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**Title**

Coral atolls are globally significant hubs for tropical seabirds

**Author list**

Sebastian Steibl1, \*, +

Simon Steiger2, +

Alex S. Wegmann3

Nick D. Holmes3

James C. Russell1

**Affiliation**

1 School of Biological Sciences, University of Auckland, Auckland, 1010, New Zealand

2 Karolinska Institute, Solna, 17177, Sweden

3 The Nature Conservancy, Sacramento, CA 95811, USA

+ shared first-authorship

**ORCiD**

Sebastian Steibl: <https://orcid.org/0000-0003-4819-8581>

Simon Steiger:

Alex S. Wegmann: <https://orcid.org/0000-0002-0595-7552>

Nick D. Holmes: <https://orcid.org/0000-0003-1740-2404>

James C. Russell: <https://orcid.org/0000-0002-5901-6416>

\* corresponding author: Sebastian Steibl; **Email:** [sebastian.steibl@auckland.ac.nz](mailto:sebastian.steibl@auckland.ac.nz)

**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 the tropical oceans. They comprise 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 atoll islands are generally depauperate fringe ecosystems with little terrestrial biodiversity and ecological value – sometimes even dubbed ‘biodiversity cool spots’ (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 large volcanic islands (Kier *et al.* 2009). Nevertheless, atoll islands house remarkable species­ communities that play critical roles in the atoll ecosystem’s functioning and resilience. Most readily evident are seabirds, which act as 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 enrichment (McMahon & Santos 2017; Young *et al.* 2010), and subsidises adjacent coral reefs and 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 has not been directly tested and quantified (Berr *et al.* 2023).

A 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 quantified and modelled seabird nesting colonies on all 280 Indo-Pacific atolls and tested the hypothesis that atoll islands are major seabird nesting hubs with global significance for species conservation. Additionally, and reciprocally, we further assessed the seabird-driven nutrient transfer systems for atoll ecosystems across the entire Indo-Pacific atoll landscape. 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 atoll islands as sites with exceptional ecological value for seabirds and, reciprocally, for seabird conservation on all atolls across the Indo-Pacific to preserve their integrity and functioning on a basin-scale.

