







Atolls are globally important sites for tropical seabirds

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Seabirds play critical roles on islands. By catalysing terrestrial and marine productivity through guano nutrient input, seabirds support natural island functioning. In the Indo-Pacific, atolls comprise one-third of all islands but only ~0.02% of island area. The importance of atolls as seabird nesting grounds has been historically neglected except on a few key atolls. We compiled a global dataset of seabird surveys on atolls and modelled seabird distribution and nutrient deposition on all Indo-Pacific atolls. We found that atolls are breeding sites for 37 species, ranging from a few dozen to more than 3 million individuals per atoll. In total, an estimated 31.2 million seabirds nest on atolls, or ~25% of the tropical seabirds of the world. For 14 species, more than half of their global populations nest on atolls. Seabirds forage more than 10,000–100,000 km² around an atoll and deposit, on average, 65,000 kg N and 11,000 kg P per atoll per year, thus acting as major nutrient pumps within the tropical Indo-Pacific. Our findings reveal the global importance of atolls for tropical seabirds. Given global change, conservation will have to leverage atoll protection and restoration to preserve a relevant fraction of the tropical seabirds of the world.

Seabirds are globally important mediators of ecological connectivity between land and sea¹. They transport nutrients in the form of guano from marine feeding grounds to terrestrial nesting sites². Owing to their gregarious nature, seabirds can form large, dense nesting colonies in incredibly spatially confined areas, which causes significant eutrophication of both terrestrial and marine environments, thereby stimulating primary productivity on land and in coastal waters around seabird colonies³. Islands are global hotspots for seabird nesting⁴ and the intertwined ecology of islands and seabirds via their nutrient subsidization has long been recognized^{2,5}.

In the Indo-Pacific, about one-third of all islands, and the most numerous island type, are formed by atolls, yet the combined land area of all the emergent land area of atolls makes up only ~0.02% of the total land area of all Indo-Pacific islands⁶. Atolls are unique systems in that they integrate marine, terrestrial and freshwater components within one ecosystem, as they consist of a ring-shaped coral reef with

islands sitting atop the reef rim (hereafter referred to as atoll islands) which together enclose a shallow lagoon⁷. Given the transboundary nature of atolls, seabirds are uniquely relevant to the ecological functioning of atolls⁸. Through their nutrient inputs, seabirds on atolls support groundwater and soil nutrient enrichment of the otherwise impoverished island carbonate sediments^{9,10}, enable atoll phosphate rock mineralization processes¹¹, shape atoll vegetation succession and dynamics¹², catalyse terrestrial primary production¹³, boost plankton and fish biomass in the adjacent atoll reefs and lagoons^{14,15}, enhance coral growth rates¹⁶ and can even facilitate local feeding aggregations of large marine species such as manta rays around atolls¹⁷. Intact seabird colonies may even elevate resilience of atolls against climate change impacts^{18,19}.

Despite the relevance of seabirds for atolls, and the general prevalence of atolls as contributing a distinct island type of the Indo-Pacific, the collective contribution of atolls in providing nesting grounds for

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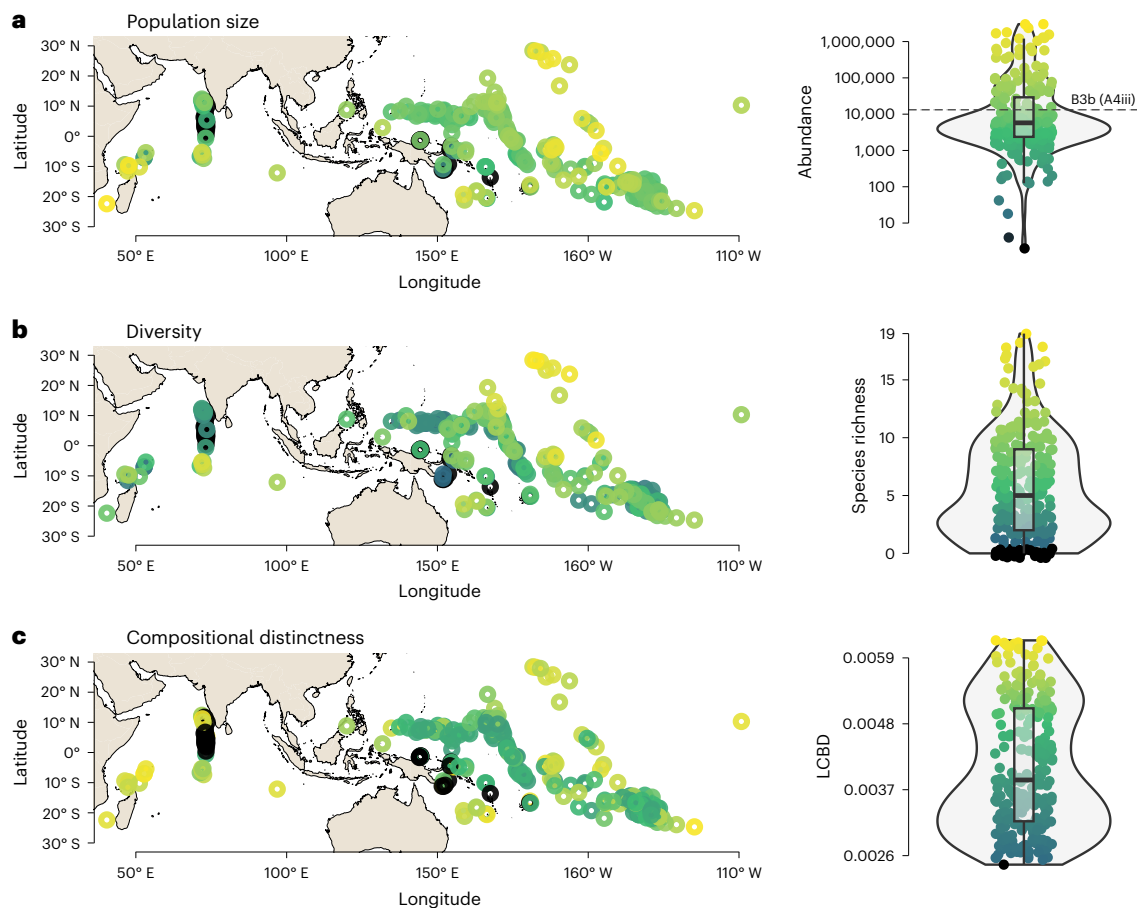


