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Abstract: The most common and numerous island type across the Pacific basin are atolls. Even though these island systems harbor only a few endemic species, atolls are globally important nesting sites for seabirds and sea turtles, roosting sites for migratory shorebirds, and refugia for Oceania's unique lowland flora and fauna. While atolls were extensively surveyed for their island biodiversity in the second half of the twentieth century, many remain unmapped, leaving important knowledge gaps for Pacific biodiversity, biogeography, and conservation. Here, we report on a terrestrial biodiversity survey of Manuae atoll, Cook Islands. Our assessment revealed that Manuae atoll harbors seabird colonies and is an important green sea turtle nesting site. Furthermore, we found at least 100 bristle-thighed curlews (*Numenius tahitiensis*) overwintering on the island (*ca.* 1% of the estimated global population), which under international evaluation criteria renders the atoll an important overwintering area that warrants protection and recognition. While our island biodiversity assessment and mapping, including vascular plants, land crabs, reptiles, and birds, reveals that Manuae atoll is an important refuge for lowland island biota within the Cook Islands, we also documented the presence of key introduced species, including Pacific rats (*Rattus exulans*) and yellow crazy ants (*Anoplolepis gracilipes*), and a colonial legacy in the overall habitat composition from the abandoned copra plantation. Our findings on the terrestrial biodiversity of Manuae atoll fill an important knowledge gap in island biodiversity data from the Cook Islands. This information can support future ecological and biodiversity research, as well as inform management, protection, and restoration planning.

Keywords: Atoll ecology, bristle-thighed curlew, island biology, overwintering site, seabirds

THERE EXIST 235 atolls across the Pacific (Goldberg 2016). Atolls constitute about one-third of all Pacific islands and are thus the most common island type within the oceanic basin (Nunn et al. 2016). Each atoll comprises an annular coral reef that encloses a central lagoon, with up to several hundred individual islands scattered along the reef rim (Steibl et al. 2024a). These unique ecosystems of the tropical Pacific were the focus of extensive biodiversity research throughout the twentieth century (*e.g.*, over 900 publications in the "Atoll Research Bulletin" journal). This work amassed substantial knowledge on the distinct island biology of atolls, which enabled insights into global patterns of island biodiversity (*e.g.*, Larrue 2024, Steibl and Russell 2024), as well as allowed recognition of the global importance of atoll biodiversity for conservation (Steibl et al. 2024b) and nature-based climate resilience-building (Steibl et al. 2024c).

While almost 100 atolls were assessed for their terrestrial biodiversity, for the majority, still no comprehensive published biodiversity data exist.

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Atolls have international importance as nesting grounds for seabirds (Steibl et al. 2024b) and for globally endangered sea turtles (Becker et al. 2019), and as overwintering sites for migratory shorebirds (Marks and Redmond 1994). Furthermore, atolls are some of the last refugia for Oceania's unique lowland floras and faunas that became widely displaced from the lowlands of high volcanic islands (Lee 1984). Therefore, continuous efforts to document the terrestrial biodiversity of the Pacific atolls remain timely and relevant endeavors for Pacific science and conservation.

Located between Aitutaki and Atiu within the southern Cook Islands group, Manuae atoll is one of only two atolls in the Cook Islands that are nowadays uninhabited (the other being Suwarrow atoll). Historical records on some aspects of Manuae atoll's biodiversity exist (*e.g.*, Frisbie 1932, Holyoak 1976, 1980), but since the atoll's abandonment in the 1970s after centuries of human occupation, no comprehensive surveys on Manuae atoll's terrestrial biodiversity have been conducted.

In October 2024, we visited Manuae atoll at the request of and with the financial and logistical support of its Indigenous landowners (represented by the Proprietors of Manuae Incorporated [PMI] and the Manuae Enua Conservation Trust [MECT]) to establish current baseline information on the atoll's terrestrial biodiversity. This work aimed to identify and map the biodiversity on Manuae atoll to facilitate biogeographic and ecological research, as well as future conservation prioritization and management planning. This study not only provides up-to-date information on the atoll's biodiversity but also sheds light on the capacity and limits of recovery of atoll ecosystems following human abandonment.

MATERIAL AND METHODS

Biogeographical background

Manuae atoll (19.27°S 158.94°W) lies in the southern Cook Islands group, Cook Islands, approximately 95 km southeast of Aitutaki, the nearest inhabited island (Figure 1). The atoll is part of the Southeast Polynesian Islands bioregion (OC3) and the Cook Islands Tropical Moist Forest ecoregion (Gillespie et al. 2012). The atoll also lies within the Polynesian biodiversity hotspot (Myers et al. 2000). Its climate under the Köppen–Geiger climate classification system is tropical rainforest climate ("Af"). The nearest permanent weather stations are on Aitutaki (*ca.* 95 km northwest) and Atiu (*ca.* 117 km southeast), with