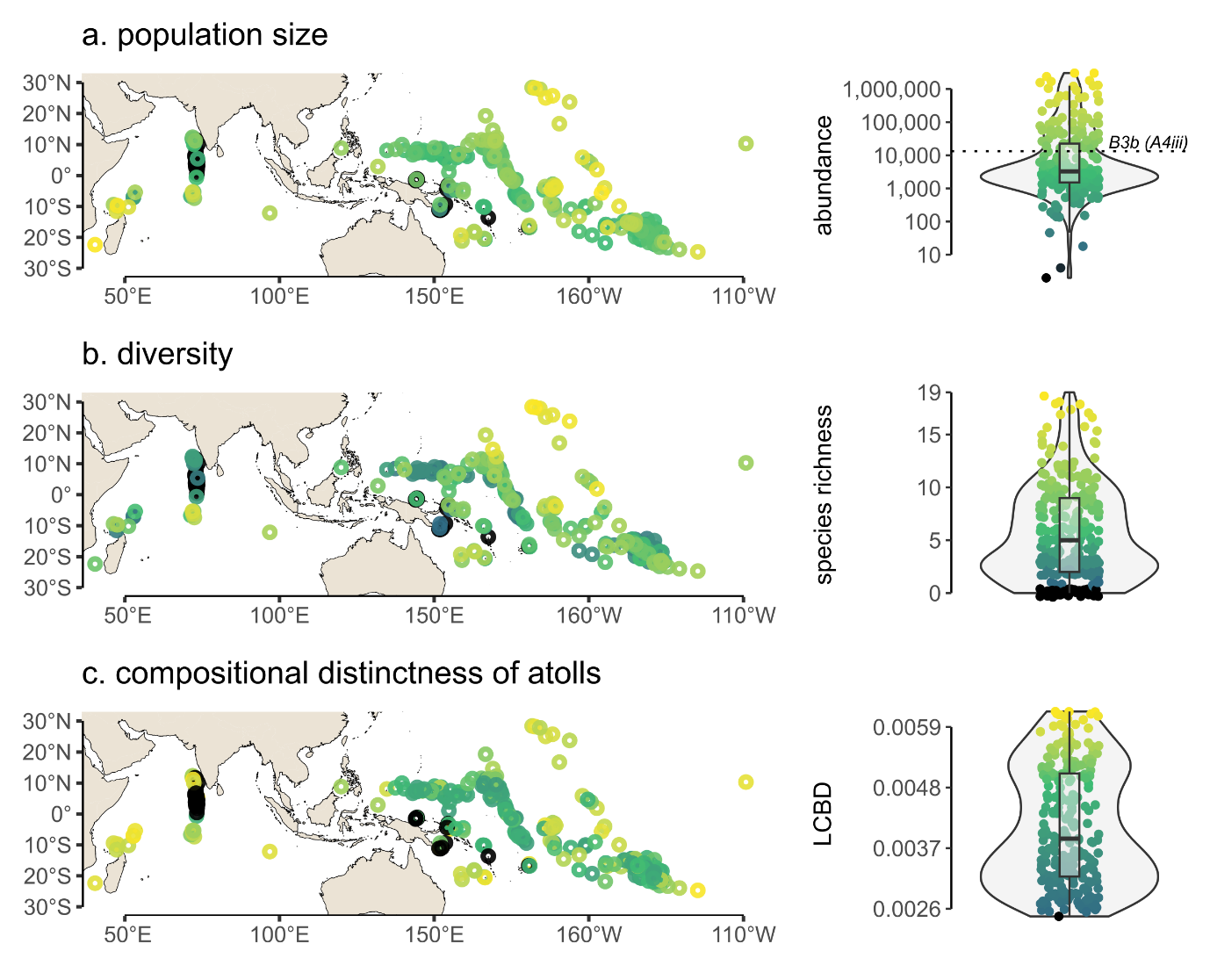
**Results**

1. *The significance of atolls for seabirds*

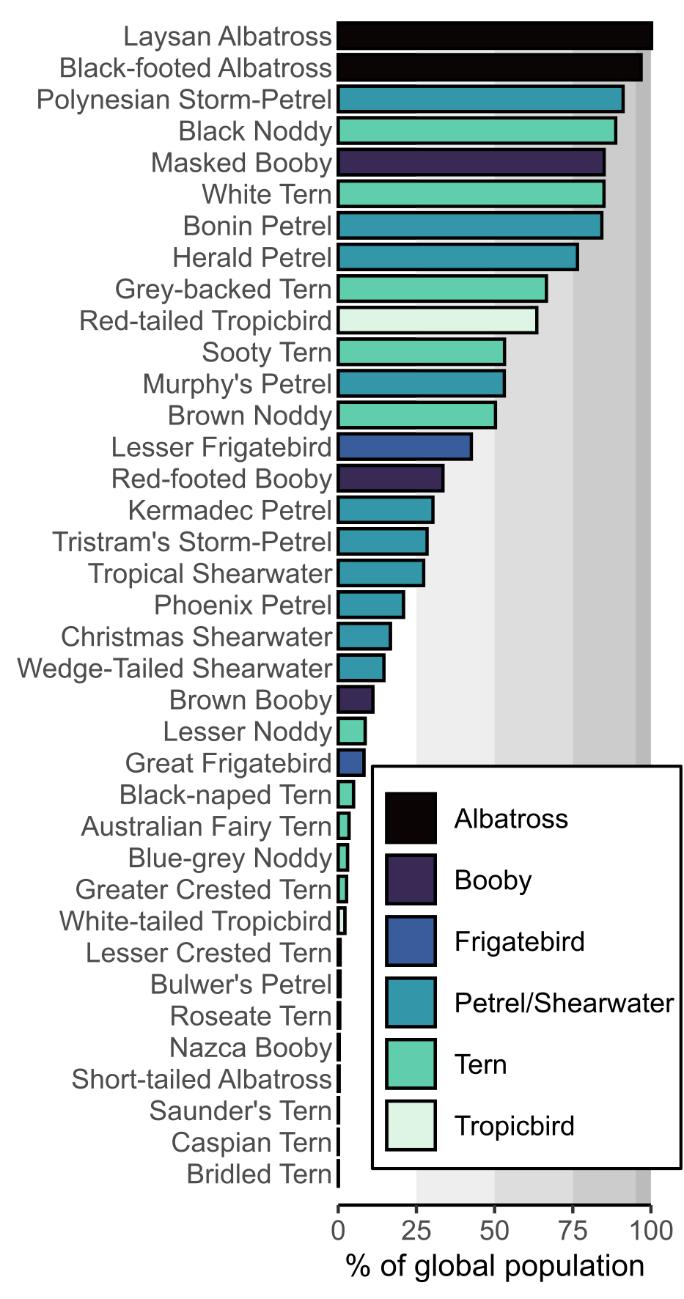
We compiled a global dataset of seabird atoll nesting colonies that comprised data for 199 of the Indo-Pacific’s 280 coral atolls. For 107 atolls, abundance-based nesting censuses were available, while for 92 atolls only incidence-based nesting censuses were available. We used a two-stage Bayesian model to predict seabird presence and breeding 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 27,993,000 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, 25% of the Indo-Pacific’s atolls (70 atolls) house 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), identifying atolls that 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 internationally recognised 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).