Fig. 1 | Seabird colonies on the 280 Indo-Pacific atolls. a–c, Total seabird colony size (a), seabird species richness (b) and compositional distinctness (LCBD score) (c). Around 26% of the Indo-Pacific atolls (74 atolls) host seabird nesting colonies above the BirdLife International threshold for significant bird areas B3b (formerly A4iii criteria; dashed horizontal line in boxplot for a²⁴). Each data point indicates the abundance for one atoll ($n = 280$). Boxplots on the

right of each panel show median, 5%, 25%, 75% and 95% quantiles of the seabird abundance (a), species richness (b) and compositional distinctness (c) per atoll and violin plot shows the underlying probability density distribution. Colour gradients in map plots on the left of each panel encode abundance (a), species richness (b) and compositional distinctness (c) for each atoll as indicated in the adjacent boxplots.

seabirds has remained largely neglected in global conservation and only recently been implied²⁰. This is a problematic knowledge gap and blind spot in both island and species conservation: atolls are at the forefront of climate change impacts, while seabirds are the most threatened bird group worldwide^{21,22}. Excluding atolls from global seabird assessments because of their small land areas, possibly perceived low ecological value or diminished stature relative to large volcanic islands²³ or simply because of scarce data, risks overlooking nascent opportunities and pressing conservation needs both for global species and ecosystem protection efforts.

In this study, we compiled a global dataset of seabird nesting surveys on atolls and modelled seabird nesting on all Indo-Pacific atolls (following published global inventorying and basin boundaries^{6,7}) using Bayesian predictive modelling. We assessed the global importance of atolls for seabirds by predicting current species richness and abundance of seabirds on all Indo-Pacific atolls and by quantifying how many of the tropical seabirds of the world are nesting on atolls. Additionally, we assessed the relevance of seabirds for atolls by quantifying seabird-driven nutrient transfers on a basin scale. By modelling seabird population sizes on atolls and their role as nutrient pumps to atoll islands and adjacent reefs, this study establishes a case for atolls as seabird nesting grounds of global importance. At the same time, it argues for seabird conservation on atolls to preserve their terrestrial and marine ecosystem services at a basin scale.

Results

The importance of atolls for seabirds

We compiled a global dataset of atoll-nesting seabird colonies comprising survey data (ranging from 1968 to 2023) for 199 of the 280 atolls of the Indo-Pacific. For 107 atolls, abundance-based nesting data were available, while for 92 atolls only presence-based nesting data were available. We used Bayesian models to predict seabird presence and breeding population size to generate a global map of seabird nesting on all Indo-Pacific atolls (see Supplementary Table 1 for an overview on the environmental variables used in the model).

Our analysis suggests that the 280 atolls of the Indo-Pacific serve as nesting sites for an estimated total of ~31.2 million seabirds (95% highest density interval (HDI): 28,100,317–42,059,815), comprising 37 different species. Nesting populations range from zero birds (on some Maldivian atolls) to >3 million birds per atoll, for example, Europa (Mozambique Channel) or Starbuck (Central Line Islands) (Fig. 1a). Notably, ~26% of the atolls (74 atolls) of the Indo-Pacific host seabird nesting populations above the threshold for Important Bird Areas (B3b, formerly A4iii)²⁴. Of these, only 55% (41 atolls) are recognized at present as Important Bird Areas under this evaluation criterion.

At least 46 atolls (~16% of all Indo-Pacific atolls) host a colony of a seabird species that constitutes >1% of the estimated global population size of the given species. Of those, 11 atolls host a colony that constitutes >10% of the estimated global population size of a seabird species and two atolls (Kiritimati and Midway) host colonies that constitute

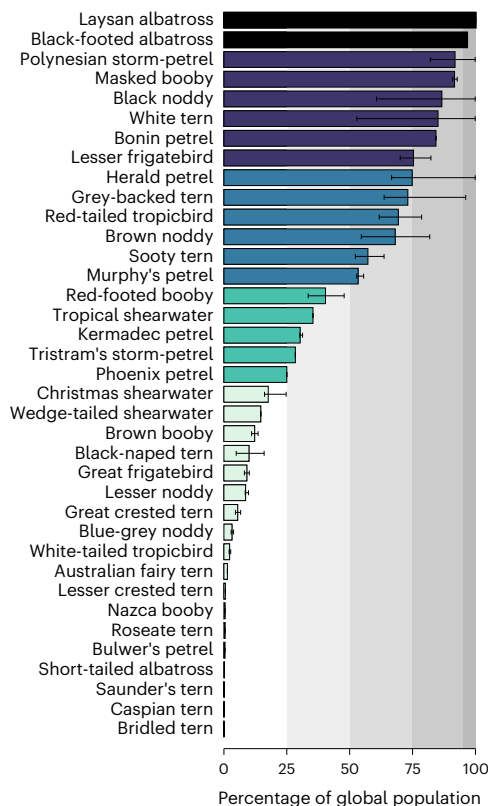


Fig. 2 | Percentage of the global population of seabird species found on atolls.

For each of the 37 atoll-nesting seabird species, the percentage of atoll-nesting birds is given based on global population size estimates from BirdLife International and Birds of the World (Supplementary Information Section 1). The colour code groups seabirds that have <25%, 25–50%, 50–75%, 75–95% and >95% (from light to dark blue, respectively) of their estimated global population nesting on atolls. Error bars indicate the 80% HDI of the predicted median total abundances across all ($n = 280$) atolls. Scientific names of all seabirds are provided in Supplementary Table 3.

>70% of the estimated global populations of these seabird species (Extended Data Fig. 1). Species richness on atolls with a seabird nesting population ranges from just a single species (for example, on some Lakshadweep atolls) to 19 species (Midway) (Fig. 1b). Community composition analysis identified several atolls that disproportionately contribute to beta-diversity (local contribution to beta-diversity, LCBD, a measure for the compositional dissimilarity between atolls). These are atolls that serve as breeding grounds for distinct seabird species assemblages, such as several petrel species only on Ducie and Oeno (Pitcairn Group) or two species of albatross only on northwestern Hawaiian atolls (Fig. 1c).

The biomass of all atoll-nesting seabirds combined totals 11,968,441 kg (95% HDI: 11,319,526–14,297,013), with an average seabird biomass of 40,628 kg per atoll (95% HDI: 39,351–55,125). Using bird biomass conversion factors²⁵, the total biomass of atoll-nesting seabirds translates to a seabird carbon stock of 4,188,955 kg C (95% HDI: 3,961,834–5,003,955) throughout all Indo-Pacific atolls or 14,220 kg C per atoll on average (95% HDI: 13,773–19,294).

