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**Title**

Coral atolls are global hubs for tropical seabirds

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**Author contributions**

Se.S. and Si.S. designed the study, conducted the model development and data analysis; Se.S. compiled the datasets; all authors contributed to the writing and proofing of the manuscript and have agreed to the submission of the final version.

**Competing Interest Statement**

The authors declare not competing interests.

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**Abstract**

**Significance statement**

**Main text**

**Introduction**

Coral atolls are unique ecosystems of tropical oceans, comprising a ring-shaped coral reef that encloses a shallow lagoon, and up to several hundred distinct islands built by reef sediments deposited along the atoll rim. Over large parts of the Indo-Pacific oceanic basin, atolls constitute the most common and numerous island type (Nunn *et al.* 2016). These low-lying islands are at the forefront of climate change and widely regarded as being among the most vulnerable ecosystems to global change (IPCC 2023). While the received wisdom of their inevitable drowning from rising sea-levels is increasingly challenged by advances in geoscience (Beetham *et al.* 2017; Masselink *et al.* 2020; Kench *et al.* 2023), major local-scale protection and ecological restoration efforts are nevertheless essential to sustain these ecosystems beyond the Anthropocene (Steibl *et al.* 2023).

Local-scale adaptation measures for future-proofing atoll islands against climate change are primarily motivated to protect human livelihoods and economies (Barnett *et al.* 2022; Brown *et al.* 2023). A conservation and protection case for atolls from a biological diversity perspective, particularly for the majority of uninhabited atoll islands, is so far limited to just a handful of selected atolls, such as Aldabra (UNESCO world heritage) or the North-western Hawai’ian atolls (National Wildlife refuges) (Stoddart 1968). This is likely reinforced by the widespread perception that atoll islands are depauperate fringe ecosystems with little terrestrial biodiversity and ecological value – sometimes even dubbed as ‘biodiversity coolspots’ (antipodal to the ‘biodiversity hotspot’ classification of most high volcanic island archipelagos) (Myers *et al.* 2000; Thaman 2008).

Atolls may not harbour the same fantastic diversities and unique ecological interactions as most large oceanic islands with their countless endemic species forms (Kier *et al.* 2009). Nevertheless, atoll islands house distinct terrestrial species­ communities that are being increasingly recognised for their detrimental role in the atoll ecosystem’s functioning and resilience. Seabirds are the major nutrient delivery system to atoll islands. Their nutrient input in the form of guano catalyses terrestrial carbon sequestration (Young *et al.* 2011), enhances soil and groundwater nutrient enrichment (McMahon & Santos 2017; Young *et al.* 2010), and subsidises adjacent coral reefs (Graham *et al.* 2018). Case studies from a limited number of atolls across the Indo-Pacific clearly suggest that atolls are reliant on the nutrient input from seabirds, and, *vice versa,* tropical seabird species are reliant on atoll islands as major nesting grounds (Berr *et al.* 2023).

Nevertheless, atoll islands are widely omitted in global assessments and censuses of seabird colonies. The significance of atoll islands and atoll island protection for seabird conservation remains to be directly quantified. In this study, we therefore tested the hypothesis that atoll islands are major seabird nesting hubs on a global scale and with international significance for seabird conservation. Additionally, and reciprocally, we further assessed the seabird-driven nutrient transfer systems for atoll ecosystems and the nutrient dynamics of the remote Indo-Pacific. By quantifying global seabird population sizes on atolls and their role as nutrient delivery system to atoll islands, this study aims to establish an empirically-tested global conservation case for atolls as sites with exceptional ecological value for seabird protection and, reciprocally, for seabird protection on atolls to preserve their integrity and functioning in the future.

**Results**

1. *The significance of atolls for seabirds*

We compiled a global dataset of seabird atoll nesting colonies that comprised data for 199 of the Indo-Pacific’s 280 coral atolls. For 107 atolls, abundance-based nesting censuses were available, while for 92 atolls only incidence-based nesting censuses were available. We used a two-stage Bayesian model to predict seabird presence and nesting population size on the missing atolls to generate a global understanding of seabird nesting on all the Indo-Pacific’s atolls.