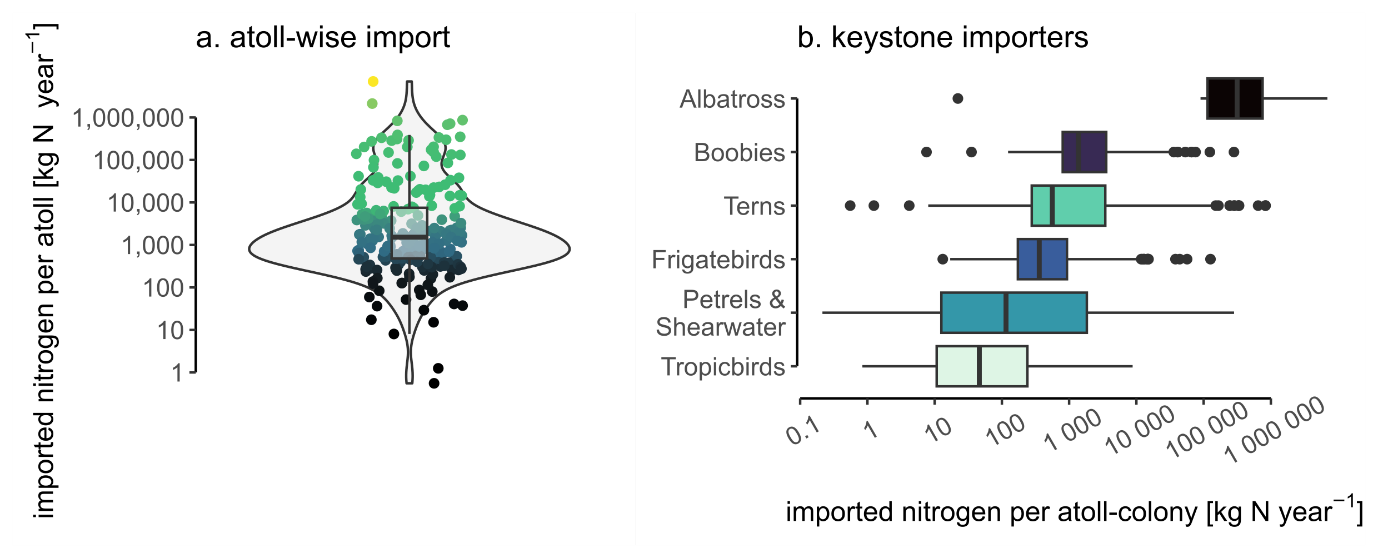
We used global population assessments from BirdLife International and Birds of the World for each of the 37 atoll-nesting seabird species to estimate how much of their world population is nesting on atolls. For 18 seabird species, more than 25% of their world population is nesting on atolls. For 13 species 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*

