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Land birds on atolls: diversity, origin, and function

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ABSTRACT

Oceanic islands are global hotspots of avian biodiversity and endemism. Their isolation and distinct environmental conditions have uniquely shaped the evolutionary trajectories of island birds, while, in turn, land bird communities have become critical providers of ecological functions to island ecosystems. However, these processes and dynamics have been studied almost exclusively on large volcanic islands. Coral atolls – the other principal type of oceanic island – remain largely absent from ecological research on island bird diversity, evolution, and functioning. This omission constitutes a major gap because atoll islands are systems with distinct geo-evolutionary histories and dynamics. Recurrent cycles of emergence and submergence of atolls with glacial sea-level fluctuations have created unique natural experiments that offer novel insights into island assembly and evolution, different to those on volcanic islands. Here, we present the first synthesis of land bird assemblages on atoll islands across the Indo-Pacific. Our quantitative review of land bird records across Indo-Pacific atolls reveals that land birds are widely occurring on atolls throughout this region, often represented by endemic species or subspecies. Building on this macroecological data, we then synthesise the evolutionary pathways of land birds in the context of the atolls' geo-evolutionary dynamics, including refugial persistence on uplifted atolls, rapid divergence following recent colonisation, and relictual persistence of bird lineages extirpated from volcanic islands. Together, this synthesis suggests that atoll islands act as unique evolutionary arenas in which avian colonisation and diversification are repeatedly 'replayed' across successive emergence–submergence cycles. In addition to the unique conditions that atolls provide for land birds, we also review the ecological functions that land birds provide to atoll island ecosystems. Despite typically low species richness, atoll land bird assemblages provide ecological functions including pollination, seed dispersal, seed predation, and insectivory. Extinctions and range contractions have eroded much of this functional spectrum from many atolls but the consequences for atoll ecosystem integrity remain virtually unstudied. By synthesising land bird diversity, evolutionary history, and functional ecology on atolls, we highlight a reciprocal relationship: atolls provide unique evolutionary arenas for land birds, while land birds support ecological functioning on atoll island ecosystems. Together, the generated insights are relevant for domain-specific knowledge of atoll ecosystems, for a more holistic theoretical understanding of island evolution processes in dynamic and young island systems, as well as for conservation and restoration actions aimed at safeguarding both Indo-Pacific avian diversity and the integrity of atoll ecosystems.

Key words: atoll, bird conservation, community assembly, ecosystem functioning, endemism, evolution, extinction, functional ecology, island biology, island biogeography.

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I. INTRODUCTION

Oceanic islands are global hotspots of terrestrial biodiversity (Myers *et al.*, 2000). Among their most recognisable features are birds, whose remarkable radiations, distinctive insular adaptations, and pivotal functional roles have long captivated scientists (Newton, 2003). The capacity of birds for active long-distance dispersal enabled colonisation of virtually all major archipelagos, where they subsequently evolved along unique trajectories shaped by the distinct biogeographical and environmental conditions of islands (Jezierski, Smith & Clegg, 2024). As a result, 19% of all extant bird species occur exclusively or primarily on islands (Newton, 2003).

While islands are often unanimously celebrated as evolutionary hotspots (Fernández-Palacios *et al.*, 2021), island biogeography theory distinguishes between two fundamentally different types of oceanic islands: volcanic islands and coral atolls (Whittaker, Fernández-Palacios & Matthews, 2023). Volcanic islands are typically high-relief landmasses with complex topography, fertile basaltic substrates, and often occur in linear archipelagic chains. Atoll islands, by contrast, are small, low-lying landforms built from infertile, unconsolidated reef-borne sediments deposited along the ring-shaped rims of atoll reefs (Steibl *et al.*, 2024). Both oceanic island types are isolated and thus meet the baseline conditions for island evolution, i.e. immigration rates lower than speciation rates ('Darwinian Islands'; Gillespie & Roderick, 2002). However, atoll islands fundamentally differ in their abiotic features and biotic context due to their dynamic geo-evolutionary history (Braithwaite, Taylor & Kennedy, 1973; Steibl *et al.*, 2024) and therefore should represent a distinct but largely overlooked evolutionary arena for land birds (Nürk *et al.*, 2020).

Volcanic islands generally persist continuously after formation, undergoing only gradual subsidence and erosion (Borregaard, Matthews & Whittaker, 2016). Quaternary glacial sea-level changes submerged the coastal fringe habitats during highstands, while the volcanic islands' interior and upland habitats remained emerged (Rijsdijk *et al.*, 2014). The long-term persistence, elevational gradients, and habitat heterogeneity of volcanic islands facilitate diversification to play out in stable and isolated environments, allowing land bird lineages to accumulate steadily over millions of years (Valente, Phillimore & Etienne, 2015; Valente *et al.*, 2020). Atolls, in contrast, are subject to cycles of complete land emergence and submergence driven by glacial sea-level fluctuations every *c.* 100,000 years since the late-Quaternary (Montaggioni *et al.*, 2015; Droxler & Jorry, 2021). These cycles repeatedly reset terrestrial community assembly and evolution processes, as atoll landforms became entirely inundated during sea-level highstands (Braithwaite *et al.*, 1973; Taylor *et al.*, 1979; Hume & Martill, 2019; Steibl *et al.*, 2024). Atolls experienced at least five such cycles during the late-Quaternary glaciations, and possibly dozens since their Cenozoic formation (Ohde *et al.*, 2002; Toomey *et al.*, 2016; Droxler & Jorry, 2021). Most modern atoll islands last emerged only after the late-Holocene sea-level highstand, rendering them just 650–6,000 years old (Kench *et al.*, 2023). Thus, most atoll islands are one to several orders of magnitude younger than even the youngest volcanic islands in the Pacific (Neall & Trewick, 2008). A small number of atolls exist across the Indo-Pacific that are tectonically uplifted and thus maintained continuous landforms during

one or several of the late-Quaternary glacial sea-level highstands. For example, the raised atoll of Aldabra, Seychelles, remained emerged during the late-Holocene highstand and last submerged only during the late-Pleistocene highstand *c.* 130,000 years BP (Braithwaite *et al.*, 1973). Despite these distinctive geodynamics, the implications for land bird assembly and evolution on atolls remain largely overlooked in island biogeography and evolution theory.

Just as islands provide unique evolutionary arenas for colonising birds, land birds are unique providers of ecological functioning to oceanic islands, such as seed-dispersal or pollination (Whelan, Wenny & Marquis, 2008; Abrahamczyk, 2019; Nogales *et al.*, 2024). On volcanic islands, land birds providing these ecological functions (e.g. fruit-doves or honeycreepers) are recognized as central to ecosystem functioning and integrity (Anderson *et al.*, 2011; Heinen *et al.*, 2023). Yet on atolls, the very same taxa (e.g. fruit-doves) or their functional analogues (e.g. myzomelas) are mostly perceived as 'supertramp' generalists with ephemeral presence (Collins, Simberloff & Connor, 2011). Consequently, the functional roles and ecological importance of land birds for atolls have widely been overlooked.

Here, we provide the first synthesis of land birds on Indo-Pacific atolls. Building on a quantitative and qualitative literature review, we (*i*) characterise Indo-Pacific atoll land bird diversity, (*ii*) contextualise the evolutionary histories of atoll land bird lineages within the unique geo-evolutionary dynamics of atolls, and (*iii*) compile information on the roles of land birds for atoll island ecosystem functioning. By integrating these perspectives, we show how atoll islands represent a unique evolutionary arena for land birds and, reciprocally, how land bird assemblages constitute unique providers of ecological functionality for atoll ecosystems.

II. LITERATURE REVIEW FOR ATOLL LAND BIRD DIVERSITY MAPPING

We based our quantitative literature review work on the global atoll data portal that lists all atolls within the boundaries of the Indo-Pacific oceanic basin and with permanently emerged and vegetated landforms (i.e. excluding drowned atolls and those with only temporarily emergent sandbanks during low tides) (Steibl *et al.*, 2026). An additional 60 atolls with emerged landforms also occur in the Banda Sea, Caribbean, South China Sea, and in the Atlantic (Goldberg & Rankey, 2025), but these were excluded as they fell outside the target biogeographical region and lacked available data. Raised atolls such as Aldabra, Niau, or Rangiroa, which experience tectonic uplift while also exhibiting the general atoll morphology of an annular reef, rim islands, and a central lagoon, were included; uplifted reef limestone islands such as Makatea, Henderson, or Nauru (sometimes referred to as Makatea-type islands), which can reach elevations of up to 80 m, were not included (Stoddart & Steers, 1977). The final dataset comprised 310 atolls across the Indian and Pacific oceanic basins.

For each atoll, we conducted literature searches on land bird occurrence in Google Scholar between 2024 and 2025. Searches were repeated where atolls had multiple synonymous names. Reported species names and subspecies statuses were validated and harmonised following the Clements taxonomy in Cornell Laboratory of Ornithology 'Birds of the World' (BOW, 2025). For each taxon, we compiled additional information on global conservation status, distribution, and endemism from 'Birds of the World' (BOW, 2025).

We restricted our dataset to land birds – as opposed to seabirds or shorebirds – based on the classification by BirdLife International (BirdLife International, 2025). Only land bird species that breed either exclusively (i.e. endemics) or as part of their range on atolls were retained. Non-breeding migratory species (e.g. long-tailed koel [*Urodynamis taitensis*] on Pacific atolls), vagrants without breeding evidence or permanent populations (e.g. occasional sightings of kingfishers on Micronesian atolls), and recent human introductions (e.g. mynas, house sparrows, and feral pigeons across Indo-Pacific atolls) were excluded. The final dataset included only native, breeding, year-round residents on atolls. Both extant and recently extinct (i.e. documented since human arrival) species were included. The full list of references for all species records can be found in Data S1 (see online Supporting Information).

For each species, we conducted literature searches on their predominant ecological function based on foraging behaviour, following Whelan *et al.* (2008). For the assignments of land birds into the five main behaviour-driven functions (pollination, seed dispersal, seed predation, insect regulation, omnivory/scavenging), we combined published field study data with avian trait databases (Wilman *et al.*, 2014; Tobias *et al.*, 2022). The assignment of atoll land birds into the five foraging categories presented here constitutes primary functional roles, but species may also provide secondary (e.g. *Myzomela* honeyeaters were considered pollinators here, but can also feed on insects and thus contribute, to some extent, to insect regulation) or additional (e.g. nutrient cycling, habitat provisioning for invertebrates through nest building) functions (Pyke, 1980; Whelan *et al.*, 2008). The full list of references for assignments of atoll land birds into the presented functional categories can be found in Table S1.