We used global population assessments from BirdLife International and Birds of the World²⁶ for each of the 37 atoll-nesting seabird species to determine how much of their estimated global population size nests on atolls. For 19 seabird species, >25% of their world population is nesting on atolls. For 14 species, >50%; for 8 species, >75%; and for 2 species (the Black-footed and Laysan albatross), >95% of their estimated global population is nesting on atolls (Fig. 2). Only one of the 14 principal atoll-nesting seabird species (that is, species with >50%

of their estimated global population nesting on atolls), the Polynesian storm-petrel (*Nesofregatta fuliginosa*), is recognized by IUCN red list criteria as globally endangered²⁷. Black-footed albatross (*Phoebastria nigripes*) and Laysan albatross (*P. immutabilis*) are considered globally vulnerable under IUCN red list criteria, while the remainder of the principally atoll-nesting seabird species are ranked 'least concern'.

The importance of seabirds for atolls

By serving as nesting sites for ~31.2 million seabirds, our analysis reveals that atolls are of exceptional importance for seabirds on a global scale. Reciprocally, seabird colonies are also important for the functioning of atolls as nutrient importers. To assess the global contribution of seabirds for the nutrient dynamics on atolls, we quantified basin-wide nutrient deposition rates (nitrogen and phosphorous) using bioenergetic models^{4,28}.

Atoll seabird breeding colonies import on average 65,171 kg N (95% HDI: 63,125–86,345) and 10,862 kg P (95% HDI: 10,521–14,391) per year and per atoll in the form of guano during breeding season (Fig. 3a and Extended Data Fig. 2a). Within a seabird colony, albatross (*Phoebastria* spp.) and booby (*Sula* spp.) colonies contribute the most N and P per atoll during breeding (Fig. 3b and Extended Data Fig. 2b). However, albatross colonies and their ecosystem subsidizing role for atolls are nowadays mostly confined to the northwestern Hawaiian atolls (yet their historic distribution may have been more widespread across Pacific atolls²⁹). Migratory seabirds during non-breeding season and non-breeding roosting aggregations of resident species can add further nutrients to atolls³⁰, rendering our estimates conservative for the total seabird-driven nutrient inputs to atolls. We estimate the total combined nutrient transport by breeding seabirds across all 280 Indo-Pacific atolls to be 19,141,075 kg N (95% HDI: 18,215,028–22,113,859) and 3,190,179 kg P (95% HDI: 3,035,838–3,685,643) per year.

Seabird guano is rapidly volatilized as ammonia and enters the atmospheric nitrogen cycle, particularly under the hot and humid conditions of atolls⁴. The estimates from our model add up to a total annual ammonia emission from atoll seabird breeding colonies across the Indo-Pacific of 2,755,922 kg NH₃ yr⁻¹ (95% HDI: 2,622,902–3,148,449). Average annual guano-borne ammonia emissions are 9,387 kg NH₃ per atoll (95% HDI: 9,091–12,442) (Fig. 4).

Using published GPS-tracking data of atoll seabird species (Supplementary Table 4 gives data sources), we estimated foraging ranges over which seabirds take up nutrients during the breeding season and concentrate them on atoll ecosystems³¹. Depending on the species, seabirds forage as close as 2–3 km (*Sternula* spp. terns) or as far as 1,500 km (*Phoebastria* spp. albatross) around an atoll during breeding season. Nutrient inputs on most atolls are derived from seabirds foraging over a core area (50% highest density region) of 10,000–100,000 km² of ocean around an atoll during breeding seasons. For those atolls with large petrel, shearwater and/or albatross colonies (for example, Ducie, Midway and Oeno), the core nutrient uptake area can extend to 100,000–1,000,000 km² of ocean because of the bird species' wider foraging ranges (Fig. 4d). As the average atoll land area is 9.7 km² (minimum 0.02 km², maximum 388 km²), seabirds are spatially concentrating nutrients onto atolls by, at least, a factor of 1,000 (but possibly up to 10,000). Outside the breeding season, seabirds can migrate and forage over even larger areas before returning to an atoll for roosting³⁰, again rendering our reported results a conservative estimate of seabird-driven nutrient concentration on atolls.

Discussion

Oceanic islands are seabird hotspots and more than one-third of Indo-Pacific islands are formed by atolls⁶, yet the global contribution of atolls to sustaining tropical seabird populations has been historically neglected. Our model predicting seabird breeding colonies on all Indo-Pacific atolls indicates that atolls are globally important sites for seabirds. At present, an estimated 31.2 million seabirds are nesting on atolls. Given that known impacts of invasive species, habitat loss and

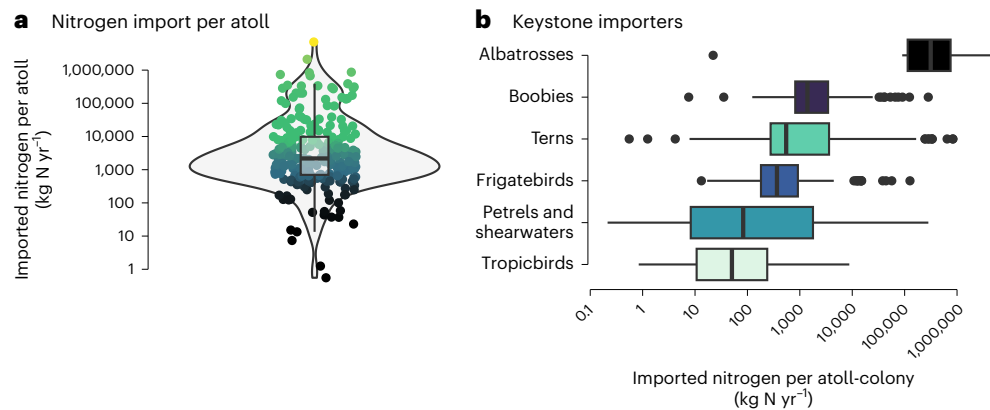


Fig. 3 | Seabird-derived nitrogen inputs on atolls. **a**, For each Indo-Pacific atoll ($n = 280$), the estimated breeding seabird-derived N input in kg N yr^{-1} is calculated using bioenergetic models. Each data point shows the N input for an atoll, with boxplots indicating the 5%, 25%, median, 75% and 95% quantiles and violin plot the underlying probability density distribution. **b**, For the six species groups of seabirds, the imported nitrogen per atoll-colony is presented. Boxplots indicate

the 5%, 25%, median, 75% and 95% quantiles of the N input per atoll and species. Atolls receive, on average, $>65,000 \text{ kg N yr}^{-1}$ from seabird breeding colonies but amounts vary greatly depending on the size of the atoll seabird colony. Albatross and booby colonies import the most N per atoll and year, on average. Phosphorous input rates are summarized in Extended Data Fig. 2.