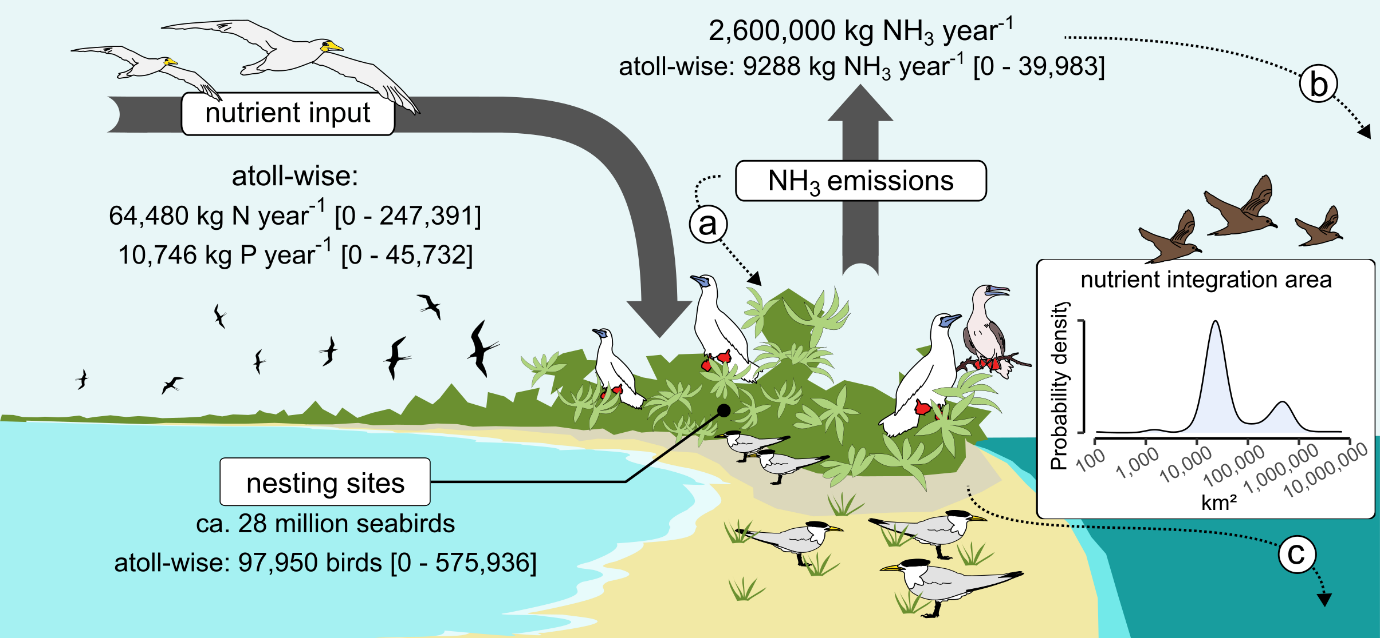
By offering suitable nesting sites to ca. 28 million seabirds, atolls are of exceptional significance for seabirds; reciprocally, the large seabird colonies are also significant for the functioning of the atoll system: to assess the global contribution of seabirds for the nutrient dynamics on atolls we quantified global nutrient deposition rates 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 atoll-seabird colony distribution was not available in most data sources, we did not further standardise nutrient input quantities by land area. Using the entire land area of an atoll would greatly underestimate the uneven and highly concentrated input rates on seabird-colony islands within an atoll.

**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 across the Indo-Pacific 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. 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 during breeding. For most atolls, seabirds are integrating nutrients over a core area (50% highest density region interval) of 10,000 – 100,000 km² of ocean around an atoll. For those atolls with large petrel/shearwater and/or albatross colonies (e.g., Ducie, Midway, Oeno), the core nutrient integration area extends to 100,000 – 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, at least, 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 enormous 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 are caused by 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 ocean (b). In addition, surface run-off and groundwater discharge directly flush seabird excrements back into the nearshore reef ecosystem (c). Values in brackets are 5% and 95% quantiles, respectively.

**Discussion**

Our global analysis of seabird colonies on all Indo-Pacific atolls demonstrates that these islands are globally significant hubs for seabirds and, reciprocally, seabirds act as a major nutrient pumps on a basin-scale. About 28 million seabirds are using atolls as nesting sites, and several species have a relevant fraction of their entire worldwide population concentrated on atolls. As a result, atoll islands are sites of extraordinarily nutrient deposition and the presence of seabirds on these remote landforms has likely relevant effects on the marine and terrestrial productivity throughout the otherwise barren and nutrient-poor tropical Indo-Pacific (de la Peña-Lastra 2021).