III. DIVERSITY OF LAND BIRDS ON ATOLLS

(1) Species richness

Our literature review yielded species occurrence data for 244 of the 310 Indo-Pacific atolls (78.7% coverage). Across the 244 atolls where records were available, 91 native land bird lineages (species or subspecies) are documented (Table 1; Table S1). These belong to 83 species, 49 genera, 24 families, and 12 orders. Seventeen species (20.5%) are

Table 1. Extant and extinct land bird species on atolls. English, scientific names, and subspecies status based on 'Birds of the World' (BOW, 2025). Species status indicates whether species is endemic to atolls ('end.') or occurs with an endemic subspecies on atolls ('ssp.-end.'). Atoll status indicates the number of atolls where a given species is present ('pr') or the population became extirpated ('ex').

Family	English name	Scientific name	Species status	Atoll status
Anatidae	Laysan duck	*Anas laysanensis*	end.	1 pr | 1 ex
	Gadwall	*Mareca strepera* (ssp. *couesi*)	ssp.-end.	0 pr | 1 ex
Megapodiidae	Micronesian megapode	*Megapodius laperouse*	-	1 pr | 0 ex
	Melanesian megapode	*Megapodius eremita*	-	8 pr | 0 ex
Columbidae	Malagasy turtle-dove	*Nesoenas picturatus* (ssp. *coppingeri*)	-	4 pr | 4 ex
	Spot-breasted cuckoo-dove	*Macropygia mackinlayi*	-	1 pr | 0 ex
	Pacific emerald dove	*Chalcophaps longirostris*	-	1 pr | 0 ex
	Bronze ground-dove	*Pampusana beccarii*	-	1 pr | 0 ex
	Polynesian ground-dove	*Pampusana erythroptera*	end.	3 pr | 17 ex
	White-throated ground-dove	*Pampusana xanthonura*	-	0 pr | 1 ex
	Nicobar pigeon	*Caloenas nicobarica*	-	4 pr | 1 ex
	Crimson-crowned fruit-dove	*Ptilinopus porphyraceus*	-	2 pr | 0 ex
	Atoll fruit-dove	*Ptilinopus coralensis*	end.	29 pr | 2 ex
	Red-bellied fruit-dove	*Ptilinopus greyi*	-	1 pr |0 ex
	Yellow-bibbed fruit-dove	*Ptilinopus solomonensis*	-	4 pr | 0 ex
	Kosrae fruit-dove	*Ptilinopus hernsheimi*	-	0 pr | 1 ex
	Comoro blue-pigeon	*Alectroenas sganzini* (ssp. *minor*)	ssp.-end.	1 pr | 4 ex
	Pacific imperial-pigeon	*Ducula pacifica*	-	20 pr | 1 ex
	Micronesian imperial-pigeon	*Ducula oceanica* (ssp. *ratakensis*)	ssp.-end.	6 pr | 1 ex
		Ducula oceanica	-	7 pr | 3 ex
	Polynesian imperial-pigeon	*Ducula aurorae*	-	0 pr | 1 ex
	Island imperial-pigeon	*Ducula pistrinaria*	-	2 pr | 0 ex
Cuculidae	Malagasy coucal	*Centropus toulou* (ssp. *insularis*)	ssp.-end.	1 pr | 1 ex
	Asian Koel	*Eudynamys scolopaceus*	-	25 pr | 0 ex
	Shining bronze-cuckoo	*Chalcites lucidus*	-	1 pr | 0 ex
Caprimulgidae	Madagascar nightjar	*Caprimulgus madagascariensis* (ssp. *aldabrensis*)	ssp.-end.	1 pr | 0 ex
Rallidae	White-throated rail	*Dryolimnas cuvieri* (ssp. *aldabranus*)	ssp.-end.	1 pr | 2 ex
	Buff-banded rail	*Gallirallus philippensis* (ssp. *andrewsi*)	ssp.-end.	2 pr | 0 ex
		Gallirallus philippensis (ssp. *tounelieri*)	ssp.-end.	2 pr | 0 ex
		Gallirallus philippensis	-	5 pr | 0 ex
	Wake rail	*Gallirallus wakensis*	end.	0 pr | 1 ex
	Eurasian moorhen	*Gallinula chloropus*	-	4 pr | 0 ex
	American coot	*Fulica americana*	-	1 pr | 0 ex
	White-browed crake	*Poliolimnas cinereus*	-	0 pr | 4 ex
	Watercock	*Gallicrex cinerea*	-	3 pr | 0 ex
	White-breasted waterhen	*Amaurornis phoenicurus*	-	34 pr |0 ex
	Spotless crake	*Zapornia tabuensis*	-	20 pr | 0 ex
	Laysan rail	*Zapornia palmeri*	end.	0 pr | 1 ex
Scolopacidae	Kiritimati sandpiper	*Prosobonia cancellata*	end.	0 pr | 1 ex
	Tuamotu sandpiper	*Prosobonia parvirostris*	end.	6 pr | 16 ex
Accipitridae	Black-winged kite	*Elanus caeruleus*	-	4 pr | 0 ex
Alcedinidae	Tuamotu kingfisher	*Todiramphus gambieri*	end.	1 pr | 0 pr
	Pohnpei kingfisher	*Todiramphus reichenbachii*	-	1 pr | 0 ex
	Sacred Kingfisher	*Todiramphus sanctus*	-	1 pr | 0 ex
	Collared kingfisher	*Todiramphus chloris*	-	7 pr | 0 ex
	Beach kingfisher	*Todiramphus saurophagus*	-	5 pr | 0 ex
	Kingfisher sp.	*Todiramphus* cf. *cinnamominus*	-	0 pr | 1 ex
Falconidae	Malagasy kestrel	*Falco newtoni* (ssp. *aldabranus*)	ssp.-end.	1 pr | 0 ex
Psittaculidae	Red-flanked lorikeet	*Hypocharmosyna placentis*	-	1 pr | 0 ex
	Kuhl's lorikeet	*Vini kuhlii*	-	3 pr | 1 ex
	Blue lorikeet	*Vini peruviana*	end.	8 pr | 7 ex
	Cardinal lory	*Chalcopsitta cardinalis*	-	1 pr | 1 ex
	Pohnpei lorikeet	*Trichoglossus rubiginosus*	-	1 pr | 1 ex
	Coconut lorikeet	*Trichoglossus haematodus* (ssp. *nesophilus*)	ssp.-end.	2 pr | 0 ex
		Trichoglossus haematodus	-	2 pr | 0 ex

(Continues on next page)

Table 1. *(Cont.)*

Family	English name	Scientific name	Species status	Atoll status
Meliphagidae	Micronesian myzomela	*Myzomela rubratra*	-	7 pr | 0 ex
	Cardinal myzomela	*Myzomela cardinalis*	-	2 pr | 0 ex
	Bismarck black myzomela	*Myzomela pammelaena*	-	2 pr | 0 ex
	Sulphur-breasted myzomela	*Myzomela jugularis*	-	1 pr | 0 ex
	Dark-brown honeyeater	*Lichmera incana*	-	1 pr | 0 ex
Rhipiduridae	Manus fantail	*Rhipidura semirubra*	-	1 pr | 0 ex
Dicruridae	Aldabra drongo	*Dicrurus aldabranus*	end.	1 pr | 0 ex
Monarchidae	Island monarch	*Monarcha cinerascens*	-	9 pr | 0 ex
	Melanesian flycatcher	*Myiagra caledonica*	-	1 pr | 0 ex
Corvidae	House Crow	*Corvus splendens* (ssp. *maledivicus*)	ssp.-end.	25 pr | 0 ex
	Pied crow	*Corvus albus*	-	5 pr | 0 ex
Cisticolidae	Madagascar cisticola	*Cisticola cherina*	-	3 pr | 0 ex
Acrocephalidae	Caroline reed-warbler	*Acrocephalus syrinx*	-	8 pr | 3 ex
	Kiritimati reed-warbler	*Acrocephalus aequinoctialis*	end.	3 pr | 0 ex
	Tuamotu reed-warbler	*Acrocephalus atyphus*	end.	48 pr | 7 ex
	Millerbird	*Acrocephalus familiaris* (ssp. *familiaris*)	ssp.-end.	0 pr | 1 ex
	Aldabra brush-warbler	*Nesillas aldabrana*	end.	0 pr | 1 ex
Pycnonotidae	Malagasy bulbul	*Hypsipetes madagascariensis* (ssp. *rostratus*)	ssp.-end.	1 pr | 2 ex
		Hypsipetes madagascariensis (ssp. *grotei*)	ssp.-end.	1 pr | 0 ex
Zosteropidae	Indian white-eye	*Zosterops palpebrosus*	-	6 pr | 0 ex
	Malagasy white-eye	*Zosterops maderaspatanus* (ssp. *voeltzkowi*)	ssp.-end.	1 pr | 0 ex
		Zosterops maderaspatanus (ssp. *menaiensis*)	spp.-end.	1 pr | 0 ex
		Zosterops maderaspatanus	-	2 pr | 0 ex
	Aldabra white-eye	*Zosterops aldabrensis*	end.	1 pr | 0 ex
	Silvereye	*Zosterops lateralis*	-	1 pr | 0 ex
	Louisiade white-eye	*Zosterops griseotinctus* (ssp. *eichhorni*)	ssp.-end.	1 pr | 0 ex
Sturnidae	Metallic starling	*Aplonis metallica*	-	1 pr | 0 ex
	Atoll starling	*Aplonis feadensis*	-	6 pr | 0 ex
	Singing starling	*Aplonis cantoroides*	-	2 pr | 0 ex
	Micronesian Starling	*Aplonis opaca*	-	13 pr | 0 ex
	Polynesian starling	*Aplonis tabuensis*	-	3 pr | 0 ex
Nectariniidae	Souimanga sunbird	*Cinnyris sovimanga* (ssp. *aldabrensis*)	ssp.-end.	1 pr | 0 ex
		Cinnyris sovimanga (ssp. *abbotti/buchenorum*)	ssp.-end.	2 pr | 0 ex
		Cinnyris sovimanga	-	1 pr | 0 ex
Ploceidae	Aldabra fody	*Foudia aldabrana*	end.	1 pr | 1 ex
Fringillidae	Laysan finch	*Telespiza cantans*	end.	1 pr | 0 ex
	Laysan honeycreeper	*Himatione fraithii*	end.	0 pr | 1 ex

endemic to atolls (of which eight species are single-atoll endemics and nine species are endemic to an atoll archipelago), while 66 species (79.5%) also occur on volcanic islands and/or continental landmasses.