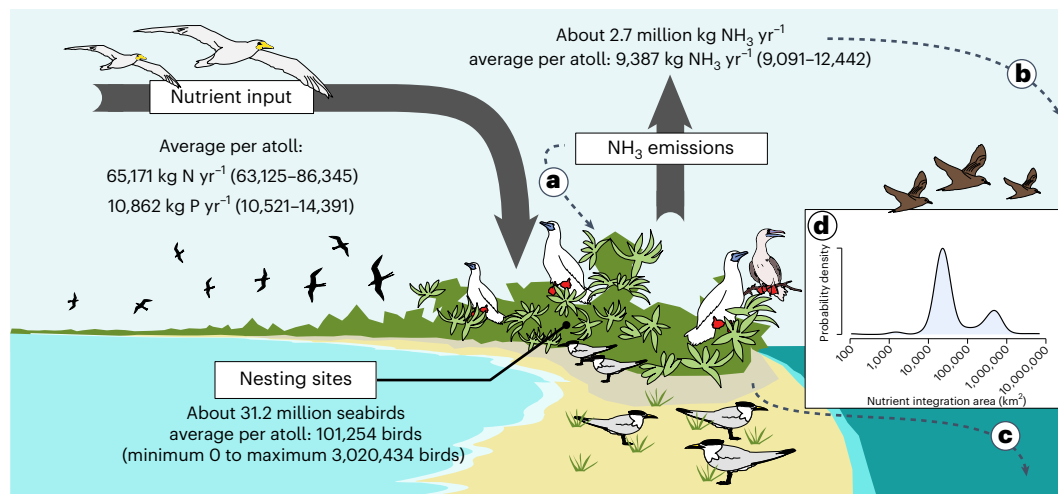


Fig. 4 | The reciprocal relationship between seabirds and atolls. All reported data in this schematic are based on the model outcomes of this study. Atolls provide nesting space for a total of ~ 31.2 million seabirds throughout the Indo-Pacific. Reciprocally, these seabirds are importing enormous quantities of nutrients in the form of guano into the atoll ecosystem, especially during breeding season, which they uptake from $>10,000$ – $100,000 \text{ km}^2$ of ocean around each atoll (inset diagram **(d)**) based on simulated foraging ranges;

see Results). Reactive nitrogen from guano is rapidly volatilized and enters the atmospheric nitrogen cycle as ammonia. **a, b**, Seabird nitrogen can either be directly re-incorporated into the atoll ecosystem via plant uptake¹⁰ (**a**) or atmospherically wet- or dry-deposited in the surrounding ocean in the form of ammonia⁵⁹ (**b**). **c**, In addition, surface run-off and groundwater discharge directly flush seabird-transported nutrients back into the nearshore reef ecosystem^{9,15}. Values are estimated averages per atoll and values in brackets are their 95% HDI.

human persecution are widespread in the Indo-Pacific, historic seabird numbers were logically far greater than our modern estimate. For 14 seabird species, the majority of their global populations are dependent on atolls as nesting grounds. The marine foraging behaviour of seabirds results in exceptionally large quantities of nutrients transported to, and concentrated on, atolls, with important basin-scale implications for nutrient dynamics in the oligotrophic tropical Indo-Pacific waters³².

Seabirds are globally the most threatened bird group yet are critical to ecosystem functioning^{3,22}. Therefore, global seabird distribution has been assessed repeatedly for conservation prioritization and management^{4,33,34}. Population models have estimated ~ 12.6 million seabirds across South America, ~ 30.5 million seabirds across Europe and ~ 73.9 million seabirds across North America⁴. Our analysis reveals that the Indo-Pacific atolls, home to ~ 31.2 million breeding seabirds, thus host about the same number of seabirds as Europe or about one-third of the total seabird population of North America⁴. Worldwide, there

exist an estimated 129 million seabirds in the tropical to subtropical regions (combining estimates for African, Atlantic, Indian Ocean, Middle Eastern, Pacific, Caribbean and Central American regions)⁴, suggesting that $\sim 25\%$ of the world's (sub)tropical seabirds are nesting on atolls. At the same time, the combined total land area of all 280 atolls equals only $2,750 \text{ km}^2$, about one-quarter of the land area of Hawaii's Big Island or $\sim 0.02\%$ of the total island land area across the Indo-Pacific basin⁶, emphasizing the extreme spatial intensity of seabirds occurring on atolls.

Our reported population sizes of seabirds on atolls represent conservative estimates. Especially for remote atolls that are difficult to access, published census data may have underestimated total seabird population sizes due to cryptic nesting behaviour, particularly in burrow-nesting petrel species. Similarly, GPS-tracking data for some atoll-nesting seabird species are scarce or have only been conducted on continental colonies, thus not capturing the full variation of at-sea

foraging ranges. Therefore, field research and ongoing surveying of seabird colonies on atolls remains a critical research endeavour for a comprehensive understanding of seabirds on atolls.

While atolls do not harbour many globally endangered or range-restricted seabird species, our analysis reveals that several common tropical seabirds have a major fraction of their global population nesting on atolls (Fig. 2). As atolls throughout the Indo-Pacific all face largely the same threats from global climate change (including increased cyclone frequencies, marine heatwaves and rising sea levels)²¹, many common Indo-Pacific seabird species thus may be considered globally vulnerable. For example, species such as the white tern (*Gygis alba*) or black noddy (*Anous minutus*) are ranked 'least concern' under IUCN criteria as they are widespread and abundant²⁷. However, our analysis suggests >75% of their global populations nest on atolls, meaning that the accelerating undermining of atoll island integrity from ongoing climate change could very quickly threaten the persistence of these seabird species³⁵. Additionally, our analysis revealed that at least 33 atolls that are currently unrecognized by conservation authorities may host seabird colonies above international thresholds for conservation (see Supplementary Information for list of atolls)²⁴. Field research to census atoll seabird colonies remains essential for establishing any legal protection. Our findings on the global importance of atolls for seabirds can help motivate such work, thereby supporting atoll conservation and restoration¹⁹.