The 280 atolls of the Indo-Pacific are nesting sites to an estimated total of 27,426,070 seabirds, comprising 37 different species. The nesting populations ranged from zero birds (on some Maldivian atolls) to over 3,000,000 birds per atoll (e.g., Europa, Starbuck) (Fig. 1a). Importantly, ca. 25% of the Indo-Pacific’s atolls have seabird nesting populations above the threshold for Important Bird Areas (B3b, formerly A4iii; BirdLife International). 47 atolls house colony that constitutes >1% of the estimated global population size of a seabird species. 12 atolls house a colony that constitutes >10% of the estimated global population size of a seabird species, and two atolls (Kiritimati and Midway) house colonies that constitutes >70% of the estimated global populations of a seabird species (Fig. S1). Species richness on atolls with a seabird nesting population ranged from just single species (e.g., on some Lakshadweep atolls) to 18-19 species (French Frigate Shoals, Kiritimati, Midway) (Fig. 1b). Community composition analysis identified several atolls that significantly contribute to the global beta-diversity (a measure for the compositional dissimilarity between atolls), as these atolls are home to distinct seabird species assemblages, such as several petrel species (*Pterodroma* spp.) on Ducie and Oeno (Pitcairn Group), or two species of albatross on the North-Western Hawai’ian atolls (Fig. 1c). Together, a large set of atolls can be identified across the entire Indo-Pacific basin, which are of great significance of tropical seabird species by providing nesting sites for either a large number of birds, often above international thresholds for important bird areas (Fig. 1a, S1), or a high diversity of different species (Fig. 1b), or a distinct composition of unique species (Fig. 1c).

A group of maps with different colored dots

Description automatically generated with medium confidence**Figure 1: Seabird colonies on the 280 Indo-Pacific coral atolls.** Total seabird colony size (a), seabird species richness (b), and compositional distinctness (local contribution to beta-diversity; LCBD score) (c) were computed using a Bayesian predictive modelling framework. Ca. 25% of the Indo-Pacific’s atolls house seabird nesting colonies greater than the BirdLife International threshold for significant bird areas B3b (formerly A4iii criteria; dashed horizontal line in boxplot a).

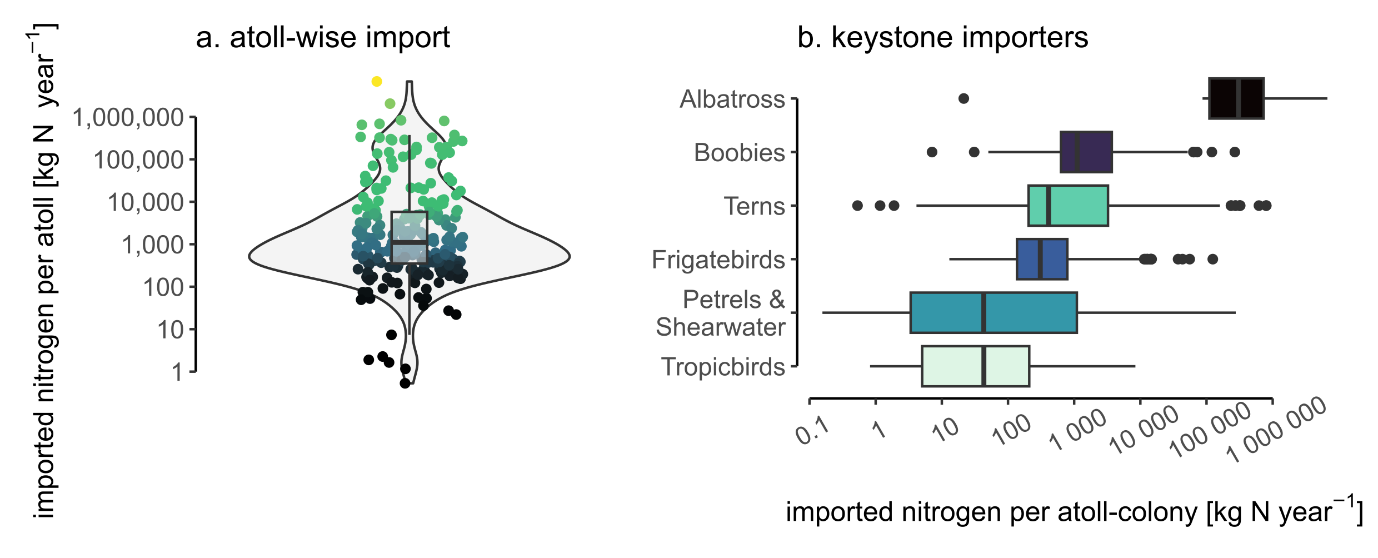
We used global population assessments from BirdLife International and Birds of the World for each of the 37 atoll-nesting seabird species to estimate how much of the world population is nesting on atolls. 18 of the 37 seabird species have more than 25% of their world population nesting on atolls, 12 more than 50%, 6 seabirds more than 75%, and two species (the Black-footed and Laysan Albatross) have more than 95% of their world population nesting on atolls (Fig. 2). Only one of the principal atoll nesting seabird species, the Polynesian storm-petrel (*Nesofregetta fuliginosa*), is currently recognised by IUCN red list criteria as endangered.