Of the 83 recorded species, 71 (85.5%) are extant, seven (8.4%) have been extirpated from atolls but persist on volcanic islands, and five (6.0%) are globally extinct, all of which were endemic to atolls. Given that island extinctions tend to rapidly follow human colonisation (Duncan, Boyer & Blackburn, 2013), which on atolls occurred as early as 2,500 years BP, and that four of the five extinction records from atolls are from the 20th century, the data on species extinction is likely biased and additional earlier extinctions were likely missed.

Beyond species extinctions, available records show severe range contractions in atoll land birds. For example, the Tuamotu sandpiper (*Prosobonia parvirostris*) has disappeared from at least 16 atolls in the Tuamotu archipelago, French Polynesia, since *c*. 1900, and nowadays persists on a few islands within only six atolls (Pierce & Blanvillain, 2004). The Polynesian ground-dove (*Pampusana erythroptera*) has disappeared from at least 17 atolls and persists nowadays on a few islands within only three atolls (Thibault & Cibois, 2017).

Despite species extinctions and range reductions, 157 atolls still house at least one species of land bird (64.3% of surveyed atolls) (Fig. 1). Conversely, native land bird populations became extirpated from 17 atolls (7.0% of surveyed atolls). On 70 atolls (28.7% of surveyed atolls), land birds have never been recorded in Western science literature. On 61 atolls (25.0% of surveyed atolls), at least one atoll-endemic land bird species occurs. Among atolls with extant and/or extinct land birds, species richness ranges from one to 14, with both mean and median values of three species per atoll (Fig. 1C). Treating each bird species per atoll as a distinct island population, a total of 404 extant land bird populations occur

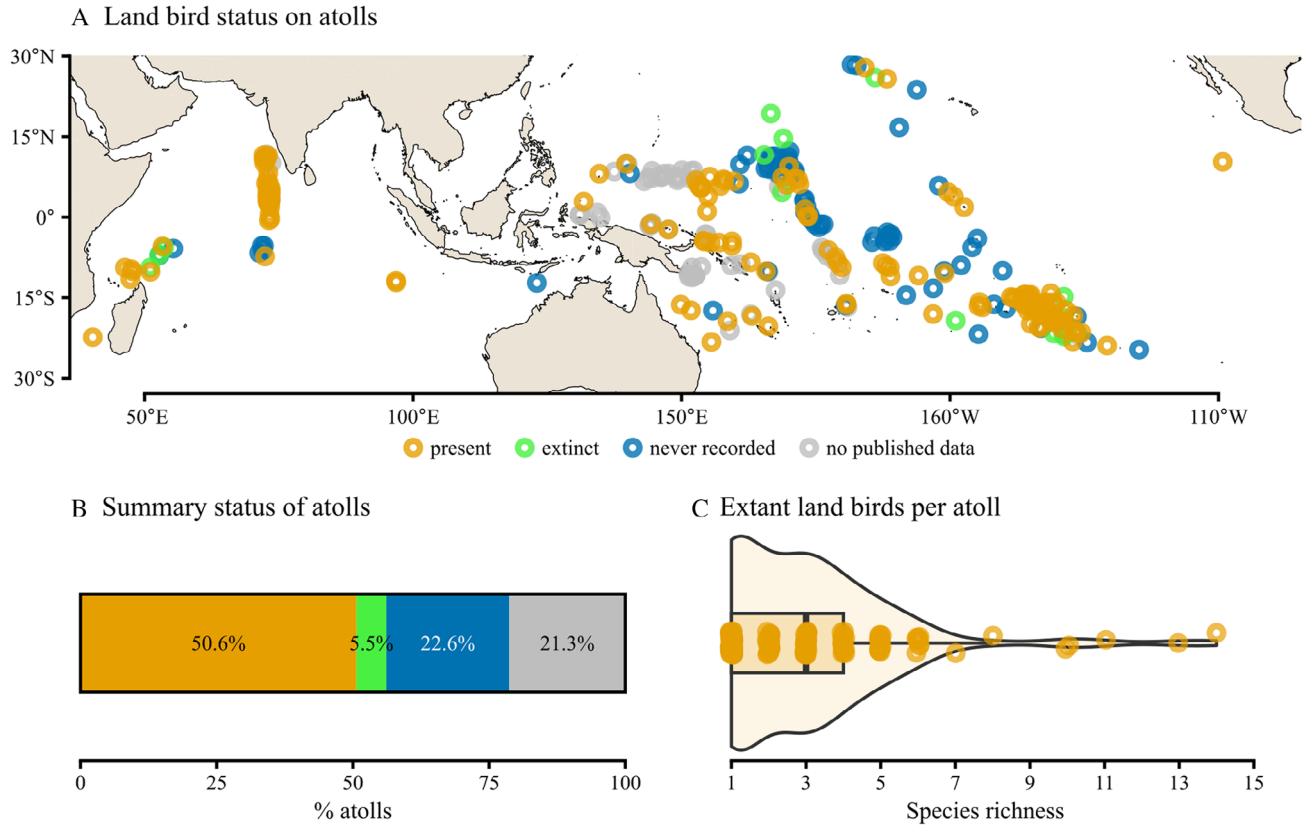

Fig. 1. Distribution and diversity of land birds on atolls. Orange: atolls with at least one recorded extant land bird species. Green: atolls with historical records but now extinct populations or species. Blue: atolls with no documented extant or extinct land birds in the available literature. Grey: atolls with no available survey data on their avifauna. (A) Geographic distribution of land bird occurrence on atolls. (B) Proportional status of land bird occurrence across all Indo-Pacific atolls ($n = 310$). (C) Species richness of extant land birds per atoll (excluding absences), with boxplot showing median (thick vertical line) and 25% and 75% percentiles, and underlying violin plot visualising kernel density distribution of species richness data. Individual data points show observed species richness per atoll.

across the 157 atolls with land birds, alongside 91 documented population extirpations.

(2) Population ecology

For the 17 land bird species with global populations restricted to atolls (i.e. atoll endemics), the intactness of the atoll ecosystems is a prerequisite for the species' survival. For the 66 species whose mapped ranges encompass both volcanic and atoll islands, apparent widespread distribution ranges can be misleading when evaluating conservation needs: several species are scarce or absent from volcanic island interiors and persist largely in coastal forest remnants or on small satellite islets, such as the island monarch (*Monarcha cinerascens*), Nicobar pigeon (*Caloenas nicobarica*), and atoll starling (*Aplonis feadensis*). Thus, atolls may support a disproportionately large share of their estimated global population sizes (Collins *et al.*, 2011; Craig & Feare, 2020a). For example, 31% of all active nests of the Palau-endemic subspecies of the Micronesian megapode (*Megapodius laperouse senex*) were found to occur on Ngcheangel atoll (*c.* 1.4 km^2 island area), Palau, where nesting densities were up to ten times higher than on the neighbouring volcanic island of Babeldaob (*c.* 400 km^2 island area), Palau (Olsen *et al.*, 2016).

Land bird populations can be abundant on single atoll islands, with recorded densities exceeding 10 individuals/ha (Buden, 1999a,b, 2006; Blanvillain, Florent & Thenot, 2002; Hockey, Wanless & von Brandis, 2011). Several species were found to achieve markedly higher densities on atolls compared to nearby volcanic islands, such as the Micronesian starling (*Aplonis opaca*) reaching 5- to 10-fold higher densities (Buden, 1998, 1999a), *Acrocephalus* reed-warblers reaching 10-fold higher densities (Buden, 1999b), and *Todiramphus* kingfishers reaching three-fold higher densities on Micronesian atolls relative to volcanic Saipan island, Northern Mariana Islands (Buden, 1996a; Camp *et al.*, 2009). These higher densities on atoll islands may partly result from competitive release, niche expansion, density compensation, and reduced territory sizes (Morse, 1977; Nilsson, 1977). However, they may also reflect the widespread loss of coastal habitats on volcanic islands due to urbanisation (accompanied by invasive predators, increased

direct human disturbances, and deforestation) (Russell & Kueffer, 2019). In this context, atolls can serve as important refugia for land bird species adapted to low-lying, dynamic, coastal habitats of oceanic islands.

The restricted land area and elevated population densities on atolls may further drive behavioural or physiological adaptations of land birds on atolls, such as cooperative breeding in trios rather than pairs as a likely strategy to minimize competition for nesting territories (Brooke & Hartley, 1995). Basal metabolic rate and body size may be reduced in species inhabiting small compared to larger oceanic islands (McNab, 1994, 2002), in line with expected bird island syndromes known from other island systems (Jezierski, Smith & Clegg, 2024).

(3) Challenges to synthesizing the diversity of atoll land birds

Three major limitations need to be considered when contextualising this quantitative review of land bird diversity on atolls.

First, the 66 atolls lacking published records are unevenly distributed geographically. Half are located within just two countries – Papua New Guinea and the Federated States of Micronesia (Fig. 1A). Survey coverage in these regions is particularly low, with only 7 of 22 atolls surveyed in Papua New Guinea, and 15 of 34 in the Federated States of Micronesia. Especially considering the geographic proximity of these un-surveyed atolls to the Papuan and Indo-Malayan regions, which represent the principal source pools for Pacific land bird lineages (Jønsson & Holt, 2015), these un-surveyed atolls may harbour additional species not captured in this review.

Second, atoll islands provide poor conditions for bone preservation and fossilization due to their highly porous carbonate soils and a lack of sheltered depositional environments, such as caves or lava tubes (Mitchell, 2015). Consequently, fossil records of extinct atoll birds are sparse, likely leading to severe underestimation of pre-human diversity, especially compared to volcanic islands (Steadman, 1995, 1997). For instance, reconstructions of the distribution of rails in the Pacific suggest that nearly all atolls (except for Johnston atoll, US Minor Outlying Islands) likely supported one rail species, resulting in an estimated total of 61 atoll-endemic rail species across the Pacific (Curnutt & Pimm, 2001). However, only two, the Wake and Laysan rails, are confirmed from historic records (Baldwin, 1947; Olson & Rauzon, 2011). Similarly, most atoll groups likely housed imperial-pigeons (*Ducula* spp.) and fruit-doves (*Ptilinopus* spp.) prior to human arrival (Curnutt & Pimm, 2001).

Third, human colonisation of atolls began as early as 2,500 years BP (Nunn, 2016). In the absence of refugia, bird extinctions may have occurred almost immediately upon first human contact and before permanent settlements were developed (Weisler, 1999). Such losses would have left little to no evidence in either archaeological sites or records by Western natural historians (Weisler, 1999). Indigenous knowledge may constitute a promising yet underutilised source for inferring historical bird occurrences on atolls (Richter-Gravier, 2022).

