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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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Biological Sciences – Ecology

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**Abstract**

**Significance statement**

**Main text**

**Introduction**

Coral atolls are unique ecosystems of the tropical oceans, comprising a ring-shaped coral reef that encloses a shallow lagoon, and up to several hundred distinct islands deposited along the atoll rim (Goldberg 2016). Over large parts of the Indo-Pacific 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 impacts 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 adaptation and restoration efforts are nevertheless essential to sustain these unique ecosystems beyond the Anthropocene (Steibl *et al.* 2023).

Local-scale adaptation initiatives to future-proof atoll islands against global change are primarily motivated to protect human livelihoods and economies (Barnett *et al.* 2022; Brown *et al.* 2023). A conservation case from a biological diversity perspective, particularly for the vast majority of uninhabited atoll islands, is so far limited to just a handful of 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 regards atoll islands as generally depauperate fringe ecosystems with little terrestrial biodiversity and ecological value – sometimes even dubbed ‘biodiversity coolspots’ (antipodal to the ‘biodiversity hotspot’ classification of most high volcanic island archipelagos) (Myers *et al.* 2000; Thaman 2008).

Indeed, atoll islands may not harbour the same endemism-rich and diverse terrestrial species communities as most large oceanic islands (Kier *et al.* 2009). Nevertheless, atoll islands house remarkable species­ communities that play critical roles in the atoll ecosystem’s functioning and resilience. The major nutrient delivery system to atoll islands is formed by seabirds. Their nutrient input in the form of guano catalyses terrestrial carbon sequestration (Young *et al.* 2011), enhances soil and groundwater enrichment (McMahon & Santos 2017; Young *et al.* 2010), and subsidises adjacent coral reefs in marine consumer communities (Benkwitt *et al.* 2022; Graham *et al.* 2018). Together, numerous case studies across the Indo-Pacific underline that seabirds are significant for the functioning and energy cycle of atolls. *Vice versa*, however, the significance of atoll islands as nesting grounds for seabirds is often implied but remains to be directly tested and quantified (Berr *et al.* 2023).

A direct global assessment of the relevance of atoll islands for tropical seabird species, and their global relevance for energy fluxes in atolls, would create a global biological conservation case for atoll island protection. Therefore, we tested the hypothesis that atoll islands are major seabird nesting hubs on a global scale and with international significance for species conservation. Additionally, and reciprocally, we further assessed the seabird-driven nutrient transfer systems for atoll ecosystems throughout the Indo-Pacific. By quantifying global seabird population sizes on atolls and their role as nutrient delivery system to atoll islands, this study establishes an empirically-tested global conservation argument for atolls as sites with exceptional ecological value for seabird protection and, reciprocally, for seabird protection on all atolls across the Indo-Pacific to preserve their integrity and functioning on a basin-scale.