A chart with different colored bars

Description automatically generated with medium confidence**Figure 2: Contribution of atolls to global population sizes of Indo-Pacific seabirds.** For each of the 37 atoll-nesting seabird species, the percentage fraction of atoll-nesting birds is given based on global population size estimates from BirdLife International and Birds Of the World (2022). 12 seabird species have more than 50% of their estimated global population nesting on atolls, two species have more than 95% of their estimated global population nesting on atolls.

1. *The significance of seabirds for atolls*

By offering suitable nesting sites to ca. 27.5 million seabirds, atolls are of exceptional significance for seabirds; reciprocally, the large seabird colonies are also significant for the functioning of the atoll system: Seabirds are major nutrient importers for island and nearshore ecosystems, and to assess the global contribution of seabirds for the nutrient dynamics on atolls we assessed global nutrient deposition using bioenergetic models.

Seabird nesting colonies on atolls import on average 63,898 kg nitrogen per year on an atoll [95% quantiles: 0 – 247,391.2], and 10,650 kg phosphorous per year [0 – 45,731.9] in the form of guano (Fig. 3a, Fig S2). Albatross (*Phoebastria* spp.) and booby (*Sula* spp.) colonies contribute the largest amounts of nitrogen per atoll-colony (Fig. 3b). As seabird nesting colonies are usually confined to just a small subset of an atoll’s islands, these inputs are unevenly concentrated to just few of an atoll’s sometimes hundreds of islands. However, because island-level information on seabird colonies was not available in most data sources, we did not further standardise nutrient input quantities by land area.

**Fig. 3 Seabird-derived nitrogen inputs on atolls.** For each of 280 Indo-Pacific atoll, the estimated seabird-derived nitrogen input in kg N per year is calculated using bioenergetic models (a). For the six species groups of seabirds, the imported nitrogen per atoll-colony is presented (b). Atolls receive a mean of over 63,000 kg N per year from seabirds, but amounts vary greatly depending on the size of the atoll seabird colony, with albatross and booby colonies contributing the largest amounts of nitrogen per atoll on average. Phosphorous input rates are summarised in supplementary figure S2.

The largest amount of seabird guano is rapidly volatilised as ammonia and enters the atmospheric nitrogen cycle. The total annual ammonia emission of atoll seabird colonies is estimated at 2,577,018 kg NH3 per year. The annual average ammonia emissions are 9203 kg NH3 per atoll [0 – 39,982.7] (Fig. 4).

Using published GPS-tracking data of the atoll seabird species, we simulated foraging ranges over which seabirds are integrating nutrients during the breeding season and concentrate them onto the atoll ecosystem in the form of guano. Depending on the species, seabirds forage as close as 2-3 km (Little terns *Sternula* spp.) or as far as 1500 km (Albatross *Phoebastria* spp.) around an atoll. For the majority of atolls, seabirds are integrating nutrients over a core area of 10,000 - 100,000 km² of ocean around an atoll. For those atolls with large petrel/shearwater or albatross colonies, the core nutrient integration area averages ca. 1,000,000 km² of ocean around an atoll (Fig. 4). The average atoll land area is 9.7 km² [0.3 – 30.1], meaning that seabirds are spatially concentrating nutrients onto the atoll islands by a factor of 1000-10,000.

A diagram of a bird life cycle

Description automatically generated**Figure 4: The reciprocal significance of seabirds and atolls.** Atolls provide nesting space for ca. 27.5 million seabirds throughout the Indo-Pacific. Reciprocally, seabirds are importing large quantities of nutrients in the form of guano into the atoll ecosystem, which they forage and integrate over large areas of ocean around an atoll. The two distinct peaks of foraging area indicate atolls with and without petrel/shearwater and albatross colonies, as these species have significantly larger foraging ranges than other atoll-nesting seabirds. A significant amount of reactive nitrogen from guano is volatilised and enters the atmospheric nitrogen cycle. Ammonia emissions can either be directly re-incorporated into the atoll ecosystem via plant stomata (a), or atmospherically wet- or dry-deposited in the surrounding open ocean (b). In addition, rainfall and groundwater discharge directly flushes seabird excrements back into the nearshore reef ecosystem (c). Values in brackets are 5% and 95% quantiles, respectively.

**Discussion**

**Materials and Methods**

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**References**

**Figures**