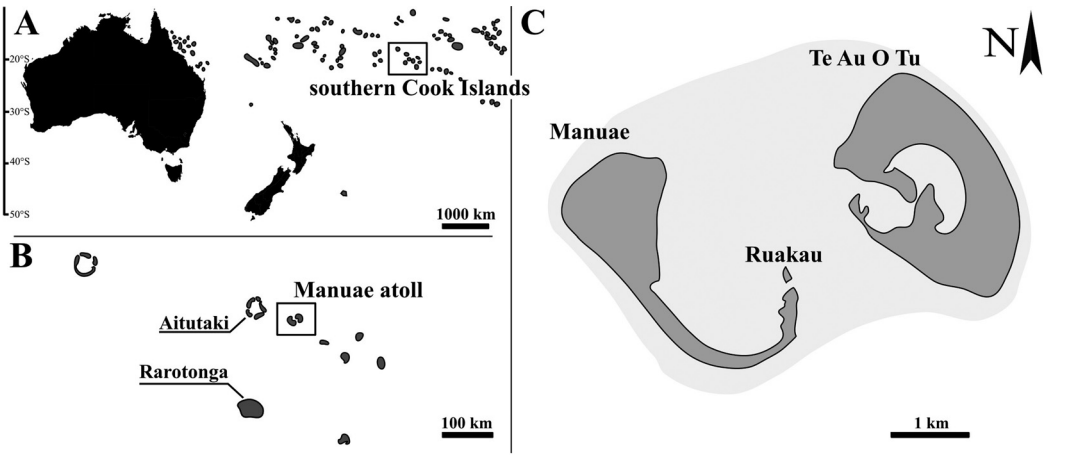

FIGURE 1. Location map of Manuae atoll. The atoll is part of the southern Cook Islands group, Polynesia (A). Manuae atoll lies *ca.* 95 km southeast of Aitutaki, its nearest neighboring island and 200 km north of Rarotonga (B). The atoll consists of three landforms (dark gray) enveloping a central shallow lagoon (light gray) from the western and eastern side (C). The size of islands in (A) and (B) map panels were inflated to visualize their location in the wide South Pacific.

recorded mean annual precipitation of approximately 1,900 and 1,930 mm, respectively, and a seasonal rainfall highest between December and March.

Historical context of human habitation and disturbance

Conflicting accounts exist in oral history around the first discovery of Manuae atoll and the origin of its name. Still, certainly, the name relates to an abundance of birds ("manu") that were once found there (Kloosterman 1976). Captain Cook was the first European to encounter the atoll in September 1773 during his second voyage, but he did not land (Hooker 1998). During his third voyage, Cook visited again in April 1777 and found the atoll inhabited by about 600 people (Kloosterman 1976). In July 1823, the atoll was visited by the London Missionary Society, who found it inhabited by only about 60 people. By 1829–1830, that number was down to just five men, three women, and a few children, whom missionaries took to Aitutaki, leaving the atoll deserted (Kloosterman 1976). In 1852, a white man and his two Polynesian wives and their children lived on Manuae atoll, and sometime before, another white man and his wife had been living on the atoll (Kloosterman 1976). In the early 1860s, a merchant vessel found William Marsters and his wives on the atoll and hired them off the atoll to become caretakers for Palmerston atoll (Hendery 2013). In August 1888, the atoll was declared a British protectorate. In 1898, it was leased out to the Cook Islands Trading Company, which at that time converted the islands to a copra plantation by planting a reported 29,300 coconut palms (Parliamentary Papers 1911). Throughout its active operation as a copra plantation between 1898 and 1969, the population on Manuae atoll generally fluctuated from 8 to 32 workers (Cook Islands Census 1936; Ward 1961; Graves and Graves 1976). By the early 1970s, only two permanent residents had remained, and the atoll has become completely abandoned soon after.

Over two months in 1981, a group from Rarotonga cleared and constructed a *ca.* 1,200-m airstrip on Manuae Island. To reinforce Indigenous ownership rights, the Proprietors of Manuae Incorporated (PMI) was established by court order in 1983. Nowadays, Manuae atoll is occasionally visited by small groups from neighboring islands to harvest giant clams ("pa'ua" *Tridacna* sp.), robber crabs (*Birgus latro*), and to fish in the lagoon and outer reefs (landowners, pers. comm.).

Field survey

We visited Manuae atoll, Cook Islands, from 14 to 17 October 2024. During our four-day visit, we surveyed the entire shoreline of the atoll's three islands (*ca.* 23.1 km) for the full day (*ca.* 08:30 to 18:15). Weather conditions throughout the visit were sunny and without any rainfall. We counted seabirds as the maximum number of birds seen simultaneously in the air at a given location. Furthermore, we counted birds flying in or out of the vegetation from their roosting or nesting trees. For shorebirds and herons along the beaches, we counted birds once they flushed and flew behind us to minimize the risk of re-counting individuals. In areas with high seabird activity, we investigated the adjacent vegetation for evidence of nesting. We also surveyed the entire atoll's shoreline for sea turtle tracks and nests. The total counts were added to generate an approximate estimate of the minimum number of birds on each island. Plant species were recorded during the shoreline survey and complemented with surveys of the islands' interior to assess inland vegetation. Other key terrestrial species groups and introduced species were also recorded. In addition to shoreline surveys during the day, we surveyed the area around our campsite on Manuae Island at night for land crab activity.

We used available satellite imagery (https://earth.google.com/web/, last accessed 30 September 2024) to identify overall vegetation features *a priori* and conducted ground surveys on the atoll during our visit to validate or update our mapping of the atoll's vegetation composition. Vegetation cover maps and seabird distribution maps were created using QGIS v. 3.10, with geographic data for coastlines and lagoon extent obtained from Toitū Te Whenua Land Information New Zealand.

Maps are indicative only, with boundaries between habitat types often more diffuse than expected from a literal reading of the maps. Measurements of island areas were done in Google Earth 10.66.0.0.

We deployed a line of 25 snap traps on both Manuae (one night) and Te Au O Tu (two nights) islands to assess the presence of invasive rodents. Snap traps were placed in low vegetation or fixed on tree trunks, baited with fresh coconut and peanut butter, and left active overnight. On Manuae Island, we deployed the traps by the campsite, repeatedly checked the traps throughout the night, removed any rats that were caught, and immediately re-baited and re-activated the traps afterward.

We followed the taxonomy of Kew Royal Botanical Gardens' Plants of the World (POWO 2024) and Cornell Lab Birds of the World (BOW 2022) for plant and bird scientific names, respectively. Indigenous names of plants and birds were taken from the Cook Islands Biodiversity & Natural Heritage Library (http://naturalheritage.gov.ck/, last accessed 22 October 2024).

RESULTS

Geography

Manuae atoll has a total area of *ca.* 20.0 km², of which *ca.* 5.5 km² is emergent land. The atoll consists of three individual islands, although the smallest, Ruakau, is sometimes not mapped as a separate landform. The land areas of the three islands are 336 (Te Au O Tu, excl. the mudflats and basins), 212 (Manuae), and 1.8 ha (Ruakau). Several sandbanks in the center of the lagoon are temporarily emergent during low tides.