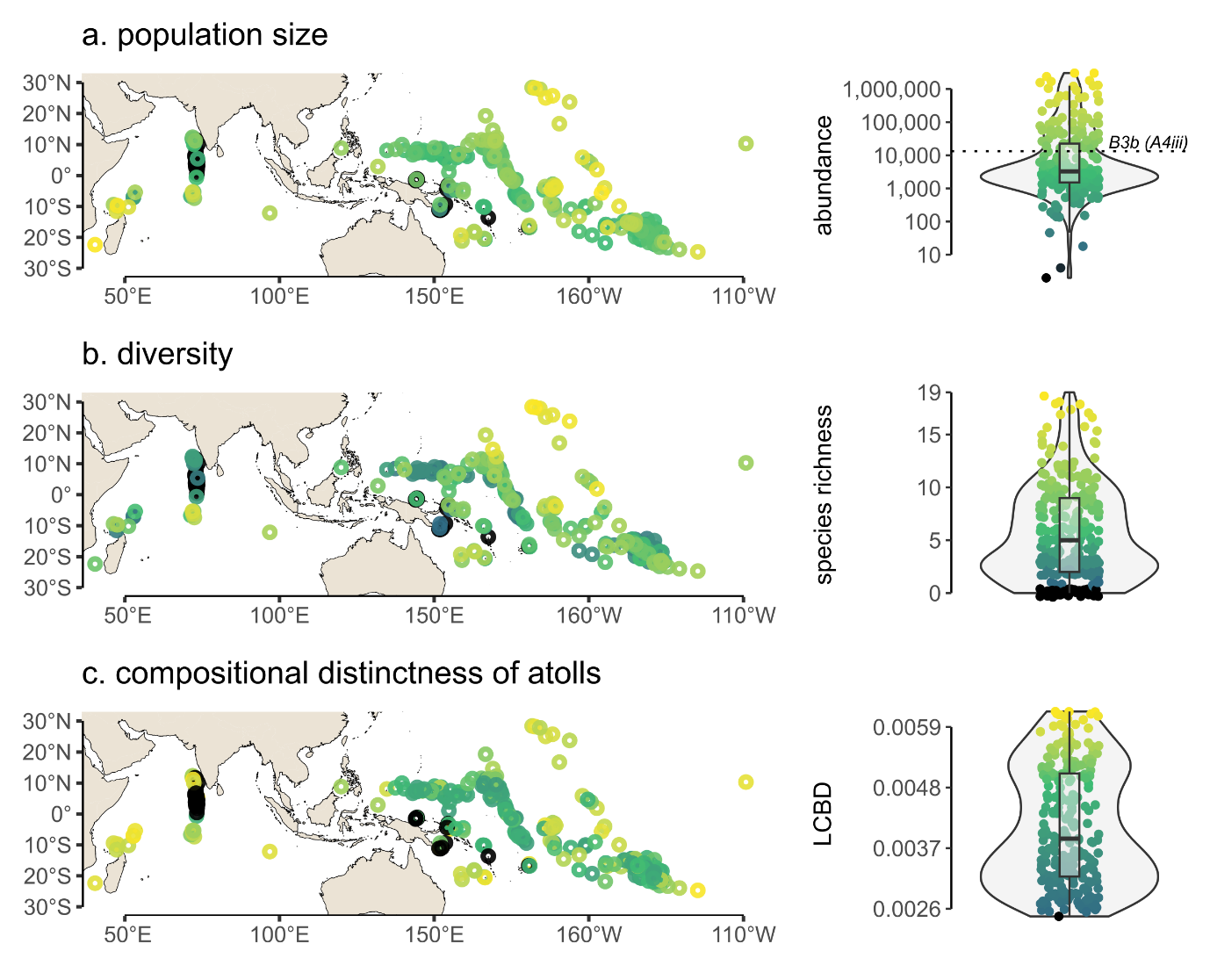
**Results**

1. *The significance of atolls for seabirds*

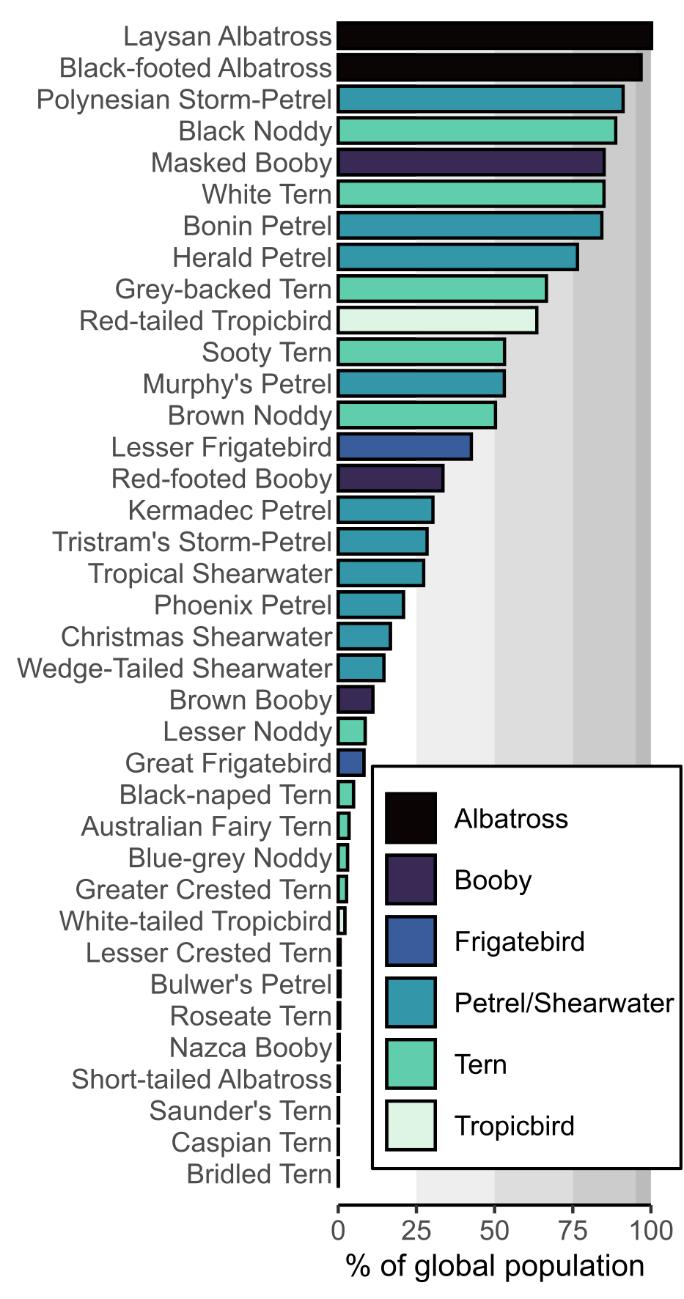
We compiled a global dataset of seabird atoll nesting colonies that comprised data for 199 of the Indo-Pacific’s 280 coral atolls. For 107 atolls, abundance-based nesting censuses were available, while for 92 atolls only incidence-based nesting censuses were available. We used a two-stage Bayesian model to predict seabird presence and nesting population size 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 27,992,662 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). 51 atolls (ca. 18% of all Indo-Pacific atolls) house a seabird 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 significant for 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 community of unique species (Fig. 1c).

