line, whereas five are from the east, including three from east of Lydekker's Line (Fig. 4). As mentioned above, the west flowing surface-water currents of the region (Supporting Information, Fig. S3) and the rafting mechanism by which the colonizations would have taken place (see Ali & Vences, 2019a) would account for this pattern. It is also worth noting that the journeys made by the ancestors of the two rodents, *Rattus macleari* (from northern Australia, ≥ 2050 km, or Aru-New Guinea-northern Australia, 3200 km) and *Rattus nativitatis* (from Sulawesi, ≥ 1650 km), are some of the longest over-water passages reported for mammals (assuming there are no unknown stepping stones). In fact, they are comparable to the ones made by the caviomorph rodents and the platyrrhine monkeys, both of which crossed from Africa to South America during the Middle Eocene (Boivin *et al.*, 2017; Silvestro *et al.*, 2018; Ali & Vences, 2019a). Although the Atlantic was narrower then (the central part of the ocean is presently widening at ~25 mm/year; Argus *et al.*, 2011), those journeys would have been ≥ 2800 km.

The ALTS spectra for the land mammals and squamates of Christmas Island are dominated by LT2 lineages, i.e. single endemic species belonging to a non-endemic genus. The lack of highly distinctive faunal components reflects the youth of the island. The absence of any *in situ* cladogenesis records (LT3 or LT5) can almost certainly be attributed to Christmas Island being insufficiently large for allopatric divergence to have occurred (see Kisel & Barraclough, 2010; Ali & Meiri, 2019).

Allowing for the fact that Christmas Island has been emergent only since ~5 Mya and that it provides only a small target to beach upon, the colonization rates, where the sweepstakes over-water dispersal process (Simpson, 1940) is invoked, must have been high. Possibly, this reflects the geography of the landmasses supplying both the waifs and the rafts, combined with the conducive regional current configuration (Supporting Information, Fig. S3).

Concerning the flying animals, there are only two bats, one from Java and the other from the near-Java satellite island of Pulau Panjang. The endemic and non-endemic resident bird species show a 1:4 west:east bias (Fig. 4), but this is tempered by the 14 that have nearest relatives or conspecifics with ranges that overlap the Wallace Line, plus *Z. natalis*, the phylogenetic affinities of which are unknown. In a related vein, we originally surmised that the pool of Christmas Island endemics would likely contain a high proportion of eastern species on the basis that with highly vagile organisms endemism might reasonably be expected to increase with the isolation of a descendant population from its source gene pool.

Unfortunately, the small size of the dataset renders it impossible to evaluate this idea.

The bat and bird ALTS are largely as anticipated: mostly LT1, with a smaller number of LT2s. However, the booby *Papasula abbotti*, which is an LT4, is noteworthy. It split from its nearest family members ~22 Mya (Early Miocene), but is endemic to a speck of an island that dates from the latest Miocene–mid Early Pliocene. It is a biogeographical conundrum. The ecology and breeding behaviour of the species (Nelson, 2004) must play a strong role in inhibiting the establishment of off-island populations. They are solitary long-distance travellers, and breeding pairs produce only one egg, typically with 3 years between successive layings (Nelson, 2004).