Taken together, these three limitations mean that our quantitative review data is restricted to only the documented extant and extinct land bird lineages. It is likely that additional land bird species existed on atolls, and that atolls nowadays devoid of land birds supported them in the past (Steadman, 1995, 1997; Curnutt & Pimm, 2001). Thus, our synthesis should be regarded as a conservative minimum estimate of both atoll bird diversity and the number of atolls that historically harboured land birds. Despite these limitations, this review shows that atolls nowadays support almost one-sixth (14.2%) of the extant Indo-Pacific land bird fauna (71 extant species on atolls and 501 recognized extant species on all Indo-Pacific islands; BirdLife International, 2025) and that about two-thirds of surveyed atolls still harbour at least one extant land bird species.

IV. EVOLUTIONARY HISTORY: ATOLLS AS UNIQUE EVOLUTIONARY ARENAS FOR LAND BIRDS

At the family level, atoll land bird assemblages broadly resemble those of volcanic islands in the remote tropical Indo-Pacific, comprising fruit-doves and imperial pigeons, rails, kingfishers, parakeets, and widespread passerine families such as reed warblers, honeyeaters, and starlings (Steadman, 2006). However, several prolific colonisers of Indo-Pacific volcanic islands such as white-eyes (Zosteropidae), fantails (Rhipiduridae), or whistlers (Pachycephalidae) are represented on only one or a few atolls, or are entirely absent (Moyle *et al.*, 2009; Jønsson *et al.*, 2010; Fabre *et al.*, 2014). To date, however, no dedicated comparative analysis has examined the consistencies and differences in land bird assemblages between atoll and volcanic islands.

Although the higher-level taxonomic composition of the atoll-inhabiting bird fauna largely mirrors that of volcanic islands, the recurrent emergence–submergence cycles of atoll islands have created markedly different conditions for avian colonisation, assembly, and diversification (Steibl *et al.*, 2024). Recognising bird occurrences on atolls not merely as a transient assemblage of generalist taxa in an ephemeral system (Collins *et al.*, 2011) but as the product of a unique geodynamic system provides new perspectives on the fundamental processes and constraints that shape island assembly and evolution.

(1) Contingency and predictability of atoll land bird assembly and evolution

The recurrent terrestrial ecological resets caused by the submergence of atoll landforms provide a unique natural experiment for testing the balance between contingency and predictability in island assembly and evolution (Blount, Lenski & Losos, 2018). In the 20th century, Stephen

J. Gould argued that "replaying life's tape" would yield wholly novel outcomes each time ('evolutionary contingency'), whereas Simon Conway Morris contended that evolutionary trajectories are constrained and therefore repeatable ('evolutionary predictability') (Gould, 1989; Conway Morris, 1985). Atoll island ecosystems furnish a real-world test of this thought experiment: with each emergence–submergence cycle, they reset their terrestrial communities, effectively 'replaying' the process of island colonisation and speciation at *c.* 100,000-year periodicity.

Fossil and contemporary records of land birds from Aldabra atoll, a raised atoll northwest of Madagascar, offer one of the few empirical datasets of island diversity spanning multiple emergence–submergence cycles (Hume, Martill & Hing, 2018). During the Pleistocene, a flightless endemic rail (*Dryolimnas cuvieri*) inhabited Aldabra but went extinct when the atoll became submerged during the late-Pleistocene highstand *c.* 130,000 years BP (Braithwaite *et al.*, 1973). Following the re-emergence of the atoll *c.* 80,000–120,000 years BP, the rail recolonised Aldabra from Madagascar and, for a second time, evolved in isolation toward flightlessness (*Dryolimnas* [*cuvieri*] *aldabranus*) (Wanless, 2003; van de Crommenacker *et al.*, 2019). This repeated evolution of flightlessness from the same ancestral source demonstrates a striking case of predictable, repeatable evolution across successive emergence–submergence cycles (Hume & Martill, 2019) (Fig. 2A).

At the same time, Aldabra's fossil record also highlights evolutionary contingency. An endemic duck (*Aldabranus cabri*) vanished with the atoll's late-Pleistocene submergence *c.* 130,000 years BP, but there is no evidence that a duck re-colonised Aldabra after this ecological reset (Harrison & Walker, 1978; Taylor *et al.*, 1979). Conversely, other endemic land birds such as the Aldabra fody (*Foudia aldabrana*) and the Aldabra brush-warbler (*Nesillas aldabrana*) are known only from the current emergence period but are absent from fossil records of earlier emergence periods (Hume *et al.*, 2018) (Fig. 2B).

Taken together, and despite limited paleontological research on atolls, these patterns illustrate that land bird assembly, genetic differentiation, and morphological adaptation on atolls can follow either predictable evolutionary routes or exhibit evolutionary contingency across successive atoll emergence–submergence cycles (Hume *et al.*, 2018).

(2) Phylogenetic histories and modes of atoll colonisation

The young age of most atoll islands (650–6,000 years) and their periodic ecological resets (Droxler & Jorry, 2021; Kench *et al.*, 2023; Steibl *et al.*, 2024) require close examination of how land birds have assembled and evolved on atolls, particularly to explain the occurrence of atoll endemism. Although phylogenetic data exist for only a subset of species, a general pattern of colonisation from nearby high islands or continental landmasses to atolls is evident (Warren *et al.*, 2005; Pasquet *et al.*, 2007; Cibois *et al.*, 2011; Fuchs *et al.*, 2016). This directionality is consistent with the accepted model of colonisation from geologically older to younger systems (Shaw & Gillespie, 2016). Within this pattern, three principal colonisation–speciation modes can be distinguished.

First, tectonically uplifted atolls can provide terrestrial refugia during sea-level highstands, allowing atoll-endemic lineages to persist through periods when low-lying atolls were submerged (Fig. 2C). The Tuamotu reed warbler (*Acrocephalus atyphus*), endemic to the Tuamotu atoll archipelago, French Polynesia, diverged 300,000–960,000 years BP from its closest known relatives in Marquesas and Mangareva, French Polynesia, thus pre-dating multiple emergence–submergence cycles (Cibois *et al.*, 2011). Genetic data indicate that Tuamotu reed-warbler populations persisted on uplifted atolls (Ana'a, Niau, Makatea, all French Polynesia), where each island harbours a distinct phylogenetic lineage, whereas the surrounding low-lying atolls share a single haplotype (Cibois, Thibault & Pasquet, 2010). These genetic patterns revealed that uplifted atolls served as refugia during sea-level highstands when low-lying atoll islands were submerged, followed by (re-)colonisation of low-lying atoll islands from uplifted atolls as sea levels fell. These refugia dynamics allowed an atoll-endemic lineage with an evolutionary divergence far older than the atoll islands themselves to persist (Cibois *et al.*, 2010; Montaggioni *et al.*, 2023). The atoll fruit-dove (*Ptilinopus coralensis*) likely owes its persistence and endemism to similar refugia dynamics (Cibois *et al.*, 2014). Divergence estimates significantly pre-dating the late Pleistocene sea-level highstand, such as in the Tuamotu sandpiper (*P. parvirostris*) (650,000–2.02 million years BP) or Kiritimati reed warbler (*A. aequinoctialis*) (560,000–760,000 years BP), suggest a complex and incompletely understood lineage history of persistence in uplifted refugia throughout multiple glacial cycles of atoll emergence and submergence (Cibois, Thibault & Pasquet, 2007; de Pietri *et al.*, 2021). In some cases, secondary differentiation occurred on low-lying atolls after colonisation from uplifted atoll refugia, as evidenced by distinct subspecies of the Kiritimati reed warbler (*A. aequinoctialis*) and multiple subspecies of the Tuamotu reed warbler across the atoll archipelago (Cibois *et al.*, 2010; Kearns *et al.*, 2024).

Second, atolls without nearby uplifted refugia were colonised anew by land bird species with strong dispersal abilities after their late-Holocene emergence, which subsequently may have initiated *in situ* differentiation on the colonised atoll (Fig. 2D). This mode is reflected in the common occurrence of atoll-endemic subspecies, which indicate early divergence and incipient allopatric speciation (Phillimore *et al.*, 2007; Hume & Martill, 2019) (Table 1). Examples include the Maldives-endemic subspecies of the house crow (*Corvus splendens maledivicus*) (Anderson & Shimal, 2020), two subspecies of the buff-banded rail (*Gallirallus philippensis andrewsi*, *G. philippensis tounelieri*) endemic to Cocos-Keeling atoll and Coral Sea atolls, Australia, respectively (Schodde & Naurois, 1982; Garcia-Ramirez *et al.*, 2017), and distinct subspecies of the Souimanga sunbird on Aldabra (*Cinnyris souimanga aldabrensis*) and Cosmoledo/Astove atolls, Seychelles (*C. souimanga buchenorum*) (Warren *et al.*, 2003) (see Table 1 for a comprehensive list of accepted atoll-endemic subspecies). Several other