The two main islands of Manuae atoll are kidney-shaped, with concave coastlines on the lagoon side of the islands. Both main islands have mudflats along their lagoonward coastlines, with the mudflats on Te Au O Tu being especially extensive (*ca.* 110.5 ha). This mudflat was largely exposed and dried out at our visit, though it is regularly flooded. There is also a large basin in the center of Te Au o Tu that occupies about 64 ha of the total area of the island and is higher in elevation than the coastline but connected with the tidal inlet on the lagoon side of Te Au o Tu by a broad, shallow channel. When we visited, this basin was completely dried out, and the *Pemphis* shrub vegetation within and around this basin had largely desiccated and died back. However, signs of regrowth were evident. Satellite imagery and landowner observations confirmed that this basin could flood (Figure 2). Whether flooding of the basin occurs periodically (*e.g.*, with seasons) or stochastically (*e.g.*, due to flooding from cyclones) could not be concluded definitively from our visit.

Vegetation

Our vegetation surveys identified 33 different vascular plant and fern species across the atoll (Table 1). Thirty species were recorded on Manuae Island, 27 on Te Au O Tu, and six on Ruakau. Of the documented flora, 27 species

FIGURE 2. Flooding and drying of the central basin on Te Au O Tu. Satellite imagery of the mudflats and central basin taken on (A) 15 November 2004, (B) 8 December 2015, and (C) 18 March 2024 [Google Earth 10.66.0.0 (2023) Maxar Technologies; https://earth.google.com/web/, last accessed 05 November 2024].

TABLE 1

The Terrestrial Flora of Manuae Atoll.

Indigenous name	Scientific name	Te Au O Tu	Manuae	Ruakau	Status
‘Utu	*Barringtonia asiatica* (L.) Kurz		X		N
Runa	*Boerhavia tetrandra* G.Forst.	X	X		N
Tamanu	*Calophyllum inophyllum* L.	X	X		N
Tainoka	*Cassytha filiformis* L.	X	X	X	N
Toa	*Casuarina equisetifolia* L.		X		I
Kotikoti	*Cladium mariscus* (L.) Pohl	X	X		N
Niu	*Cocos nucifera* L.	X	X		I
Tou	*Cordia subcordata* Lam.	X	X		N
Vayavaya	*Cyanthillium cinereum* (L.) H.Rob.		X		I
Totototo	*Euphorbia fosbergii* (J.Florence) Govaerts	X	X		N
Mauku	*Fimbristylis cymosa* R.Br.	X	X		N
‘Ano	*Guettarda speciosa* L.	X	X		N
Ngātoro	*Heliotropium anomalum* Hook. & Arn.	X	X	X	N
Tai’inu	*Heliotropium arboreum* (Blanco) Mabb.	X	X	X	N
‘Au	*Hibiscus tiliaceus* L.	X	X		N
Po’ue	*Ipomoea violacea* L.		X		N
Naunau	*Lepidium bidentatum* Montin	X			N
Matie	*Lepturus repens* (G.Forst.) R.Br.	X	X		N
Nono	*Morinda citrifolia* L.	X	X		I
-	*Moringa oleifera* Lam.	X			I
Tūroutou	*Nephrolepis biserrata* (Sw.) Schott	X	X		N
‘Ara	*Pandanus tectorius* Parkinson	X	X		N
Ngangie	*Pemphis acidula* J.R.Forst. & G.Forst.	X	X		N
Maire ‘Enua	*Phymatosorus grossus* (Langsd. & Fisch.) Brownlie	X	X		N
‘Orongā	*Pipturus argenteus* (G.Forst.) Wedd.		X		N
Pukatea	*Pisonia grandis* R.Br.	X			N
Toatoa	*Psilotum nudum* (L.) P.Beauv.	X	X		N
Kōpara	*Scaevola taccada* (Gaertn.) Roxb.	X	X	X	N
Tiāki	*Stachytarpheta urticifolia* Sims		X		I
Ngangie Moe	*Suriana maritima* L.	X	X	X	N
Pia Māori	*Tacca leontopetaloides* (L.) Kuntze	X	X		N
Kōpara	*Timonius uniflorus* (Banks ex C.F.Gaertn.) Govaerts	X	X	X	N
Ngau	*Triumfetta procumbens* G.Forst.	X	X		N

The presence or absence of the plant species on each of Manuae atoll’s three islands is indicated. Distribution status (N: native, I: introduced) is based on POWO (2024).

are native, and six species have been introduced (POWO 2024).

Coconut palms are the dominant, and sometimes the only, plant species across much of the atoll’s interior (Figures 3 and 4*A*). At times, however, the coconut monostands are interspersed with patches of understory vegetation of *Morinda citrifolia*, *Guettarda speciosa*, and *Pandanus tectorius*. There are also more open coconut woodland areas, where thickets of *Euphorbia fosbergii* and *Timonius uniflorus* and ground cover of *Frimbistylis cymosa* grew in open areas between coconut stands. Despite the heavy alteration of the interior