The combined biomass of all atoll-nesting seabirds combined totals 11,264,618 kg, with an average seabird biomass of 40,231 kg per atoll [95% quantiles: 0 –164,445]. Using bird biomass conversion factors in Bar-On *et al.* (2018), the total biomass of atoll-nesting seabirds translates to a carbon stock of 3,942,616 kg throughout all Indo-Pacific’s atolls, or 14,081 kg per atoll on average [0 – 57,556].

**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).

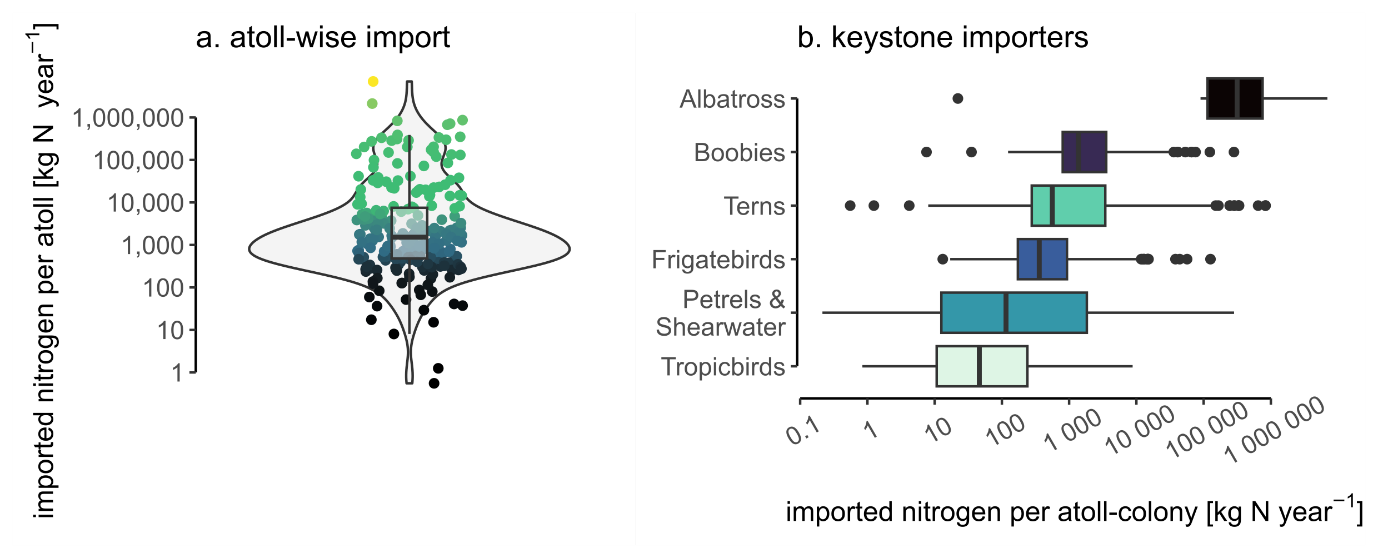
We used global population assessments from BirdLife International and Birds of the World for each of the 37 atoll-nesting seabird species to estimate how much of the world population is nesting on atolls. For 18 of the 37 seabird species, more than 25% of their world population is nesting on atolls. For 13 species more than 50%, for eight seabirds more than 75%, and for two species (the Black-footed and Laysan Albatross) more than 95% of their world population is 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.