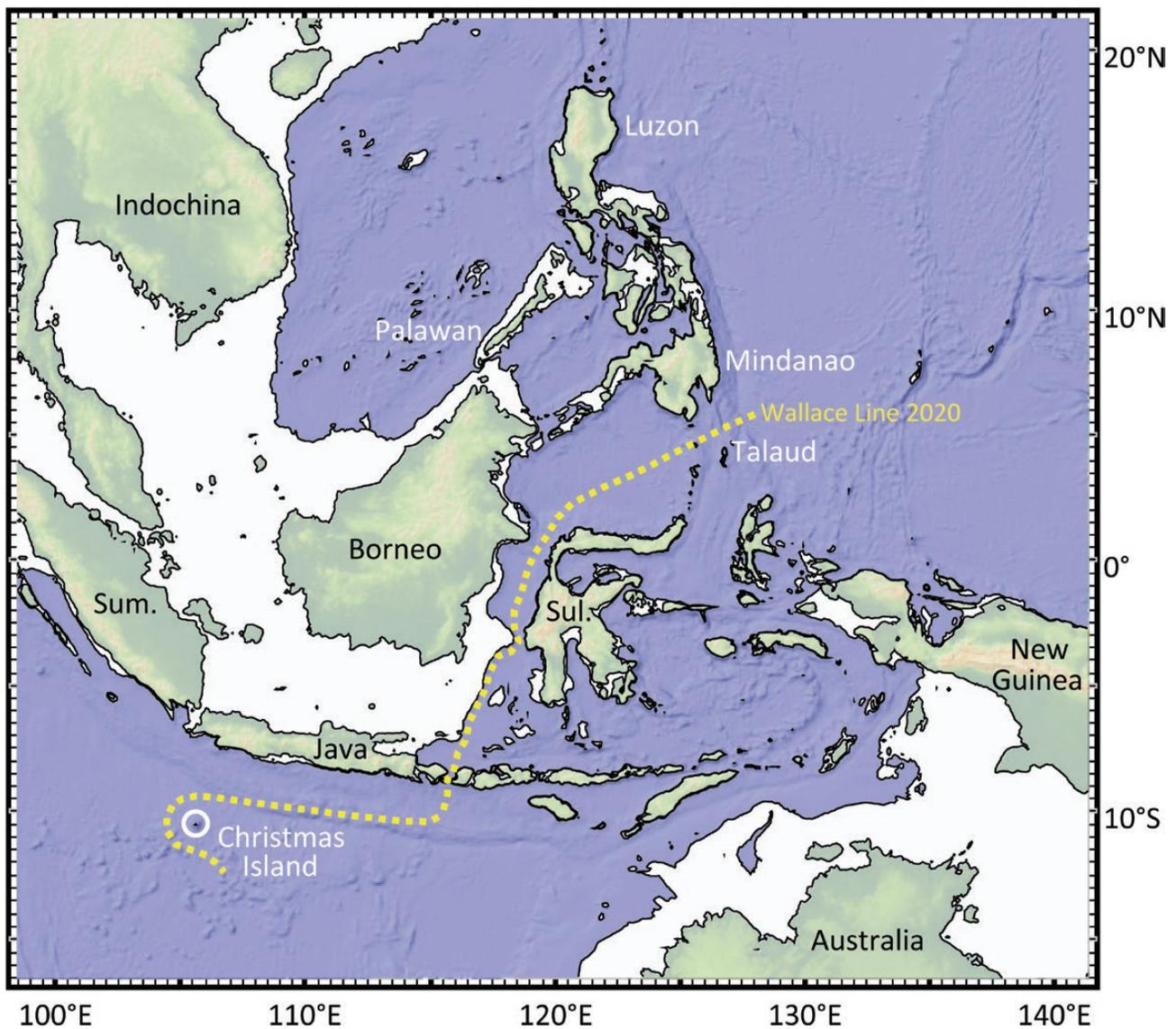


Figure 5. Map showing Wallace's Line drawn such that Christmas Island (circled) is sited on the Australasian side of the biogeographical divide. Abbreviations: Sul., Sulawesi; Sum., Sumatra. The base image was generated using GeoMapApp (Ryan *et al.*, 2009).

Focusing on the land-dwelling mammals and squamates, do the occurrence patterns have a bearing on the way the southern end of the Wallace Line is drafted? As explained above, the Christmas Island faunal suite was unknown when Wallace (1859, 1860, 1863) proposed his boundary separating the Oriental and Australasian biogeographical realms. Moreover, although his 1863 publication included a detailed regional map spanning the Andaman Islands to New Caledonia (89–167°E) and Shark Bay to Hainan (26°S–19°N), Christmas Island was not portrayed despite the fact that many tens of similarly small islands were shown. If a simple definition of the Wallace Line is adopted, i.e. it being the western limit of Australasia-derived species, then the Christmas Island suite suggests that upon exiting the Lombok Strait the boundary should track sharply to the west and hook around the northern side of the landmass. However, would Wallace have given two rats, two skinks and a gecko the same weighting as a single marsupial? Obviously, we will never know, but his discussion of the Sulawesi fauna in *Island Life* (Wallace, 1880: 426) suggests that the presence of Australasian realm rats on Christmas Island might have led him to look favourably upon the idea. We therefore contend that future discussions of the Wallace Line need to consider the Christmas Island fauna fully. There is an argument for placing the island and its vertebrate suite on the Australasian side of the boundary (Fig. 5). At the very least, it needs to be recognized that, despite its proximity to Sundaland, it contains an unexpectedly large fraction of species whose origins are east of Wallace's Line, and even some from beyond Lydekker's divide.

CONCLUSIONS

We were intrigued by the presence on Christmas Island of several land-mammal and land-squamate species whose ancestors appear to have originated on lands to the east of Wallace's Line, 1100 km away (for reference, western Java, to the north, is one-quarter of that distance). To this end, we carried out a comprehensive appraisal of the vertebrate assemblage of the landmass. Using published phylogenetic data, we established, for 28 out of 31 species, their nearest extant relatives and the geographical areas they occupy. The non-flying animals yield the most interesting results, with five having affinities east of the Wallace Line: the rodents *Rattus macleari* and *Rattus nativitatis*, the skinks *Cryptoblepharus egeriae* and *E. nativitatis*, and the gecko *L. listeri*. There is, therefore, a case for redrafting the Wallace Line such that the Christmas Island faunal assemblage is included within the Australasian biogeographical realm (Fig. 5). At the

very least, the 'data point' has to be reflected upon in future discussions of this fundamental biogeographical divide. It is also notable that the Christmas Island assemblage contains land-locked mammals that result from some of the longest known over-water dispersal colonizations of any members of this group. As a whole, the suite is 'evolutionary immature', because there are only small levels of differentiation of individual species with respect to their mainland relatives, and there are no records of *in situ* cladogenesis. The former reflects the youth of the island, the latter its small size.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Map of the Indo-Australian archipelago and adjacent areas, providing a key to the various geographical features mentioned in the text and depicted in [Figure 1](#) (Christmas Island is circled).

Figure S2. Map of the Indo-Australian Archipelago and adjacent areas (Christmas Island is circled), showing the tectonic plates in Southeast Asia and Western Pacific based on the work of [Bird \(2003\)](#) and [Hall \(2013\)](#).

Figure S3. Map summarizing the principal surface-water currents (pale blue dashed arrows) and the July winds (red continuous arrows) in the eastern Indian Ocean, Indo-Australian Archipelago and Western Pacific (Christmas Island is circled).