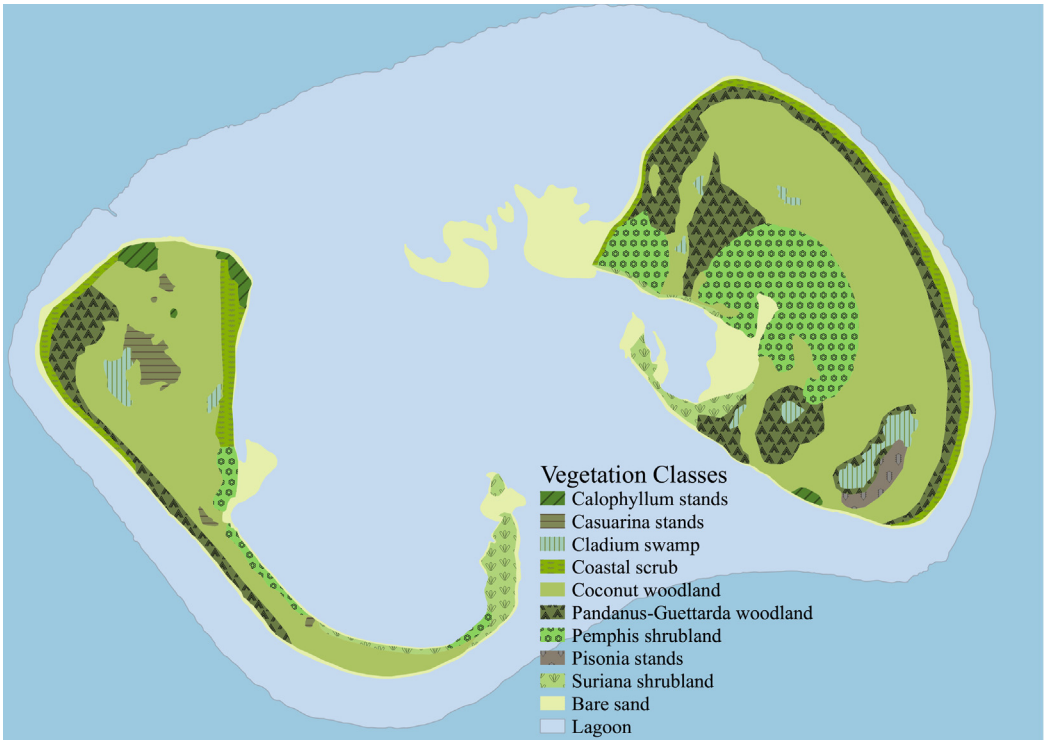

FIGURE 3. Vegetation map. The main vegetation features and habitat composition of Manuae atoll. For photographic images of vegetation types, see also Figure 4. The vegetation map was based on an a-priori assessment of key vegetation features visible from satellite imagery, that was then validated or updated during the atoll survey. Additional vegetation features that were not visible from satellite imagery, such as the *Pisonia* woodland, were also included.

forest, the islands of Manuae atoll possess a largely intact and native coastal shrub vegetation belt. In areas where conglomerate outcrops or beach rock are present, this shrub vegetation is dominated by *Pemphis acidula* (Figure 4*B*). In contrast, sandy beaches are mostly stabilized by a mixed shrub community consisting of *Suriana maritima*, *Scaevola taccada*, *T. uniflorus*, and *E. fosbergii*, that vary in their relative dominance along the atoll shoreline (Figure 4*C*). The smallest of the three islands, Ruakau, possesses only a mixed *Suriana* shrub vegetation and no soil development is visible. On the two larger islands, a narrow belt of mixed *P. tectorius* and *G. speciosa* broadleaf trees sits in the transition zone between the coastal shrub community and the interior coconut woodland (Figure 4*D*). On the southeastern side of Te Au O Tu, a stand of *Pisonia grandis* trees, interspersed with individual *Hibiscus tiliaceus*, is present (Figure 4*E*). Throughout Manuae Island and Te Au O Tu, there exist several brackish to freshwater swamps with small areas of standing water that are surrounded by a belt of *Cladium mariscus* reed grass and *P. tectorius* trees (Figure 4*F*). Areas of past human settlements, such as the former copra station, have stands of introduced *Casuarina equisetifolia* and *Calophyllum inophyllum*.

Land crabs

The terrestrial decapod fauna includes three species of shell-bearing hermit crabs (*Coenobita brevimanus*, *Coenobita perlatus*, and

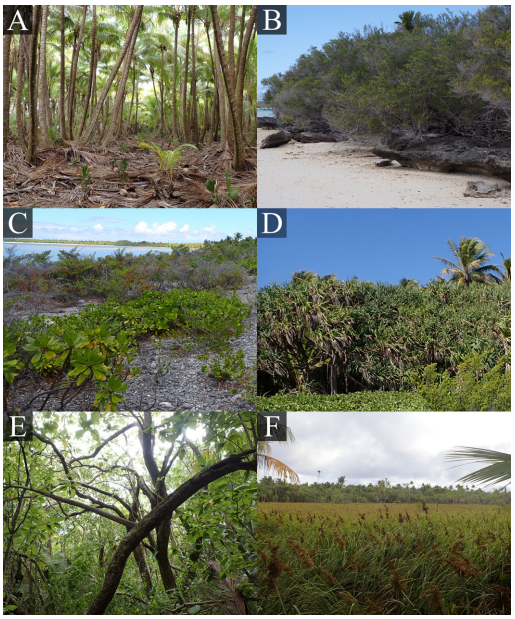

FIGURE 4. Habitat types on Manuae atoll. The majority of Manuae atoll's interior forest is dominated by coconut woodland (A). The shoreline vegetation belt consists of *Pemphis* shrubs in areas with conglomerate rock substrate (B). The sandy beaches of the atoll's lagoon- and ocean-facing beaches are covered by a low shrub vegetation belt consisting of *Scaevola*, *Timonius*, *Suriana*, and *Euphorbia* (C). Over most parts of the atoll, there exists a distinct broadleaf vegetation belt in the transition zone between the shrub vegetation along the beaches and the coconut woodlands, consisting of *Pandanus* and *Guettarda* (D). On the southern-eastern side of Te Au O Tu, a *Pisonia* stand exists (E). Swamp areas in the interior of both islands have extensive *C. mariscus* reed grass vegetation (F).

Coenobita spinosus), as well as the large robber crab (*B. latro*), all observed on both main islands. Around swamp areas, extensive burrow colonies of the land crab *Cardisoma carnifex* can be found. In the interior of the islands, only a few individuals of *Geograpsus crinipes* and *Tuerkayana rotundum* were noted. Small numbers of ghost crabs, *Ocypode* sp., on the sandy beaches, were present. In areas with conglomerate outcrops or beach rock, shore crabs *Grapsus tenuicrustatus* were present. In the coastal mudflats of Te Au O Tu, we found carapace pieces of the mud crab *Scylla serrata* and fiddler crabs *Uca (Gelasimus)* sp.