**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). For 13 seabird species, more than 50% of their estimated global population are nesting on atolls, and for two species more than 95% of their global population is nesting on atolls.

1. *The significance of seabirds for atolls*

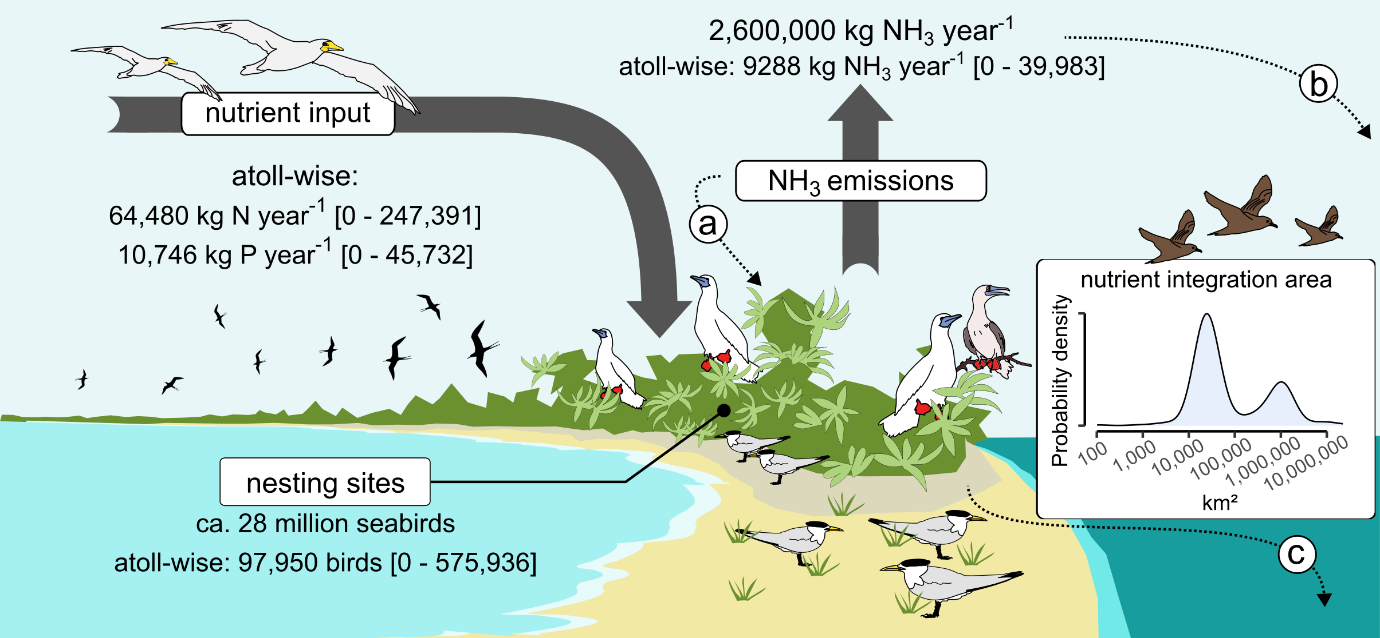
By offering suitable nesting sites to ca. 28 million seabirds, atolls are of exceptional significance for seabirds; reciprocally, the large seabird colonies are also significant for the functioning of the atoll system: to assess the global contribution of seabirds for the nutrient dynamics on atolls we assessed global nutrient deposition using bioenergetic models (Otero *et al.* 2018; Wilson *et al.* 2004).

Seabird nesting colonies on atolls import on average 64,480 kg nitrogen per year on an atoll [95% quantiles: 0 – 247,391], and 10,746 kg phosphorous per year [0 – 45,732] 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 on average of over 64,000 kg N per year from seabirds, but amounts vary greatly depending on the size of the atoll seabird colony. Albatross and booby colonies import 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 2,600,723 kg NH3 per year. The annual average ammonia emissions are 9288 kg NH3 per atoll [0 – 39,983] (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, atoll-nesting 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 and/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.

**Figure 4: The reciprocal significance of seabirds and atolls.** Atolls provide nesting space for ca. 28 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 each atoll (10,000 – 100,000 km²). The two distinct peaks of foraging area indicate atolls with and without petrel/shearwater and/or 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 as ammonia. Ammonia emissions can either be directly re-incorporated into the atoll ecosystem via plant uptake (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**