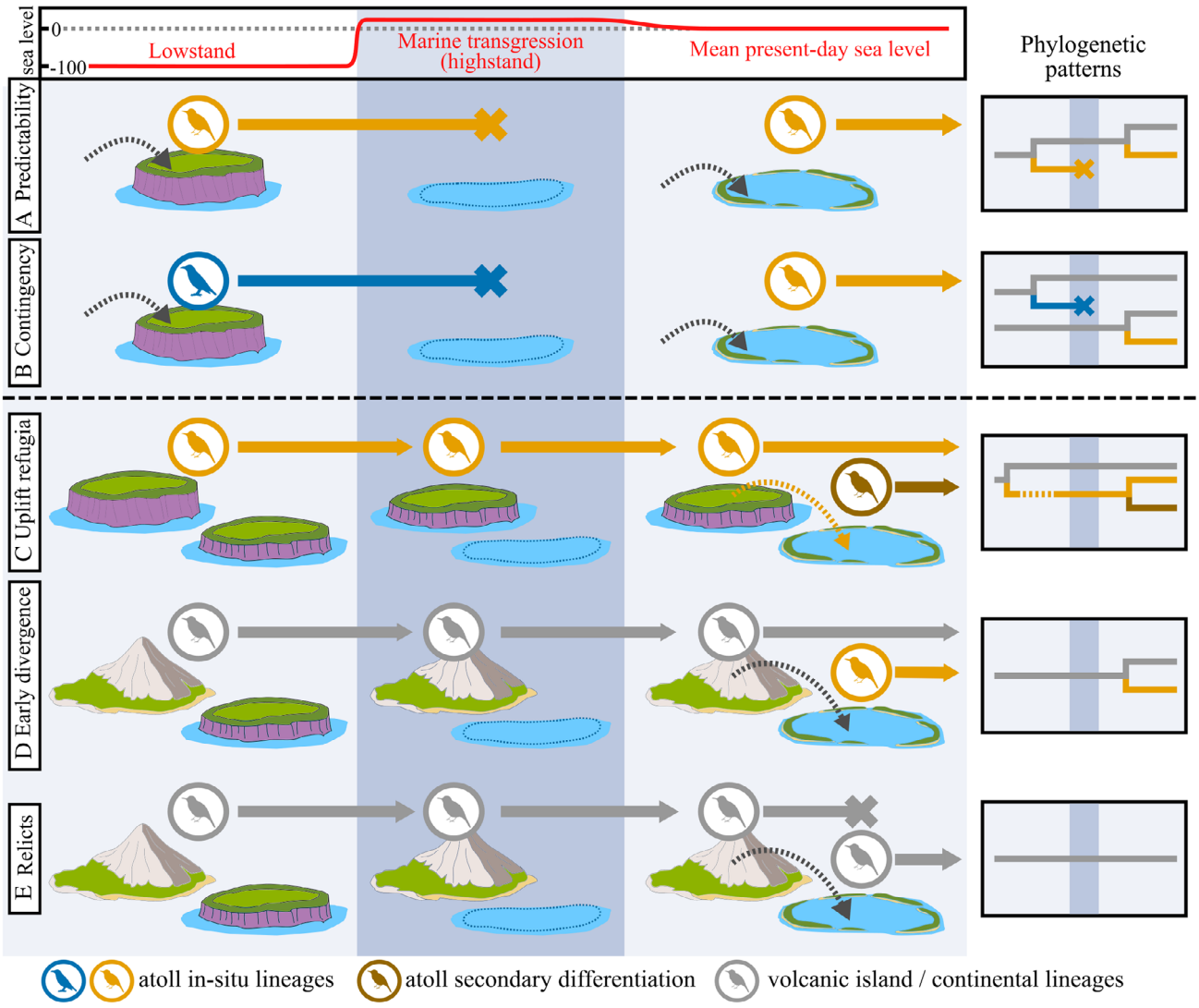

Fig. 2. Atoll island emergence–submergence dynamics and resulting scenarios of diversity and speciation in land birds. Quaternary sea-level changes (schematic mean sea-level curve simplified, in red) shifted atolls through stages of large carbonate platform islands during lowstands, complete landform submergences during highstands, and rim-island configurations as in present-day sea levels. The figure illustrates one simplified cycle of lowstand–submergence–rim configuration and the resulting modes of land bird colonisation and differentiation identified from palaeontological and phylogenetic studies. Phylogenetic trees show simplified, expected patterns for each mode.

land birds on atolls remain grouped within volcanic islands/continental populations as a single subspecies. However, to the best of our knowledge, phylogenetic testing has not confirmed how similar or diverged any of these atoll populations actually are from their closest mainland or volcanic island population. Notably, whenever morphological and/or phylogenetic testing has been undertaken explicitly for an atoll population, the populations have been confirmed as atoll-endemic subspecies (Warren *et al.*, 2003, 2005, 2006, 2012; Fuchs *et al.*, 2016; Martins *et al.*, 2020). Recent range expansions, such as the recent spread of the white-breasted waterhen (*A. phoenicurus*) into Micronesian atolls (Buden & Retogral, 2010), may reflect ongoing assembly processes due to the atoll islands' young age. Some recent colonisations, however, may also represent replacements following undocumented prehistoric extinctions, as argued for the buff-banded rail (*G. philippensis*) on Pacific atolls (Kirchman, 2009).

Third, species once widespread across both volcanic islands and atolls have been extirpated from volcanic islands and consequently have become restricted to atolls (Fig. 2E). Even though these land bird species appear as endemic to atolls, they do not reflect *in situ* speciation events but rather relicts of formerly more widespread lineages (McCulloch & Waters, 2019). Bone records of the Laysan duck (*Anas laysanensis*) and Laysan honeycreeper (*Himathione fraithii*) on the volcanic islands of Hawai'i (James & Olson, 1991; Lavretsky

et al., 2015), or historical records of the blue lorikeet (*Vini peruviana*) on Tahiti, French Polynesia (Medway, 2004), reveal that these species became restricted to atolls only after becoming extirpated from volcanic islands. Divergence times for such species therefore predate Quaternary atoll submergences (Lavretsky *et al.*, 2015).

Together, these three modes – refugial persistence, recent colonisation with rapid divergence, and relictual persistence following extirpations from volcanic islands – capture the known, principal evolutionary pathways by which land birds assemble and evolve on atolls. They underscore how atoll islands, despite their young age and cyclical ecological resets, provide a mosaic of recurrent opportunities for persistence, novel colonisation, diversification, and relictual lineage survival in the face of repeated ecological resets.

V. ECOLOGICAL FUNCTIONING: LAND BIRDS AS PROVIDERS OF ECOLOGICAL FUNCTIONING FOR ATOLLS

(1) Functional diversity and prevalence on atolls

Birds fulfil a wide range of ecological functions including pollination, seed dispersal, seed predation, nutrient cycling, and habitat provisioning (Whelan *et al.*, 2008). On oceanic islands, reliance on avian contributions for these functions is often amplified by the absence of other vertebrate groups, particularly mammals (Nogales *et al.*, 2024). The functions provided by land birds to island ecosystems are oftentimes connected to endemic, specialised, and, today, often critically endangered or extinct species, such as the dodo as seed-disperser or the endangered Hawai'ian honeycreepers as pollinators (Heinen *et al.*, 2018, 2023; Smith *et al.*, 1995; Aslan *et al.*, 2014). However, widespread and generalist land birds can also play important roles for island ecosystem functioning (Thornton *et al.*, 1988; Thornton, Compton & Wilson, 1996).

Based on existing trait databases and classifications of avian ecological functions (Whelan *et al.*, 2008; Wilman *et al.*, 2014), we grouped atoll land birds into five categories based on foraging behaviour: pollinators, seed dispersers, seed predators, insect population regulators, and generalist foragers (Fig. 3). Across the 157 atolls that presently support land birds, 70 (44.6%) host a single functional group, 42 (26.7%) host two, 30 (19.1%) host three, nine (5.7%) host four, and six (3.8%) support all five of these identified functional groups. Land bird-driven seed dispersal is the most widespread function, documented on 103 atolls (65.6% of atolls with extant land birds) (Fig. 3).

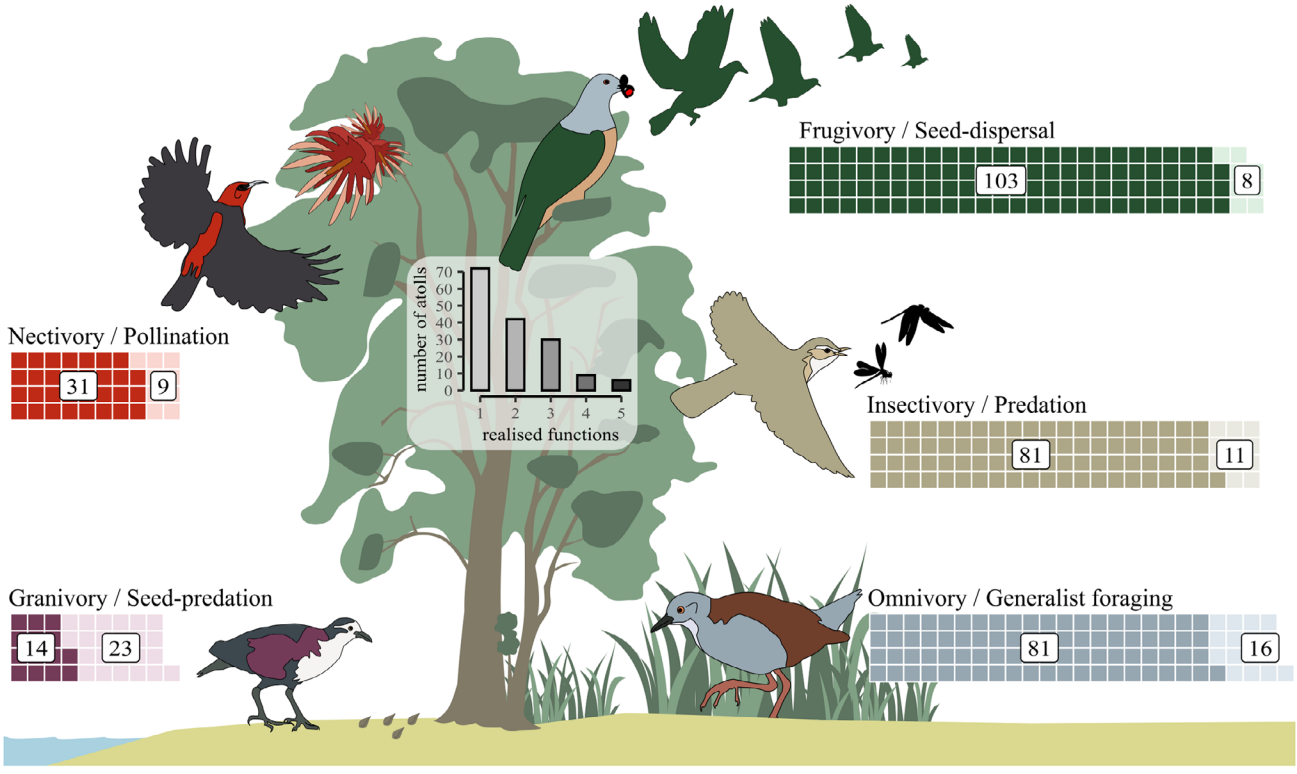

Fig. 3. Functional diversity and prevalence of land-bird-provided ecological functions on atolls. Atoll land birds were classified into five key avian ecological functions based on foraging behaviour (Whelan *et al.*, 2008; Wilman *et al.*, 2014). The bar chart at the centre shows the number of avian functions realised per atoll ($n = 157$ atolls with extant land birds). Waffle plots depict, for each function, the number of atolls where a function is realised by an extant species (darker shade), and the number of atolls where a function has been lost through bird extinction (lighter shade).

Whether all five land bird functions were historically realised on every atoll remains uncertain. Functional diversity was likely greater before human arrival on atolls; while human-mediated species introductions may have increased functional diversity in some cases, concomitant extinctions of indigenous species and populations would have weakened or eliminated many other ecological functions from atolls (Heinen *et al.*, 2025). For example, Steadman (1995, 1997) argued that fruit-doves, imperial-pigeons, and ground-doves once occurred on most Pacific atolls, implying that land bird-driven seed dispersal and seed predation were historically more widespread across Pacific atolls.