Reptiles

While traversing the entire coastline, we did not record any recent turtle tracks that indicated active nesting. However, we found at least 10 old turtle nests on Te Au O Tu and approximately 40 old turtle nests on Manuae Island. Nests on both islands were concentrated on the oceanward beaches and located within the mixed *Suriana* shrub vegetation (Figure 5). In the interior of the islands, we observed blue-tailed copper skink (*Emoia impar*) and snake-eyed skink (*Cryptoblepharus poecilopleurus*) in low numbers.

Birds

We identified 15 bird species on Manuae atoll, all of which are native to tropical Polynesia (Table 2). We found direct evidence of nesting for four species: red-tailed tropicbirds (*Phaethon rubricauda*), brown noddy (*Anous stolidus*), white tern (*Gygis alba*) and a species of yet unidentified burrowing petrel/shearwater, based on down and fledgling feathers found in procellariid burrows. For three seabird species, the red-footed booby (*Sula sula*), brown booby (*S. leucogaster*), and great frigatebird (*Fregata minor*), we could not find direct evidence for nesting on the atoll. However, we observed a high fraction of immature/sub-adult brown boobies, alluding to potential breeding of this species on the atoll. Besides the resident seabirds, a group of three sooty terns (*Onychoprion fuscatus*) was seen passing over the atoll on two occasions, and less than five black noddy (*Anous minutus*) were seen foraging in the lagoon.

Particularly noteworthy were the large numbers of overwintering bristle-thighed curlews (*Numenius tahitiensis*) on both Manuae Island (at least 36 individuals) and Te Au O Tu (at least 64 individuals), with likely more birds present in the islands' interior. Throughout the atoll, we also recorded 30 Pacific golden plover (*Pluvialis fulva*), 25 wandering tattlers (*Tringa incana*), and one flock of at least seven ruddy turnstones (*Arenaria interpres*). Reef herons (*Egretta sacra*) were occurring in dark (15 individuals), white (12 individuals), and intermediate

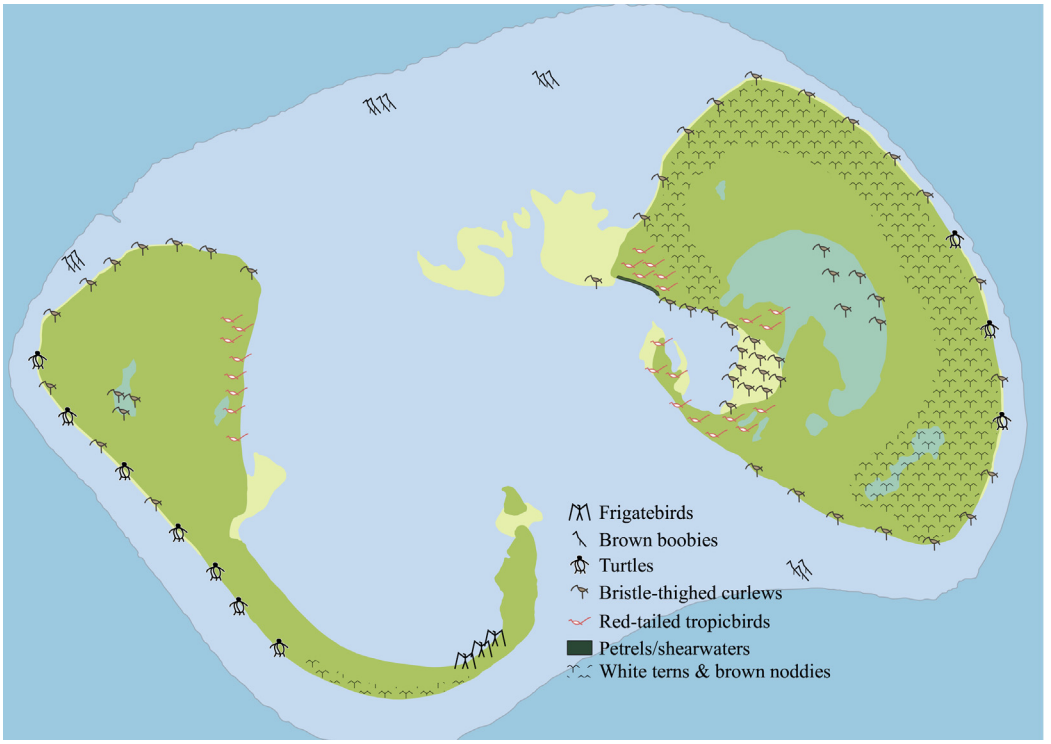

FIGURE 5. Spatial separation of bird occurrence and sea turtle nesting sites of Manuae atoll. Icons (see legend) indicate location of key bird roosting and/or nesting areas; turtle icons further indicate the sections of beach where old turtle nests were found.

(three individuals) morphs. Reef herons were observed flying in and out of the dense coastal vegetation, suggesting potential breeding on both Manuae and Te Au O Tu islands, but no direct evidence for nesting was found. The only land bird found on the atoll was the migratory long-tailed cuckoo (*Urodynamis taitensis*), where we observed one bird harassing a nesting brown noddy.

The distribution of bird nesting and roosting sites on Manuae atoll was spatially segregated (Figure 5). The petrel/shearwater burrows were located along a 10-m section of eroded beach facing the lagoon (Figure 6*A*). Ground-nesting red-tailed tropicbirds nested in the lagoon-facing dry areas of low and open coastal shrub vegetation, with at least 30 active nests of juveniles all close to fledging (Figure 6*B*). Brown noddies and white terns were mostly nesting within the coastal mixed *Pandanus*—*Guettarda* belt facing the open ocean, and in interior patches of *Pandanus* stands, but concentrated to the eastern, ocean-facing side of Te Au O Tu. The frigatebird roosting colony was located at a short section of *Pemphis* coastal shrub vegetation on Manuae Island, which was the only over-water vegetation on the atoll in a wind-sheltered area facing the lagoon. Brown boobies were roosting on large storm-deposited coral blocks along the atoll reef rim. Bristle-thighed curlews and other migratory shorebirds occurred throughout the ocean- and lagoon-ward beaches in small groups of usually no more than two to three birds, but a single congregation of 32 bristle-thighed curlew was observed on the mudflats of Te Au O Tu (Figure 6*C*). We also observed individual bristle-thighed curlews in the interior open coconut forest and heard birds calling in the interior swamps.