Because of their ecological significance as biological pumps between marine and terrestrial ecosystems, global seabird distribution and conservation priorities have been assessed repeatedly (Chown *et al.* 1998; Paleczny *et al.* 2015; Otero *et al.* 2018). However, atoll have been generally omitted from large-scale efforts to identify global priority areas for seabird conservation. Global studies estimated total seabird population sizes at ca. 12.6 million birds throughout South America, 30.5 million birds throughout Europe, or 73.9 million birds throughout North America (Otero *et al.* 2018). Our global analysis revealed that the 280 atolls of the Indo-Pacific are housing about the same number of seabirds as the entire European peninsula, or about one third of the total seabird population of entire North America – on a combined total land area of less than 2750 km², or about a quarter of the land area of Hawai’i’s Big Island (ca. 10,430 km²). This unequivocally demonstrates the global significance of atoll islands as prime focus sites for seabird conservation.

While atolls do not harbour critically endangered or range-restricted seabird species, several common seabirds of the tropical Indo-Pacific have a relevant fraction of their global population nesting on atoll islands. As atolls throughout the Indo-Pacific face the same challenges from climate change (incl. increase in storm surges, marine heatwaves, rising sea levels) (Barnett *et al.* 2022), a significant fraction of many common seabird species may thus actually be considered vulnerable. For example, species such as the White tern (*Gygis alba*) or Black Noddy (*Anous minutus*) are widespread and common, and thus ranked ‘least concern’ under IUCN criteria. However, our analysis suggests more than 75% of their global populations are found on atolls, meaning that an increasing undermining of atoll islands’ integrity with ongoing global change threatens the global persistence of these species.

Many features of atoll islands, such as their small land areas, isolation, or low habitat complexity, render them ideal sites for ecological restoration actions. Removal of invasive mammal predators, native forest diversification and clearing of abandoned monoculture copra plantations have been conducted on atolls and created safe havens for tropical seabird species throughout the Indo-Pacific (Carr *et al.* 2021). The ecological value of atoll islands for seabirds on a basin-scale thus places a premium on atoll restoration as a key conservation tool for seabird protection with global relevance. Additionally, nature-based resilience-building measures on atoll islands against climate change will be critical to implement across the entire Indo-Pacific to protect a significant number of the world’s seabirds (Steibl *et al.* 2023).

Reciprocally, the protection or active restoration of seabird colonies is an essential instrument for maintaining critical energy and nutrient fluxes throughout the Indo-Pacific (Sandin *et al.* 2022). The large biomasses of atoll seabird colonies may contribute significantly to terrestrial carbon stocks throughout the Indo-Pacific, particularly on arid atolls with otherwise only sparse grass and shrub vegetation (e.g., Malden, Starbuck). More importantly is the enormous concentration of nutrients, integrated over 10,000 – 100,000 km² of open ocean around an atoll, onto the comparably small island and reef ecosystem. Our assessment of nutrient and phosphorous loads throughout all Indo-Pacific atolls offers the opportunity to incorporate atoll ecosystems into basin-wide analysis of element cycles. The estimated total ammonia emissions from atolls of over 2.6 million kg per year makes up as much as 40% of total Indo-Pacific wide emission estimates (ca. 6.28 million kg) (Riddick *et al.* 2018). Case studies on ammonia emissions from atoll seabird colonies suggest that these emissions can be rapidly re-integrated into the atoll ecosystem, either through direct uptake by plants or re-deposited within few kilometres into the ocean (Schmidt *et al.* 2004, 2009). Ammonia emissions from seabird colonies together with the direct run-off into the adjacent coastal ecosystems can stimulate and amplify oceanic productivity in otherwise nutrient- and particularly nitrogen-limited surface waters (Duce *et al.* 2008; Martino *et al.* 2014). Our quantifications suggest that atoll seabird colonies may be an important yet overlooked contributor to remote oceanic nitrogen cycles where otherwise significant continental inputs are negligible (Altieri *et al.* 2021; Paulot *et al.* 2015).

Atolls are unique trans-boundary ecosystems where marine and terrestrial ecological processes and functioning are tightly intertwined. Seabirds are major nutrient pumps and thus a critical element to atoll ecosystems (Berr *et al.* 2023). Reciprocally, atoll islands are globally significant hubs for tropical seabirds. As many atoll islands are severely degraded from local-scale human impacts, the carrying capacities and seabird colonies on atolls can be even further expanded through ecological restoration (Carr *et al.* 2021). Ultimately, the restoration of atoll seabird colonies will contribute towards restoring the integrity of atoll ecosystems themselves, offering a nature-based opportunity for resilience building against future climate change (Benkwitt *et al.* 2023; Steibl *et al.* 2023).

**Materials and Methods**

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**References**

**Figures**