The presence of large seabird colonies on atolls makes these systems focal nutrient sites of the Indo-Pacific, a phenomenon well-known historically which gave rise to the guano mining industry. Particularly during the nineteenth and twentieth centuries, up to 160,000 t of seabird guano were extracted from single atoll islands in just a few years³⁶. The nutrients that form these rich guano soils are being taken up by seabirds from >10,000–100,000 km² around each atoll. Our estimates suggest that an atoll receives on average 337 kg N per hectare land area per year (compared to the European Union's legal maximum of 220 kg N ha⁻¹ yr⁻¹ for farmland fertilization). However, given the strong spatial clustering of seabird colonies within atolls, the nutrient input loads are unevenly distributed over the land area of an atoll and thus significantly larger in nesting areas, reaching locally up to 1,500 kg N ha⁻¹ yr⁻¹ (ref. 10). Once deposited, the immediate area of influence where seabird-derived nutrients have been shown to cause measurable physiological effects on atolls is limited to just a few hundred metres offshore^{16,37}. However, under certain oceanographic enabling conditions, such as stationary eddy formations around atolls, seabird nutrients may be exported far offshore³⁸. These phenomena remain poorly studied but invite a critical re-evaluation, considering that atolls constitute major nutrient reservoirs within the otherwise oligotrophic tropical seas.

The imported nutrients on atolls from breeding seabirds are probably of basin-scale relevance for remote tropical oceanic nutrient dynamics³⁹. For example, our estimated total ammonia emissions from atoll seabird colonies of >2.7 million kg yr⁻¹ makes up as much as 40% of total Indo-Pacific-wide emission estimates from seabirds (~6.28 million kg)⁴⁰. Considering and including atolls and their large seabird breeding colonies in future analyses of oceanic nutrient dynamics is critical to achieve a more refined and realistic understanding of basin-wide nutrient dynamics, especially given the already well-established importance of seabird nutrient subsidies for nearshore marine systems^{14,15}. Relative to the major nitrogen and phosphorous contribution of seabirds to atolls, their average carbon biomass is only of minor importance for atoll ecosystem nutrient and energy budgets compared to terrestrial primary production and carbon above-ground biomass⁴¹.

Our reported seabird nutrient inputs to atolls must be considered only a conservative estimate of the total contribution of atolls to nutrient dynamics. Besides being seabird breeding sites, atolls also can be important roosting sites for migratory seabirds during their non-breeding season, which import additional nutrients to atolls³⁰. For

example, several seabird species ceased breeding in the Maldivian atolls due to intense anthropogenic disturbances, yet thousands of lesser noddies (*Anous tenuirostris*), as well as other tern species and frigatebirds, migrate annually to the Maldives during the non-breeding season where they use the islands for roosting⁴². Besides seabirds, atolls are also stopover or wintering grounds for migratory wader species, which bring additional, seasonally pulsed nutrient subsidies to atolls and further add to claims of atolls as important sites for bird conservation⁴³.

Together, our finding that tropical seabirds are nesting at globally important numbers on atolls should galvanize a critical re-evaluation of the present role and future potential of atolls for seabird conservation. Importantly, however, our analysis is only an assessment of present seabird population sizes on atolls under present-day conditions in which the survey data were collected. Atolls and their seabird colonies have experienced severe degradation from direct human poaching²⁹, destructive resource extraction practices such as guano mining³⁶, urbanization⁴⁴, monoculture crop plantations¹⁰ and invasive species introductions⁴⁵. Therefore, seabird colony sizes today are probably only a fraction of what would have been found historically on atolls⁴⁶. Addressing these local-scale impacts has the potential to amplify even further the global importance of atolls for seabirds. For example, one study from the Chagos archipelago estimated that clearing one of its atoll islands from invasive rats could result in an estimated 84-fold increase in seabird breeding numbers, with an additional potential 32-fold increase if copra monoculture plantations are restored to native atoll vegetation⁴⁷. These numbers give an indication of the extent of seabird loss attributable to two human impacts and the restoration potential for one atoll island; such an approach could be scaled globally to all atolls before copra plantations and invasive species were established, along with other anthropogenic impacts (for example, urbanization, intense local fishing pressures or direct seabird poaching). However, without reliable data quantifying these impacts across the entire Indo-Pacific, which do not exist at the moment, we caution against simple extrapolations of our estimated population sizes.

Many atoll islands that bear legacies of colonial exploitation are today uninhabited. Building on the here-established global importance of atolls for seabird conservation, these uninhabited atoll islands offer themselves as prime target sites for future seabird conservation and restoration initiatives. However, only 42 of the worldwide 998 documented vertebrate invasive species eradication operations have been conducted on atolls (DIISE, <http://diise.islandconservation.org/> last accessed 29 February 2024)⁴⁸. Furthermore, <10 of 851 active seabird restoration projects involving social attraction or conservation translocation have occurred on atolls (Seabird Restoration Database <https://www.seabirddatabase.org> last accessed 22 March 2024)⁴⁹. This under-representation of atolls in seabird conservation indicates an underused opportunity to remove invasive species permanently from what are some of the smallest, and therefore easiest, islands to manage.

Overall, our global analysis of seabird nesting colonies on atolls establishes a compelling case for atolls as underappreciated seabird nesting sites of global importance. Despite, or perhaps because of, their smallness, atolls are globally relevant to conservation as they offer tractable systems which allow implementing whole-ecosystem restoration actions that may not be feasible on continental or high-island settings. The protection of atolls against climate change impacts will need to become a priority for seabird conservation in the tropics. Through the protection and active restoration of seabirds on atolls, ecological cascades can be triggered that benefit wider atoll biodiversity on land and in coastal waters and may improve the resilience of atolls to climate change^{18,19}.

Methods

Data compilation

We compiled an Indo-Pacific database of seabird colonies on an atoll-level. For a list of references see Supplementary Information

Section 1. Seabird surveys were only included where authors indicated a complete assessment of all seabird species; records of just single species from atolls were excluded. We used the global atoll checklist⁷ for identifying all atolls that fall within the boundaries of the Indo-Pacific basin⁶. Even though our article refers to ‘Indo-Pacific atolls’, it is a comprehensive analysis of all atolls worldwide, with only one other atoll existing in the Atlantic (Rocas) that was not included for biogeographic reasons in our model framework⁷. Reef islands in the South China Sea, the Banda Sea and the Caribbean are sometimes also treated as atolls but were excluded from our analysis for falling outside the biogeographic boundaries of the Indo-Pacific basin and for resembling, in many cases, barrier reef islands instead of oceanic atolls in the Darwinian sense^{50,51}. These exclusions make our estimates more, rather than less, conservative.