TABLE 2

Bird Species on Manuae Atoll.

English name	Indigenous name	Scientific name	Manuae	Te Au O Tu	status
Bristle-thighed curlew	Teuea	*Numenius tahitiensis*	36	64	ow
Wandering tattler	Kuriri	*Tringa incana*	9	16	ow
Pacific golden-plover	Tōrea	*Pluvialis fulva*	12	18	ow
Ruddy turnstone	Parau'unga	*Arenaria interpres*	2	7	ow
Long-tailed cuckoo	Karavia	*Urodynamis taitensis*	1	1	ow
Reef egret	Kōtuku	*Egretta sacra*	17	13	b?
Great frigatebird	Kōta'a	*Fregata minor*	20	7	r
Brown booby	Toroā	*Sula leucogaster*	2	36	b?
Red-footed booby	Toroā	*Sula sula*	1	3	r
Red-tailed tropicbird	Tavake	*Phaethon rubricauda*	14 ad, 3 nests	55 ad, 27 nests	b
Brown noddy	Ngōio	*Anous stolidus*	52	215	b
Black noddy	Ngōio	*Anous minutus*	-	2	r
White tern	Piraki	*Gygis alba*	7	168	b
Sooty tern	Tara	*Onychoprion fuscatus*	-	2	r
Burrowing Procellaridae		Procellariidae	-	10 burrows	b

The number of counted animals per species during our surveys is given for each island. Status indicates where we found direct evidence for breeding ("b"), suggest that breeding is likely but could not be directly confirmed ("b?"), are overwintering ("ow") or roosting ("r") on the atoll. No sign of nesting or roosting of any birds was found on Ruakau Island.

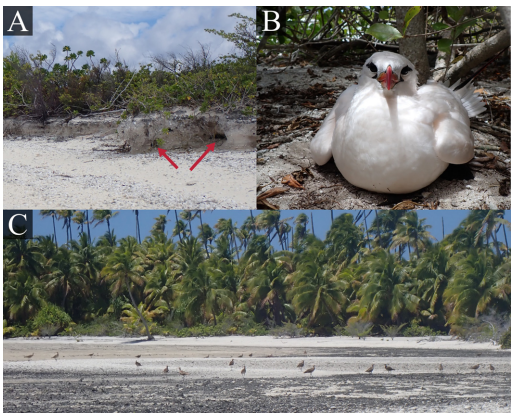

FIGURE 6. Bird fauna of Manuae atoll. A short (*ca.* 10-m long) section of eroded beach on the lagoon side of Te Au O Tu served as nesting site for a yet unidentified burrowing petrel/shearwater species; arrows identify two of the burrows (A). Red-tailed tropicbirds (*P. rubricauda*) are using Manuae atoll as nesting ground (B). The extensive mudflats and beaches of Manuae atoll serve as an important overwintering site for bristle-thighed curlews (*Numenius tahitiensis*) (C).

Introduced species

We readily trapped the Pacific rat (*R. exulans*), confirming its exclusive presence on both Manuae and Te Au O Tu islands. We caught 32 rats on Manuae Island (one-night trapping effort) and 19 on Te Au O Tu (two-nights trapping effort). We also confirmed the presence of the yellow crazy ant (*A. gracilipes*) on both islands, although it appears to be only patchily distributed. The most widespread introduced species across the atoll was the coconut (*Cocos nucifera*), resulting from the former copra monoculture farming. Several introduced species with historical records from Manuae atoll, such as common myna (*Acridotheres tristis*), domestic junglefowl (*Gallus gallus*), and pigs (*Sus scrofa*) (Frisbie 1932), were not detected.

DISCUSSION

The common interpretation of Manuae's Polynesian name origin ("manu enua"—home of birds) suggests an abundance of birds on its islands at the time of first human contact.

However, Manuae atoll has had a long history of human presence, which impacted its terrestrial biodiversity. After centuries of human habitation, extraction of natural resources, and copra plantation farming, the atoll was deserted in the 1970s. Our biodiversity survey of Manuae atoll, *ca.* 50 years after its abandonment, offers valuable insights into its present-day state. Manuae atoll's island biodiversity still bears a deep legacy of human impact. Still, at the same time, it is recovering as a regionally important nesting site for seabirds and sea turtles in the southern Cook Islands, as well as an overwintering ground for bristle-thighed curlews with regional to potentially international conservation importance.

Vegetation

We documented 33 vascular plant and fern species on Manuae atoll, of which 27 are native. About 19 years earlier, 45 different vascular plant and fern species were recorded on the Manuae atoll, of which 25 are native (Rongo 2006). Of the 27 native species found in 2024, 20 (*ca.* 74%) were already on the atoll in November 2005, while seven were not recorded in 2005. Five native plant species were recorded on Manuae atoll in 2005 but not found by our survey (*Colubrina asiatica*, *Hernandia nymphaeifolia*, *Laportea ruderalis*, *Stenotaphrum micranthum*, and *Vigna marina*). Most plant species that were present in 2005 but absent in 2024 (16 out of 21, or *ca.* 76%) are introduced species (*e.g.*, papaya, lemon, breadfruit) and were specifically recorded only around the former copra station settlement area (Rongo 2006). While the ratio of appearing-to-disappearing native species from 2005 to 2024 is approximately balanced (seven and five, respectively), the main change to the plant community over the 19 years was the disappearance of 16 introduced plant species. These shifts allude to the capacity of atoll floral communities to recover, suggesting that many ornamental and agricultural introductions on atolls can naturally disappear after the abandonment of human cultivation (Uhl et al. 1988). Whether the loss of these introduced species appeared successionally or abruptly following a key disturbance event cannot be concluded unambiguously. Studies of cyclone impacts on atolls have reported that agricultural and ornamental plants are disproportionately impacted by saltwater intrusion, wind forcing, or overwash from cyclones (Blumenstock 1958, Duvat et al. 2017). The most recent cyclone passed Manuae atoll in January 2013 and within 30 km distance (NOAA historical hurricane tracks database https://coast.noaa.gov/hurricanes/, last accessed 01 November 2024), which may have driven the disappearance of several introduced plant species from the atoll.