(2) Pollination

Nectivorous land birds can play important roles in plant–pollinator mutualisms when pollen is effectively transferred during feeding (Pauw, 2019). On atolls, the principal nectar-feeding land bird species include six lorikeets (Psittaculidae: *Vini* spp., *Trichoglossus* spp., *Chalcopsitta cardinalis*, and *Hypocharmosyna placentis*), five honeyeaters (Meliphagidae: *Myzomela* spp., and *Lichmera incana*), and one sunbird (Nectariniidae: *Cinnyris sovimanga*). The *Vini* lorikeets are found on Polynesian atolls, while the other lorikeets and honeyeaters are found on Micronesian and Melanesian atolls, and the sunbird on western Indian Ocean atolls (Fig. 4A, Fig. S1). In addition to these extant taxa, the Laysan honeycreeper (Fringillidae: *Himatione fraithii*) formerly occurred on Laysan atoll in the Hawaiian archipelago until its extinction in 1923 (Ely & Clapp, 1973). Besides these established nectivorous species, there exist observations that the Tuamotu sandpiper (Scolopacidae: *P. parvirostris*), a relict shorebird endemic to eastern Polynesian atolls, also exhibits unusual nectar-feeding behaviour in tree canopies, coconut palms, and bushes, suggesting a tentative pollinating role (Pierce & Blanvillain, 2004; Howell & van der Vliet, 2014; Ducatez & DeVore, 2024).

The honeyeaters, lorikeets, and the Souimanga sunbird are generalist nectivores and do not exhibit the same degree of host–plant-specificity as other nectar-feeding taxa (e.g. hummingbirds), in line with island biogeography principles whereby there is a selection for generalists on islands (Scott *et al.*, 2003; Norman & Christidis, 2014). On Aldabra atoll, the Souimanga sunbird's diet consists of 61% nectar and 39% arthropods, predominantly spiders (Frith, 1979). Its breeding on the atoll is synchronised with the predominant flowering period, suggesting dependence on nectar resources (Frith, 1979). Diet studies of myzomelas indicate a similar mix consisting, on average, of 56% nectar and 41% insects (Pyke, 1980). Historical records of the Laysan honeycreeper also describe insect supplementation to its diets (Rothschild, 1893; Fisher, 1903), but its extinction was ultimately linked to the disappearance of key nectar-providing plants following herbivore pressure from introduced rabbits (Ely & Clapp, 1973). Lorikeets are almost exclusive pollen- and nectar-feeders (Richardson & Wooller, 1990; Schweizer *et al.*, 2015). However, a study on the feeding behaviour of Stephen's lorikeet (*V. stepheni*), endemic to the raised Makatea-type island of Henderson, Pitcairn Islands, showed that lorikeets can also supplement their diet substantially with insect larvae and fruit (Trevelyan, 1995).

Despite known physiological adaptations in lorikeets, honeyeaters, and sunbirds for effective pollen transfer and their established importance as plant pollinators in volcanic island and continental systems (Ford, Paton & Forde, 1979; Paton & Collins, 1989; Zilko, Hoebee & Edwards, 2017; Sazima & Sazima, 2025), bird–plant pollination mutualisms remain incompletely understood on atolls. Evidence for bird–flower interactions is limited to observations of the blue lorikeet (*V. peruviana*) feeding on coconut (Gerischer & Walther, 2003) and *Pemphis acidula* flowers (J. DeVore & S. Ducatez, personal observation) on Rangiroa atoll, French Polynesia; of the Souimanga sunbird feeding on flowers of different coastal and mangrove plants (*Abutilon angulatum*, *Allophylus aldabricus*, *Ceriops tagal*, *Cocos nucifera*, *Cordia subcordata*, *Guettarda speciosa*, *P. acidula*, *Scaevola taccada*, *Sophora tomentosa* and *Suriana maritima*) on Aldabra (Frith, 1979; Woodell, 1979; Safford & Hawkins, 2013); and of the Laysan honeycreeper feeding on flowers of *Capparis sandwichiana*, *Portulaca spp.*, and *Sesuvium spp.*, as well as in not-further-specified bushes (Ely & Clapp, 1973).

Given the relatively young age of atoll islands, the generalist nature of their nectivorous birds, and the widespread distribution of bird-pollinated plants on atolls with and without these avian pollinators, it is unlikely that specialised plant–pollinator interactions have co-evolved in atolls (Pauw, 2019). Nonetheless, the presence (or extinction) of land bird pollinators may still influence plant community composition, the relative dominance of bird-pollinated species, and forest demography on atoll islands (Bond, 1994; Anderson *et al.*, 2011; Pauw, 2019). On the volcanic island of Guam, Northern Mariana Islands, the disappearance of the Micronesian myzomela (*M. rubratra*) due to invasive vertebrate predators resulted in reduced recruitment of the orange mangrove (*Bruguiera gymnorrhiza*) and the tree *Erythrina variegata*, as the myzomelas accounted for 98% of flower visits to the mangrove while insect or geckos were not compensating for the role of mangrove pollination (Mortensen *et al.*, 2008). Both the orange mangrove and Micronesian myzomela occur also on nearby atolls, implying that similar dynamics could apply, although this has not been directly tested. Studying these plant–pollinator dynamics and downstream implications for plant recruitment explicitly in atoll systems is particularly relevant as mangroves and other bird-pollinated trees and shrubs contribute to shoreline stability and coastal protection for atoll islands (Duvat, Magnan & Pouget, 2013).

(3) Seed dispersal

Avian seed dispersal is a key ecological function in island ecosystems (Nogales *et al.*, 2024). On atolls, the principal seed-dispersing land bird species include five starlings (Sturnidae: *Aplonis* spp.), four imperial-pigeons (Columbidae: *Ducula*

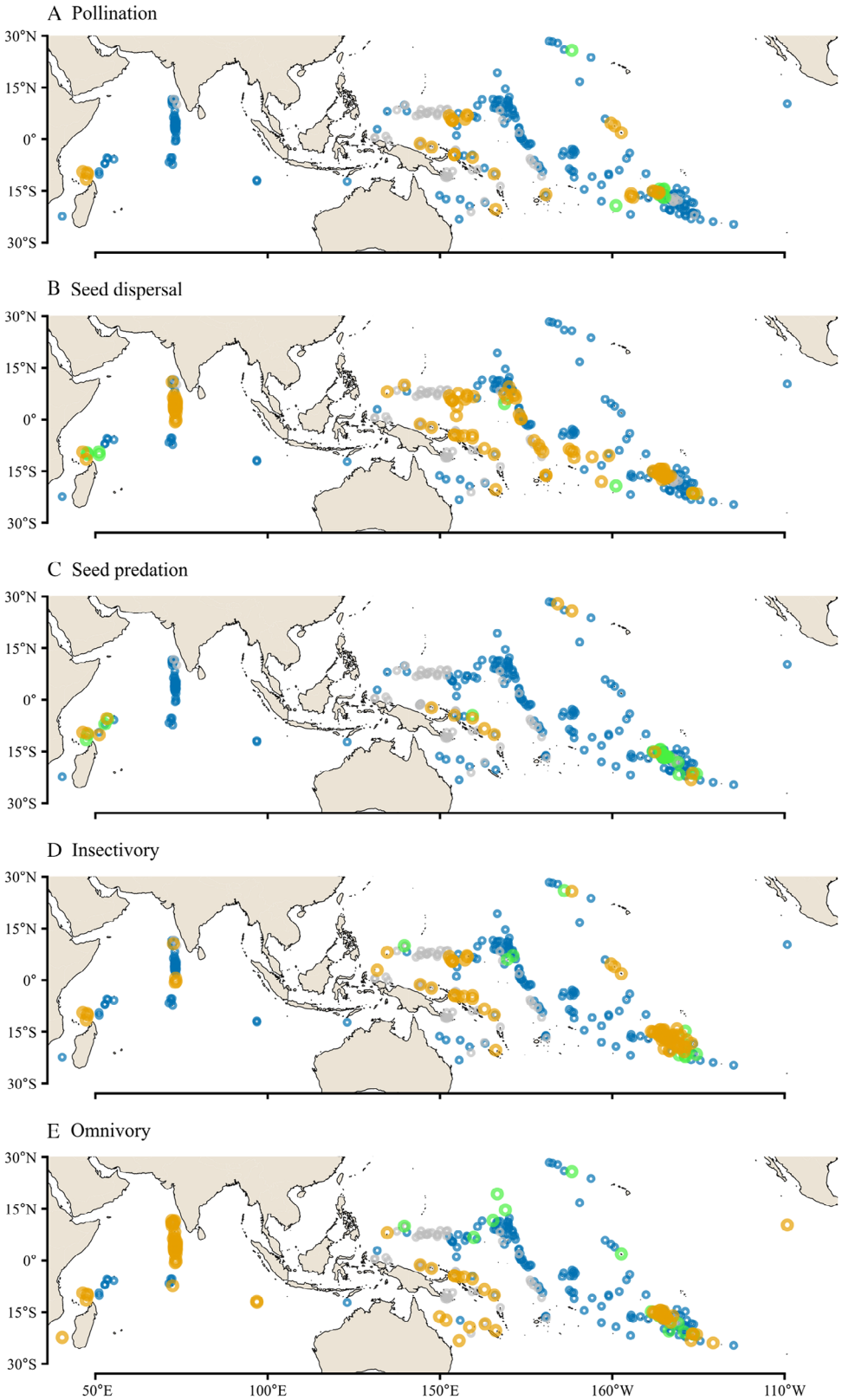

Fig. 4. Biogeographic distribution of land bird functions across the Indo-Pacific atolls. Orange: atolls with at least one recorded extant land bird species that is providing the function. Green: atolls with historical records but now extinct populations or species that once provided the function. Blue: atolls with no documented land birds of the given functional guild A–E in the available literature. Grey: atolls with no available survey data on their avifauna.

spp.), five fruit-doves (Columbidae: *Ptilinopus* spp.), as well as the Comoro blue-pigeon (Columbidae: *Alectroenas sganzini*), Malagasy bulbul (Pycnonotidae: *Hypsipetes madagascariensis*), and the Asian koel (Cuculidae: *Eudynamys scolopaceus*), one of only two predominantly frugivorous cuckoos worldwide (Corlett, 1998, 2017). The bulbul and blue-pigeon occur on western Indian Ocean atolls, the Asian koel on Lakshadweep and Maldivian atolls, and starlings on Micronesian and Melanesian atolls, whereas imperial-pigeons and fruit-doves are found across Pacific atolls (Figs 4B and S2). Although largely allopatric over most of their current range, on 13 atolls (*c.* 12.6% of atolls with extant seed-dispersing land birds) more than one seed-dispersing land bird species occurs. Historical records indicate that such co-occurrences of multiple seed-dispersing land birds were more widespread (Steadman, 1997; Steadman & Freifeld, 1999). For example, both fruit-doves (*P. hernsheimi*) and imperial-pigeons (*D. oceanica ratakensis*) were recorded on Ebon atoll, Marshall Islands, prior to their extirpation (Spennemann, 2006).