For each atoll, we compiled a set of environmental and biogeographic variables that can be broadly grouped in four categories: oceanographic variables (net primary productivity, chlorophyll concentrations, phytoplankton concentrations, sea surface temperature and wave velocity), biogeographic variables (distance to nearest atoll, distance to nearest high island, distance to nearest continent, number of islands per atoll and total land area per atoll), environmental variables (annual rainfall) and disturbance variables (hurricane frequency, frequency of tropical storms, El Niño/Southern Oscillation (ENSO)-driven precipitation anomalies and human population size). These variables were chosen because they are known correlates of tropical seabird colonies (Supplementary Table 1 gives details on each variable)^{44,52,53}. Other known drivers of seabird occurrence on atolls, including invasive species, could not be directly included as covariates in the model framework. This is because invasive species are often present on only a subset of the islands within an atoll but seabird and invasive species data (where available) are typically only available at the atoll-level (and not island-within-atoll-level). Thus, it was not possible to account for within-atoll co-occurrence patterns of invasive species and seabirds. However, we included human population size per atoll as a covariate to our model framework, which is considered a reliable correlate with invasive species presence on islands⁵⁴.

The oceanographic variables were obtained from the EU Copernicus Marine Service Information data hub (<https://data.marine.copernicus.eu/products> last accessed 24 May 2023) and measured as 30-year long-term average at -100 km circumference around each atoll, measured from the geographic centre of the atoll. Biogeographic and environmental variables were compiled from literature data and distances measured in Google Earth 10.40.0.2. Disturbance variables were obtained from the Historical Hurricane Tracks database of the National Oceanic and Atmospheric Administration (NOAA) (<https://coast.noaa.gov/hurricanes/> last accessed 25 February 2023) and measured as 90-year cumulative sum at a 50 km polygon around each atoll. Data on ENSO-driven rainfall anomalies were obtained from the Global Precipitation Climatology Project of the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) (<http://research.jisao.washington.edu/data/gpcp/> last accessed 24 May 2023).

To approximate how much of the estimated global population size of each seabird species is nesting on atolls, we obtained global population estimates for each species from BirdLife International and Birds of the World²⁶.

Bayesian predictive model for seabird distribution on atolls

All statistical analysis was done in Julia programming language and the ‘Turing’ ecosystem for Bayesian modelling^{55,56}. Presence-based data on seabird nesting were available for 92 atolls and abundance-based for 107 atolls, while no data were available for the remaining 81 atolls. Atolls with missing data were relatively homogeneously distributed across the four main oceanic regions (Indian Ocean, 21; Melanesia, 14; Micronesia, 24; and Polynesia, 22; for a detailed analysis of missingness see Supplementary Figs. 1 and 2). We conducted a principal component

analysis (PCA) for the environmental variables (z-scoring variables to ensure equal weighting) to account for potential interactions and multicollinearity (Supplementary Fig. 3). We used the first six principal components for downstream modelling (cumulative explained variance 81.4%). We used a two-stage model to first predict the presence/absence and then the population sizes of each seabird species. Both the presence-based model and the abundance-based model use the same independent variables to model outcome (presence or abundance) of species *s* of nesting type *n* (burrow nesting, ground nesting and vegetation nesting²⁶) on atoll *a*, with environmental variables *E* (obtained from a PCA of the environmental variables using the first six principal components) in region *r* (Indian Ocean, Micronesia, Melanesia and Polynesia).

For predicting seabird presence, we fitted a Bayesian multilevel logistic regression model to presence/absence data from 199 surveyed atolls: let $Y_{asnr} \in \{0,1\}$, denote the presence of species *s* (*s* = 1, ..., *S*) of nesting type *n* (*N* ∈ {1,3}) on atoll *a* (*a* = 1, ..., *A*) with environmental variables E_{aj} (*j* ∈ {1,6}) where *j* is the index of the principal component, in region *r* (*R* ∈ {1,4}).

$$\begin{aligned}
 y_{asnr} &\sim \text{Bern}(P_{asnr}) \\
 \text{logit}(P_{asnr}) &= \beta_{0s[r]} + \beta_{1n[s]j} \times E_{aj} \\
 \beta_{0sr} &\sim \mathcal{N}(0, 1) \\
 \beta_{1nj} &\sim \mathcal{N}(\tilde{\beta}_{1nj}, \tau_{nj}) \\
 \tilde{\beta}_{1nj} &\sim \mathcal{N}(0, 0.2) \\
 \tau_{nj} &\sim \text{InvGamma}(3, 0.5)
 \end{aligned} \tag{1}$$

The tilde symbol means ‘distributed as’. The parameter β_{0sr} encodes the probability that species *s* occurs in region *r*, in which atoll *a* is located. The parameter β_{1nj} encodes how environmental variables of atoll *a* affect the probability that species *s* within a nesting type *n* occurs on atoll *a*. This effect is allowed to differ between nesting types, such that the probability that a ground-nesting species occurs on atoll *a* increases with some environmental variable, while the probability of a vegetation-nesting species may remain unaffected. By partially pooling species within nesting types, we express our assumption that species within the same nesting type *n* are similarly affected by certain environmental variables.

For predicting seabird population sizes, we specified a Bayesian multilevel model using the same value sets as above, as follows: let Y_{asnr} denote the log-transformed count of birds of species *s* of nesting type *n* on atoll *a* in region *r*.

$$\begin{aligned}
 y_{asnr} &\sim \mathcal{N}(\mu_{asnr}, \sigma) \\
 \mu_{asnr} &= \beta_{0s} + \beta_{1nj} \times E_{aj} \\
 \sigma &\sim \text{InvGamma}(3, \sqrt{2}) \\
 \beta_{0s} &\sim \mathcal{N}(\tilde{\beta}_{0s}, \tau_0) \\
 \beta_{1nj} &\sim \mathcal{N}(\tilde{\beta}_{1nj}, \tau_{nj}) \\
 \tilde{\beta}_{0s} &\sim \mathcal{N}(M_s, 1) \\
 \tilde{\beta}_{1nj} &\sim \mathcal{N}(0, 1) \\
 \tau_0 &\sim \text{InvGamma}(3, \sqrt{2}) \\
 \tau_{1nj} &\sim \text{InvGamma}(3, \sqrt{2})
 \end{aligned} \tag{2}$$

The parameter β_{0s} encodes the abundance of species *s* across regions, by nesting regional estimates within species. As such, $\tilde{\beta}_{0s}$ is the average abundance of species *s* across regions. The hyperparameter on τ_0 encodes the variation between regions across species. By partially pooling regions within species, we express our assumption that species *s* forms colonies of similar size across regions. This is unlike the

presence model, where the fixed effect β_{osr} prevents information flow between estimates for species s for different regions.