The native plant assemblage on Manuae atoll resembles the plant communities on other southern Polynesian atolls, such as Maria atoll (31 native species; Meyer 2013), Suwarrow atoll (23 native species; Woodroffe and Stoddart 1992), Manihiki atoll (20 native species; Cranwell 1933), or Tongareva atoll (18 native species; Linton 1933). The vegetation-forming shrub and tree species are all consistently represented throughout these atolls. Differences in species numbers between these atolls are mostly due to the presence or absence of a few herb and grass species (*e.g.*, *Ipomoea* spp., *Laportea* sp., and *Digitaria* sp.). Overall, the high similarity between Manuae atoll's native flora and other Polynesian atolls underpins the strong environmental filters that the atoll environment exerts on its biota. These conditions allow only specialized species to establish that can cope with the depauperate nutrient conditions, high disturbance regimes, continuous salt sprays, and limited water availability (Lee 1984)—likely the same conditions that extirpated many introduced ornamental and agricultural plants around the settlement area.

Even though the vascular plant community on Manuae atoll has likely maintained all or most of its original species, the relative vegetation composition and cover have changed since human arrival, especially through the influence of the copra plantation. Over 86% of Manuae atoll's vegetated land is coconut woodland (Burnett et al. 2024), which became the dominant land cover when Manuae atoll was developed into a coconut plantation for copra production (Frisbie 1932). Coconut palms maintain their monodominance over atolls due to their heavy burden on groundwater resources, soil nutrients, and faunal

decomposer communities that keep even long-abandoned plantations in a positive feedback loop favoring palm recruitment while restricting native atoll broadleaf forest regeneration (Young et al. 2010a, 2010b, 2017). Areas of *Pandanus*, *Guettarda*, or *Pisonia* stands across the atoll's interior may be either remnant patches of uncleared native forests or small pockets of native vegetation recovery where cyclone damages to the copra forest created new colonization opportunities for native broadleaf species (Blumenstock et al. 1961, Russell et al. 2025). Overall, the introduced coconut palm maintains its dominance over most parts of the atoll, a colonial legacy of copra plantation farming.

Land crabs

The terrestrial decapod fauna across the tropical Indo-Pacific shows high similarities and little species turnover due to the marine larval dispersal of land crabs, which enables these species to maintain connected meta-populations across Oceania (Drew et al. 2010). Therefore, the land crab community on Manuae atoll is similar, if not identical, to most other Polynesian atolls. Nevertheless, we noted land crabs, particularly ghost crabs (*Ocypode* sp.) and smaller inland-dwelling crabs (*Geograpsus* sp.), to be in noticeably low densities compared to our observations on other atolls. The beach decapod fauna on atolls is generally consistently active throughout the day and primarily influenced in its relative abundance by tides but with otherwise little seasonality (Steibl and Laforsch 2019), suggesting that our observations of a relative paucity in land crabs are not principally caused by environmental conditions. Introduced rats can significantly suppress land crab population sizes (Nigro et al. 2017, Samaniego et al. 2019), and their omnipresence on Manuae atoll likely impacts land crab abundance, with potentially cascading negative effects to forest recruitment and succession processes that land crabs naturally mediate (Lindquist et al. 2009).

Reptiles

The sandy beaches of atolls can be important nesting grounds for globally endangered sea turtles (Becker et al. 2019). Given that sea turtle nesting is seasonal, our survey likely failed to capture the annual nesting season. In November 2005, 12 active turtle nests were recorded on Manuae Island (Rongo 2006). In October 2019, at least 26 active nests on Manuae Island and 31 nests on Te Au O Tu of the globally endangered green sea turtle (*Chelonia mydas*) were recorded (Morejohn et al. 2019). Green sea turtle nesting is known from atolls in the northern Cook Islands group, as well as from Palmerston atoll and Aitutaki in the southern Cook Islands group (White 2014). Tongareva atoll is thereby the most important sea turtle nesting site (*ca.* 500–1,000 nests per year), followed by Palmerston atoll (*ca.* 100 nests per year) (White 2014). Given previous surveys (Rongo 2006, Morejohn et al. 2019) and our observation of at least 50 old nests on Manuae atoll, the atoll may also be considered a regionally important green sea turtle nesting ground in the Cook Islands, particularly because of the absence of coastal development, the intactness of the coastal shrub vegetation belt, and low overall human disturbance (Donlan et al. 2010).

Birds

The avifauna of Manuae atoll had been recorded repeatedly over the past. At the time of habitation by Polynesians during Captain Cook's voyages, no mention of seabird presence was made (Hooker 1998). In the early 1900s, during active copra plantation farming, red-tailed tropicbirds and bristle-thighed curlews were present and hunted by the copra station workers as a food source (Frisbie 1932). Both species were also present in September 1973, with a single nesting red-tailed tropicbird recorded on Manuae Island, and 22 bristle-thighed curlews across both islands. Additionally, nine white terns and other overwintering shorebirds were reported (Holyoak 1976, 1980). Noddies, frigatebirds, and boobies were not mentioned to be present on the atoll in the 1930s and 1970s, but brown noddy eggs had been collected from Manuae atoll *ca.* 1899–1904 (Gill 1996). In November 2005, only two nesting red-tailed tropicbirds were

recorded on Te Au O Tu, and no nests were found on Manuae Island (Rongo 2006). Boobies, frigatebirds, and terns were specifically stated to be noticeably absent from the atoll in 2005 (Rongo 2006).