Alternative modes of zoochorous seed dispersal exist in atoll systems, including long-distance dispersal of *Pisonia* seeds through external attachment to seabirds (Burger, 2005) or localised transportation of *Pandanus* fruits by *Cardisoma carnifex* land crabs (Lee, 1985). However, consumption by frugivores is particularly effective because gut-passage of fruits can increase germination and plant recruitment success (Fricke *et al.*, 2019). Gape width of frugivorous birds is a primary constraint on internal seed dispersal, as it sets the upper limit of fruit and seed size that can be swallowed, thereby restricting the suite of plant species a bird can disperse (Wheelwright, 1985; Meehan, McConkey & Drake, 2002). Published gape width measurements are available for only a subset of atoll land birds: *Ptilinopus porphyraceus* (11.2–17.1 mm gape width), *Ducula pacifica* (26.2–33.4 mm), *D. latrans* (24.5–31.9 mm), *Aplonis opaca* (14.6–15.9 mm), and *Eudynamys scolopaceus* (19.3–20.1 mm) (Meehan *et al.*, 2002; Naniwadekar *et al.*, 2019; Rehm *et al.*, 2019). Although limited, these measurements provide an initial, trait-based approach for identifying which atoll plants fall within the ingestible size spectrum of resident avian dispersers and thus are likely to be dispersed by land birds, at least opportunistically.

Direct studies of avian seed dispersal on atolls are scarce, and available data is limited to feeding observations, including lists of dietary items of the atoll fruit-dove (*Ptilinopus coralensis*) on Ana'a atoll, French Polynesia (Beaune & Butaud, 2018), and notes on foraging behaviour of the Malagasy bulbul on Aldabra (Frith, 1979). To the best of our knowledge, no germination experiments, recruitment studies, or quantitative assessments of seed-dispersal effectiveness by land birds on atoll islands have been conducted. Nonetheless, given the known generalist feeding ecology of fruit-doves, imperial-pigeons, starlings, and bulbuls, together with the available gape width data, many common trees and shrubs with fleshy fruits found on atoll islands are likely, at least opportunistically, bird-dispersed when land birds are present (but may also utilise other dispersal mechanisms, such as dispersal by reptiles, fruit bats, or ocean currents) (Wickens, 1979). Plant species likely utilising land bird dispersal include *Allophylus* spp., *Ficus* spp., *G. speciosa*, *Heliotropium arboreum*, *Morinda citrifolia*, *Pipturus argenteus*, *Premna serratifolia*, *S. taccada*, *Terminalia spp.*, and *Timonius uniflorus* (Benson & Penny, 1971; Frith, 1979; Banack, 1998; Freifeld, 1999; Steadman & Freifeld, 1999; McConkey, Meehan & Drake, 2004; Beaune & Butaud, 2018; Pollock *et al.*, 2020). Several of these plant species are not obligate endozoochorous but also disperse via oceanic drift (e.g. *S. taccada* and *H. arboreum* being able to float up to 120 days and retain germination capacity), which may complement or substitute frugivore dispersal, particularly when the original frugivorous bird community has been lost (Carlquist, 1967; Lesko & Walker, 1969; Heinen *et al.*, 2025). Other plant species that are widely occurring on atoll islands, however, are predominantly animal-dispersed (e.g. *Ficus* spp.), which Steadman (1997) used to infer that even remote atoll archipelagos such as Tokelau and Tuvalu must once have supported fruit-doves.

The influence of seed-dispersing land birds on atoll forest structure and demography remains unstudied. However, studies from other island systems allude to the likely role of avian dispersers (Wandrag *et al.*, 2015; Nogales *et al.*, 2024). Imperial-pigeons can fly up to 3 km over open ocean, suggesting they enable plant gene flow between, and rapid (re-)colonisation of, islands within atolls (McNab, 1994; McConkey *et al.*, 2004). On Guam, where imperial-pigeons, fruit-doves, and *Aplonis* starlings became largely extirpated, forest seedling recruitment was reduced by 87–92% (Rogers *et al.*, 2017), and seedling species richness under canopy gaps was reduced by 50% (Wandrag *et al.*, 2015), whereas in sites retaining *Aplonis* starlings, seedling abundance and richness were elevated (Kastner *et al.*, 2021). Losses of seed-dispersing land birds from many atolls may have created similar impacts to their broadleaf forests (Steadman & Freifeld, 1999).

Besides seed-dispersing land birds on atolls, other taxa also contribute to dispersal via gut passage. The migratory bristle-thighed curlew (Scolopacidae: *Numenius tahitiensis*), which overwinters exclusively on Pacific tropical islands, feeds on fruits of various plant species during its stay on atoll islands and may thus be an overlooked, relevant seed-disperser on atolls (Fosberg, 1953; Walker, Gessel & Held, 1997). Fruit bats, where present, provide analogous long-distance dispersal services (Banack, 1998). Skinks, geckos, and, in the case of Aldabra, giant tortoises, can also fulfil analogous or complementary seed-dispersal functions on atolls (Hnatiuk, 1978; Wickens, 1979). However, given their inability to undertake regular, directed, and active overwater movement, reptiles primarily contribute to within-island rather than between-island seed dispersal (Valido & Olesen, 2019). Studies of land crab effects on plant recruitment on atoll islands suggested they are primarily acting as seed predators, not dispersers, even though some seeds can be moved undamaged by land crabs (Lee, 1985; Louda & Zedler, 1985; Lindquist *et al.*, 2009). Ultimately, only birds

and bats are capable of maintaining inter-island and inter-atoll dispersal networks (Ando, 2025).

(4) Seed predation

In contrast to the fruit-dispersing imperial-pigeons and fruit-doves, a second guild of pigeons and doves that predominantly feed on the dry seeds of plants occurs on atolls. Owing to their muscular, grit-bearing gizzards, these species mostly destroy plant seeds during digestion, thus acting foremost as seed predators rather than dispersers, though limited dispersal may still occur (Lambert, 1989; Corlett, 1998; Fricke *et al.*, 2019; Rehm *et al.*, 2019). On atolls, the seed-predating land birds comprise three ground-doves (Columbidae: *Pampusana* spp.), the Pacific emerald dove (Columbidae: *Chalcophaps longirostris*), the spot-breasted cuckoo-dove (Columbidae: *Macropygia mackinlayi*), the Nicobar pigeon (Columbidae: *Caloenas nicobarica*), the Malagasy turtle-dove (Columbidae: *Nesoenas picturatus*), as well as the Laysan finch (Fringillidae: *Telespiza cantans*) (Figs 4C and S3). Biogeographically, the turtle-dove occurs on the western Indian Ocean atolls. The Laysan finch is found on two northwestern Hawai'ian atolls, where a second population outside Laysan atoll had been established via translocation at Pearl-and-Hermes atoll (Morin & Conant, 2020). Ground-doves are nowadays found only on atolls in the Tuamotu archipelago as well as on Nissan atoll, Solomon Islands, but historical records note that the shy ground-dove (*P. stairi*) and Polynesian ground-dove (*P. erythropterus*) occurred on Nonouti and Abemama atolls, Kiribati (Amerson, 1969), and the White-throated ground-dove (*P. xanthonura*) on Ulithi atoll, Federated States of Micronesia, last recorded in 1922 (Steadman & Intoh, 1994).

The Laysan finch is the only seed-predator species with available, detailed dietary studies. Its diet is dominated by seeds of *Tribulus* and *Eragrostis*, along with seeds and buds of *Boerhavia* and *Portulaca* (Ely & Clapp, 1973). Another study found seeds of *Eragrostis* (8.7%), *Rhododendron* (8%), *Cenchrus* (6.8%), *Cyperus* (8%), and *Portulaca* (6.2%) as the major dietary items (Morin & Conant, 2020). On Aldabra, the Malagasy turtle-dove feeds on fallen seeds in the mixed scrub and *Pemphis* vegetation as well as in coconut groves (Frith, 1979). Stomach content analysis showed prevalence of seeds of *S. taccada*, *Flacourtia*, *Triainolepis*, and *Apodytes* (Benson & Penny, 1971). On Tuamotu atolls, the Polynesian ground-dove was observed feeding on seeds of *H. arboreum*, *M. citrifolia*, and *Digitaria* (Blanvillain *et al.*, 2002).

The broader ecological influence of avian seed predators on seed bank and plant recruitment in atolls has not been assessed, but the importance of these antagonistic bird–plant interactions in structuring island plant communities is known for volcanic islands (Carpenter *et al.*, 2020). However, on atoll islands the relative influence of land birds as seed predators is likely minor compared to that of terrestrial hermit crabs (*Coenobita* spp.), which are ubiquitous on virtually all atolls and act as major seed predators (Niering, 1963; Lindquist *et al.*, 2009). For example, on Eniwetok atoll, Marshall Islands, terrestrial hermit crabs consumed up to 100% of seeds of *Terminalia spp.*, 79% of *Scaevola* seeds, or 63% of *Guettarda* seeds, effectively preventing any seedling recruitment (Louda & Zedler, 1985). Given this strong influence of terrestrial hermit crabs on seedling recruitment in the atoll ecosystem, the wider ecological influence of avian seed predators is likely subordinate.

(5) Insectivory

Insectivorous birds can influence prey populations and, thereby, modulate insect herbivory and other insect-driven functions, albeit this functional role is primarily assessed in the context of continental, agricultural ecosystems (Sherry, 2021). On atolls, insectivorous land bird species include six kingfishers (Alcedinidae: *Todiramphus* spp.), five reed-warblers (Acrocephalidae: *Acrocephalus* spp., and the extinct *Nesillas aldabrana*), two monarch flycatchers (Monarchidae: *Monarcha cinerascens*, *Myiagra caledonica*), the Madagascar cisticola (Cisticolidae: *Cisticola cherina*), Aldabra drongo (Dicruridae: *Dicrurus aldabranus*), Manus fantail (Rhipiduridae: *Rhipidura semirubra*), black-shouldered kite (Accipitridae: *Elanus caeruleus*), and Laysan duck (Anatidae: *Anas laysanensis*). Additionally, the insectivorous Madagascar nightjar (Caprimulgidae: *Caprimulgus madagascariensis* ssp. *aldabrensis*), Malagasy kestrel (Falconidae: *Falco newtoni* ssp. *aldabranus*), and Malagasy coucal (Cuculidae: *Centropus toulou* ssp. *insularis*) occur on Aldabra as endemic subspecies.