The parameter β_{inj} encodes how environmental variables affect the abundance of species within a nesting type. This effect is allowed to differ between nesting types, such that the abundance of a ground-nesting species may be positively related to some environmental variables, while the abundance of a vegetation-nesting species may be negatively related. By partially pooling species within nesting types, we express our assumption that species from the same nesting type n_i are similarly affected by certain environmental variables. For more extensive details on model parameters and hyperparameters, see Supplementary Table 2.

We validated model outcomes using standard Bayesian diagnostics, leave-one-out cross-validation and out-of-sample validation, and computed prior predictive checks, prior sensitivity analyses and posterior predictive checks (Supplementary Figs. 4–9 provide details on model validation). The final models were computed using weakly informative priors, which act as soft constraints on our parameters, thus allowing us to keep model inference stable in the overall sparse data situation.

We summarized total seabird population sizes and species richness per atoll and computed the LCBF metric for each atoll using the ‘adespatial’ package in R v.3.4.1 (ref. 57). LCBF is a comparative measure for how much a given site contributes to the total beta-diversity and can be interpreted as the compositional distinctness of seabird assemblages on atolls.

Annual nutrient inputs

Annual nitrogen and phosphorous inputs were calculated using bio-energetic models^{4,28}. Body weight measurements for each seabird species were obtained from the AVONET global bird trait database⁵⁸. Total excreted nitrogen or phosphorous were calculated using

$$N(\text{or } P)_{\text{excr}} = \frac{9.2M^{0.774}}{F_{\text{EC}}A_{\text{eff}}}F_{\text{NC(or PC)}} \quad (3)$$

M is the body mass per bird (in g), F_{EC} the energy content of seabird diets (in kJ g^{-1}), A_{eff} the assimilation of food (in kJ kJ^{-1}) and F_{NC} or F_{PC} , respectively, are the nitrogen or phosphorous content of the food (in g N or g P g^{-1} wet mass). Values were taken from published literature data⁴. Calculated amounts of excreted nitrogen and phosphorous were adjusted for length of breeding period for each species, its attendance time at the colony during breeding and nesting behaviour (burrow nesting, ground nesting and vegetation nesting)²⁸. We also incorporated seabird chick excretion rates using the above equation, adjusted for chick attendance time, body mass of chick at fledging and the number of chicks per breeding pair, using published literature data⁴.

As seabird nesting colonies are usually confined to just a subset of the islands of an atoll, the calculated nutrient inputs are unevenly concentrated to just a few of the sometimes hundreds of islands of an atoll⁵¹. However, because island-level data on seabird colony distribution were not available in most data sources, we could not further adjust nutrient input quantities to colony 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.

Ammonia emissions were calculated using the mass ratio of 17/14 of NH_3 to nitrogen and assuming a volatilization rate of 0.7 based on literature values from in situ measurements on Indo-Pacific reef islands⁵⁹. The conversion of total seabird biomass to carbon stock was calculated using biomass conversion factors in ref. 25, which approximates carbon content assuming 70% water content of bird biomass and 50% carbon content of bird dry weight.

Seabird foraging ranges around atolls

While the land areas of atolls generally do not exceed a few hundred to thousand hectares, seabirds are foraging over vast areas of open

ocean even during the breeding season, meaning that seabirds are greatly transporting and concentrating pelagic nutrients into the atoll ecosystem. To approximate by how much marine nutrients are being concentrated onto atolls, we estimated seabird foraging areas around each atoll on the basis of the predicted seabird colony sizes and available seabird foraging data. Data on maximum and mean seabird foraging ranges were obtained from published GPS-tracking studies (Supplementary Information Section 1 gives list of data sources). We only included studies that tracked seabird foraging during nesting season. For each seabird species, we used the mean maximum foraging distance and reported variabilities (standard deviations) to simulate foraging distance under a Gaussian distribution, assuming no biased directionality of each simulated foraging trip. This foraging radii method is a pragmatic, yet generally robust, method for assessing seabird foraging distribution around nesting colonies^{31,60}. We then calculated the 50% highest density region around each atoll where its seabird colony forages during the breeding season and calculated the ratio between pelagic foraging range of the seabird community and total land area (in km^2) of each given atoll.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All raw data can be accessed under <https://doi.org/10.5281/zenodo.12622076> (ref. 61). Marine data were obtained from EU Copernicus Marine Service Information (<https://data.marine.copernicus.eu/products> last accessed 24 May 2023). Tropical cyclone and storm data were obtained from the Historical Hurricane Tracks database of NOAA (<https://coast.noaa.gov/hurricanes/> last accessed 25 Feb 2023). Data on ENSO-driven rainfall anomalies were obtained from the Global Precipitation Climatology Project of JISAO (<http://research.jisao.washington.edu/data/gpcp/> last accessed 24 May 2023). Seabird trait data were from the AVONET trait database (<https://opentraits.org/datasets/avonet> last accessed 1 December 2023).

Code availability

All statistical code can be accessed from <https://doi.org/10.5281/zenodo.12622076> (ref. 61).

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Author contributions

S. Steibl and S. Steiger designed the study and conducted the model development and data analysis. S. Steibl compiled the datasets. All authors contributed to the interpretation, writing and proofing of the manuscript and have agreed to the submission of the final version.

Competing interests

The authors declare no competing interests.