Although some of the differences between earlier reports and our findings may be due to different environmental conditions (*e.g.*, seasonal conditions), comparing these historical records with our seabird assessments still suggests that the seabird community on Manuae atoll is recovering. We recorded at least 175 white terns, over 260 brown noddies, and at least 30 nests of red-tailed tropicbirds across the atoll, along with burrows of unidentified shearwaters/petrels and numerous roosting great frigatebirds and brown boobies, for which no previous published records from the atoll exist. The abandonment of the copra plantation likely significantly reduced the direct and permanent human pressure in the form of hunting, thus allowing seabird populations to partially recover (Lopez-Darias et al. 2011). Nevertheless, 50 years following the abandonment of the atoll, the seabird community of Manuae atoll is far from the carrying capacity that atolls can generally achieve, and several widespread atoll breeding species are noticeably absent as breeding species, such as sooty terns, crested terns, or black noddies (Steibl et al. 2024b). The dominance of coconut palms over the atoll interior greatly reduces potential nesting habitat, as most vegetation-nesting seabird species, except for brown noddies, cannot nest on the palms but require either broadleaf tree species (Young et al. 2017) or open grassland habitat (Carr et al. 2021). Furthermore, invasive rats on Manuae atoll likely negatively affect hatching success and the establishment of rat-sensitive species such as small ground-nesting seabirds (Harper and Bunbury 2015).

In addition to the apparent slow and partial recovery of seabirds, the presence of at least 100 overwintering bristle-thighed curlews are of particular conservation importance. This migratory shorebird species nests only in two locations in North-western Alaska and migrates annually to tropical Pacific islands, its exclusive overwintering grounds (Marks and Redmond 1994). Only about 3,200 breeding pairs of this species remain (Marks et al. 2020), with a global population estimate of 10,000 mature individuals (BirdLife International 2020)—although these estimates have high uncertainty due to scarcity in thorough breeding population census. Nevertheless, it suggests that, at the order of magnitude, *ca*. 1% of the global population of bristle-thighed curlews are using Manuae atoll as wintering ground. Bristle-thighed curlew is unique among shorebirds in that up to 50% of an overwintering population can become entirely flightless when they molt on their overwintering tropical islands, rendering them vulnerable to hunting and invasive mammal predators (Marks et al. 1990, Marks 1993). The extensive mudflats of Manuae atoll, together with the end of direct human pressure from hunting since the end of the copra plantation (Frisbie 1932), have likely made this atoll important as an overwintering ground for bristle-thighed curlews. Given the high site fidelity in the curlews' annual return to their overwintering grounds (Marks and Redmond 1994), Manuae atoll could potentially qualify as an internationally recognized important bird area (IBA) for overwintering bristle-thighed curlew. Repeated surveys in the following years will be necessary to confirm a consistent usage of Manuae atoll by large numbers of bristle-thighed curlew over multiple seasons.

Introduced species

The habitation of Manuae atoll by Polynesians, Western settlers, and copra plantation workers has been accompanied by the introduction of invasive species. The omnipresence of the Pacific rat (*R. exulans*) on the atoll tentatively dates back to the first settlement by Polynesian seafarers. During the times of copra plantation farming, common myna (*A. tristis*), domestic junglefowl (*G. gallus*), domestic turkey (*Meleagris gallopavo*), and pigs (*S. scrofa*) were introduced (Frisbie 1932). All these species have now disappeared from the atoll. The common myna was abundant in the 1930s (Frisbie 1932) and in 1973 (Holyoak 1976) and last reported in very low numbers on the atoll in 1997 (McCormack, pers. comm.) but was not found in 2005 (Rongo 2006). Similar to the disappearance of many agricultural plant species from Manuae

atoll since its abandonment, the disappearance of several introduced bird species without management intervention is likely also due to the near complete absence of humans. Nevertheless, key introduced species with negative impacts on atoll biodiversity and functioning remain, including rats and coconut palms (Young et al. 2017, Graham et al. 2018). Another introduced species of major conservation concern, yellow crazy ants (*A. gracilipes*), was recorded to be present only on Manuae Island but not Te Au O Tu in the 1960s (Taylor 1967), but in 2024, the ant was readily observed on both islands. Biosecurity strategies, mainly managing and controlling the transport of goods to the atoll, will be necessary to protect Manuae atoll from the arrival of invasive species that are established on other islands in the Cook Islands, such as black rats (*Rattus rattus*) (Corson 2023).

Conclusion

Pacific atolls can be hotspots and refugia for Oceania's unique lowland island biodiversity when free of human disturbance or actively restored (Lee 1984, Becker et al. 2019, Steibl et al. 2024b). Manuae atoll, a large and, nowadays, uninhabited atoll, has had a long history of permanent human occupation, resource exploitation, and monoculture farming. When the first avifaunal records of Manuae atoll were made, many bird species that our survey recorded were largely absent. In the nineteenth century, the atoll changed from Indigenous to Western human disturbances, which introduced additional species to the atoll, continued to deplete its natural resources, and shifted its vegetation into coconut dominance (Russell and Kueffer 2019, Steibl et al. 2024a). With the abandonment of settlement in the 1970s, Manuae atoll's terrestrial biodiversity initiated a partial recovery. Formerly established introduced plant and animal species have disappeared from the atoll by 2024, and other native species, particularly seabirds, but also pockets of native broadleaf vegetation, appear to be recovering and re-establishing. At the same time, Manuae atoll still bears an ongoing legacy of human disturbance, including introduced rats and the monodominant coconut palms from plantation farming, that restrict the atoll's capacity to fully recover. Direct restoration interventions, such as rat eradication and forest restoration, thus promise to accelerate the natural recovery process of Manuae atoll and enable more atoll-dwelling species to recover or return (Dunn et al. 2024). Beyond returning island biodiversity, the natural recovery and active ecological restoration of Manuae atoll will contribute to local-scale resilience against sea-level rise and climate change (Benkwitt et al. 2023, Steibl et al. 2024c).

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