Biogeographically, reed-warblers are the most widespread avian insectivores on Indo-Pacific atolls, ranging from western Micronesian to eastern Polynesian atolls. Ulithi atoll marks the known western distributional limit, where the Caroline Islands reed-warbler (*Acrocephalus syrinx*) existed up until its extirpation between 1891 and 1915 (Steadman & Intoh, 1994). Kingfishers are largely confined to Micronesian and Melanesian atolls, though one endemic species (*Todiramphus gambieri*) occurs on Niau atoll, French Polynesia. The Laysan duck persists on Laysan atoll, with additional translocated populations on Midway and Kure atolls, Northwestern Hawaiian Islands. The remaining insectivorous land bird species are restricted to atolls in the western Indian Ocean and Melanesia (Figs 4D and S4).

Dietary data are available for only three of the 20 insectivorous atoll land birds. On Niau atoll, analysis of 186 faecal pellets of the Tuamotu kingfisher revealed a diet of arthropods (>50%), lizards (40%), and land crabs (9%), with coleopterans (23%), hymenopterans – primarily ants – (10%), and dictyopterans (9%) constituting the dominant arthropod diet items (Zarzoso-Lacoste *et al.*, 2019). On Laysan atoll, the Laysan duck is largely insectivorous with a primarily crepuscular to nocturnal feeding activity (Ely & Clapp, 1973). They feed by sweeping through swarms of ephydrid flies along the lagoon shores with their heads close to the ground, often multiple birds side-by-side, and rapidly opening and closing their bills to ingest the clouds of flies that rise from the ground (Caspers, 1981). Faecal analyses showed a broad, opportunistic insectivorous diet, consisting of flies and their larvae (48%), brine shrimps from the hypersaline lagoon of the atoll

(21%) and lepidopteran larvae (8%), with minor additional contributions of plant seeds and fibres (Reynolds, Slotterback & Walters, 2006). On Aldabra, the Aldabra drongo preys on small lizards and insects (including coleopterans, ants, cicadas and other homopterans, orthopterans, and hymenopterans), while the Malagasy kestrel on Aldabra atoll is feeding on larger insects, geckos, and skinks (Benson & Penny, 1971; Frith, 1979; Rocamora & Yeatman-Berthelot, 2020). The extinct Laysan millerbird (*Acrocephalus familiaris* ssp. *familiaris*) preyed primarily on moth larvae gleaned from the low *Portulaca* mat vegetation surrounding the lagoon (Fisher, 1903). Given the dependence on insects, different insectivorous land birds were found to time their breeding to coincide with peak insect abundance, usually at the beginning of the wet season (Frith, 1975a).

By preying on insect herbivores, detritivores, saprotrophs, and pollinators, insectivorous land birds may regulate invertebrate ecosystem functions on atoll islands. No study has quantified whether insectivorous land birds meaningfully reduce herbivory rates, alter pollination dynamics, or influence detrital processing on atoll islands. Dedicated studies in atoll systems are needed to assess how land bird insectivory influences insect guilds and to evaluate possible consequences of insectivore extinctions or translocations for atoll ecosystem functioning (Vernet *et al.*, 2024).

(6) Omnivory

Omnivorous land birds are not immediately recognised as providers of ecological functions as compared to pollinators or seed dispersers. Nevertheless, through their generalist diets, omnivores may contribute opportunistically to pollination, seed dispersal, insect regulation, as well as carrion removal and nutrient cycling (de Ruyck & Koper, 2024). On atolls, omnivorous land birds include 11 extant and extinct rails (Rallidae: *Gallirallus* spp., *Zapornia* spp., *Amaurornis phoenicurus*, *Dryolimnas cuvieri*, *Fulica americana*, *Gallicrex cinerea*, *Gallinula chloropus*, *Poliolimnas cinereus*), five white-eyes (Zosteropidae: *Zosterops* spp.), two megapodes (Megapodiidae: *Megapodius* spp.), two crows (Corvidae: *Corvus* spp.), and the Aldabra fody (Ploceidae: *Foudia aldabrana*).

Biogeographically, rails are the most widespread group of land birds on atolls, occurring from the western Indian Ocean to eastern Polynesia (Fig. 4E, Fig. S5). Megapodes nowadays persist only on Melanesian atolls and Ngcheangel atoll, Palau, though fossil records from volcanic islands suggest a historically broader distribution across Micronesia and Melanesia, as far as their natural dispersal barrier in western Polynesia, potentially also including additional atolls (Steadman, 1999). White-eyes occur on western Indian Ocean atolls, Lakshadweep atolls, as well as in Melanesia. Crows are limited to western and central Indian Ocean atolls, while the Aldabra fody is a localised endemic.

Observations of omnivorous land bird foraging on atolls reveal broad and opportunistic diets. The flightless Aldabra rail (*D. cuvieri aldabranus*) forages in leaf litter for insects and land snails, and actively hunts for land crabs, skinks, and geckos; furthermore, it scavenges on dead land crabs and gleans insects from tortoise carcasses (Penny & Diamond, 1971; Alexander, 1979). The extinct, flightless Laysan atoll rail (*Z. palmeri*) fed on insects, primarily Sarcophagid flies, moths, caterpillars, Dermestid beetles, spiders, as well as on seabird carcasses, green plant material, and seeds (Baldwin, 1947). It also opportunistically preyed on seabird eggs and chicks and entered petrel burrows (Baldwin, 1947). The extinct, flightless Wake rail (*Gallirallus wakensis*) consumed seeds, insects, lizards, and hermit crabs, and gleaned moths and caterpillars from *Cordia* trees (Olson & Rauzon, 2011). On Aldabra, feeding observations and gizzard content analyses of the Aldabra fody documented generalist feeding on insects, seeds, nectar, and berries across mixed scrub, mangrove, and palm grove habitats with no observed seasonal variations in uptake preferences (Frith, 1976). Its distinct brush tongue, together with feeding observations in *Pemphis* and *Cocos* flowers, may also contribute to opportunistic pollination (Frith, 1976). Similar insect feeding supplemented with nectar has been noted in the Aldabra white-eye (*Zosterops aldabrana*) (Frith, 1979). In contrast, the two crow species (*Corvus albus*, *C. splendens*) rely on human presence (Benson & Penny, 1971). In the Maldivian atolls, crows are therefore largely confined to inhabited islands (Anderson & Shimal, 2020).

Despite rails being recognised as the most extinction-prone land bird family on islands (Lévêque *et al.*, 2021; Matthews *et al.*, 2022), little is known about their functional roles provided to island ecosystems, and the implications of their extinctions for island ecosystem integrity. Their ground-foraging omnivory likely contributes to nutrient cycling and soil turnover and may exert some influence on insect populations. Megapodes, though poorly studied on atolls, can uniquely affect nutrient dynamics through their mound-building behaviour, which enhances soil nutrient contents and decomposition rates (Neilly, Cale & Eldridge, 2022; Decker *et al.*, 2023).

The functional roles of land birds on atolls highlighted in this review position land birds as important components of conservation strategies that seek to restore atoll ecosystems and enhance their resilience to global change. Yet, few studies have directly examined how land birds influence atoll island ecosystem functioning, creating a substantial research gap, even though some mechanisms and processes can be implied from studies on volcanic islands. It remains unclear whether the functional ecology and wider ecosystem influence of land birds on atolls align with their established roles and importance on volcanic islands, or whether there exist distinct dynamics shaped by atoll-specific environmental and biogeographic conditions. Addressing the gaps identified in this review is not just important for generating domain-specific knowledge on the functioning of atoll systems, but also for guiding conservation reintroductions of land birds, including critically endangered species. Atoll islands represent highly suitable candidate sites for such efforts, as their small size and isolation facilitate restoration interventions (e.g. invasive species eradications) and enable stringent biosecurity and population monitoring, which are key prerequisites for both translocation actions and for successful long-

term outcomes (Laws & Kesler, 2012; Vernet *et al.*, 2024), as demonstrated by the recent translocation of the extinct-in-the-wild Guam kingfisher (*Todiramphus cinnamominus*) to Palmyra atoll, Line Islands.

VI. CONCLUSIONS

(1) Across 244 Indo-Pacific atolls with published records, our quantitative review documented 91 native resident land bird lineages, including 17 species and 18 subspecies endemic to atolls. Resident native land birds occur on *c.* 65% of surveyed atolls, with endemic species on *c.* 25% of surveyed atolls, revealing that land bird residency and endemism are widespread rather than exceptional.
(2) Atoll islands constitute a distinct evolutionary arena for land birds, as Quaternary sea-level fluctuations repeatedly emerged and submerged atoll landforms, thereby imposing periodic ecological resets on land bird assembly and diversification that contrast with the relative persistence and stable lineage accumulation on volcanic islands. This dynamism results in unique evolutionary trajectories of atoll land birds, with endemism arising via refugial persistence on uplifted atolls, rapid divergence after island emergence and colonisation, or relictual persistence after extirpations from volcanic islands.
(3) Atoll land birds support ecosystem functioning, including seed dispersal, pollination, seed predation, and insect regulation.
(4) Human impacts have reduced atoll land bird diversity through extinctions and extirpations with largely unexplored consequences for atoll ecosystem functioning. The true magnitude of human-driven land bird loss from atolls is likely underestimated because preservation and fossilisation of bone material in atoll island sediments are limited and availability of historic records is temporally biased.
(5) Empirical research remains largely missing for (*i*) systematic comparative studies between atoll and volcanic island land bird assemblages, particularly considering their different geo-evolutionary settings, (*ii*) phylogenetic resolution of many putatively endemic atoll land bird subspecies, and (*iii*) direct assessments of functional roles of land birds for atoll island ecosystem integrity. This review provides a knowledge base for developing hypothesis-driven empirical research that can address these open research questions.
(6) Recognising land birds as important providers of natural atoll ecosystem function, as well as atoll islands as suitable candidate sites for land bird translocations, would benefit conservation and restoration efforts, given that the conditions on atoll islands enable effective conservation management.

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VIII. AUTHOR CONTRIBUTIONS

S. S. conducted the data compilation and led the conceptualisation, writing, and created the figures. All authors contributed to writing and editing and have approved upon the final manuscript version prior to original submission.

IX. DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

X. REFERENCES

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XI. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Occurrence of pollinating land birds on atolls.
Figure S2. Occurrence of seed-dispersing land birds on atolls.
Figure S3. Occurrence of seed-predator land birds on atolls.
Figure S4. Occurrence of insectivorous land birds on atolls.
Figure S5. Occurrence of omnivorous land birds on atolls.
Table S1. Assignment of land birds into functional groups based on foraging behaviour.
Data S1. Reference list for atoll land bird occurrences.

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