Additional information

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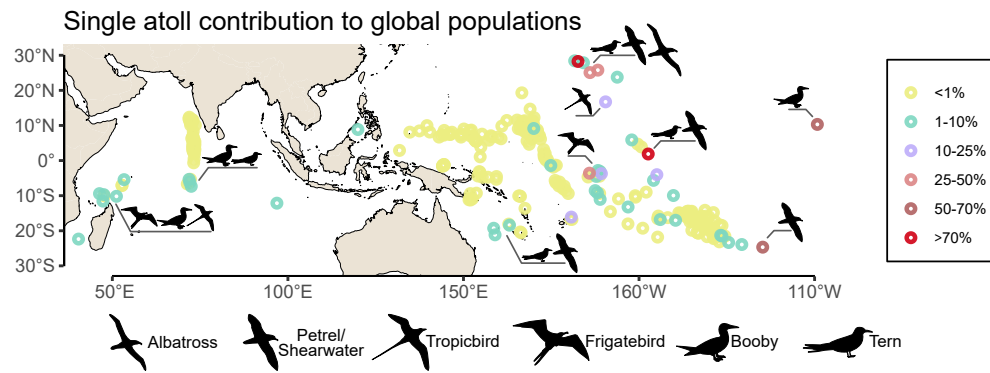
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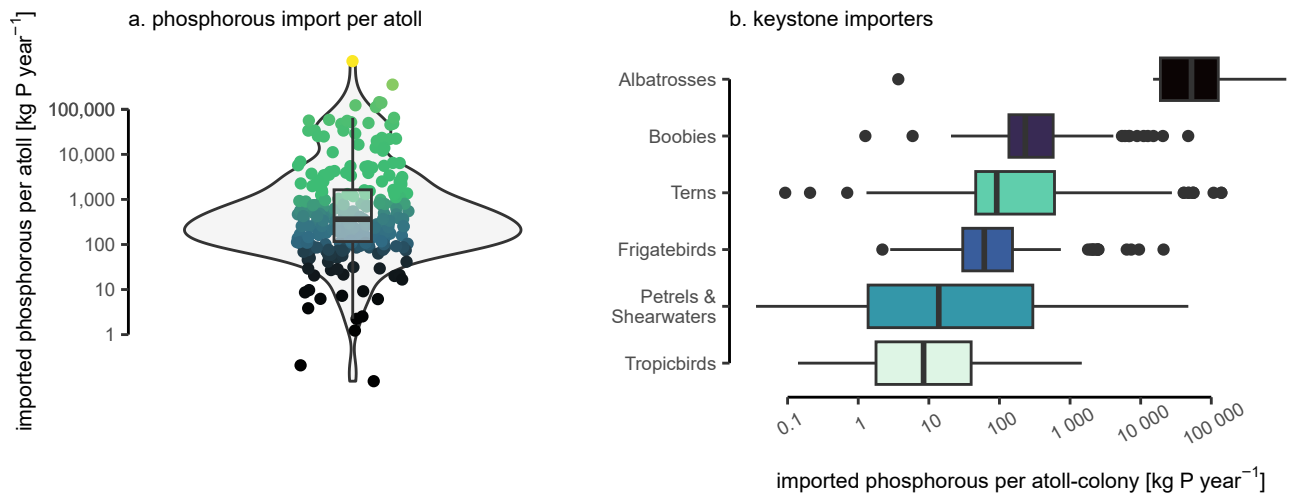
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Extended Data Fig. 1 | Atoll contribution to global seabird populations. Colour code indicates which atolls host a colony of a seabird species that constitutes >1% of the estimated global population of this species. Bird icons indicate to which taxonomic group the species on a given atoll belongs to (albatross, boobies, frigatebirds, petrel/shearwater, tern, tropicbird).



Extended Data Fig. 2 | Seabird-driven phosphorous input on atolls. For each Indo-Pacific atoll ($n = 280$), the estimated breeding seabird-derived phosphorous input in kg P per year is calculated using bioenergetic models (a). Each data point shows the P input for an atoll, with boxplots indicating the 5%, 25%, median,

75%, and 95% quantiles, and violin plot the underlying probability density distribution. For the six species groups of seabirds, the imported phosphorous per atoll-colony is presented (b). Boxplots indicate the 5%, 25%, median, 75%, and 95% quantiles of the P input per atoll and species.

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Software and code

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Data collection

No field data collection was conducted.

Data analysis

All data extractions and statistical analyses were done using the Julia programming language (<https://julialang.org/>). The Bayesian predictive modelling was done using the 'Turing' package in Julia version 1.10.3 (<https://turing.ml/>). Data summary and visualization were created in R version 4.3.1., using the package 'adespatial' for diversity analysis (<https://www.r-project.org/>). All raw data and statistical code can be accessed via Github using <https://doi.org/10.5281/zenodo.12622076>

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Seabird nesting were collected from literature reports; atoll biogeography data obtained from Google Earth version 10.40.0.2 (<https://earth.google.com>); marine data obtained from Copernicus Marine Services (<https://data.marine.copernicus.eu/products/>); storm and hurricane data obtained from NOAA Hurricane Tracks database (<https://coast.noaa.gov/hurricanes/>); rainfall anomaly data from JISAO database (<https://research.jisao.washington.edu/>); seabird morphological traits data obtained from the AVONET trait database (<https://opentraits.org/datasets/avonet.html>).

All compiled and generated raw data for this study can be accessed via GitHub under <https://doi.org/10.5281/zenodo.12622076>.

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Study description	We compiled a novel global dataset on atoll seabird nesting distribution and used environmental data on the atoll-level (incl. biogeographic parameters, terrestrial and marine environment parameters, disturbance parameters, and human population sizes per atoll) to model and predict the seabird nesting species richness and population sizes on all atolls of the Indo-Pacific.
Research sample	Seabird nesting data were collected from published literature reports. A detailed list of references for each atoll can be found in the supplementary file accompanying the publication. Atoll biogeographic and environmental data were collected from published literature reports, Google Earth, Copernicus Marine Services, NOAA Hurricane Tracks database, and JISAO. The raw datasets and summary of results can be accessed via GitHub using https://doi.org/10.5281/zenodo.12622076 .
Sampling strategy	Not applicable.
Data collection	Data collection was done by S. Steibl and S. Steiger using the above described databases and code written in Julia to extract and convert data tables (accessible in the statistical code, see GitHub: https://doi.org/10.5281/zenodo.12622076).
Timing and spatial scale	Not applicable.
Data exclusions	Only seabird nesting data was included, where authors indicated a full reporting of seabird nesting. Accidental sightings were excluded. If more than one report was available for an atoll, we used the most recent seabird nesting survey.
Reproducibility	The entire analysis can be fully reproduced using datasets and statistical code under the following GitHub link: https://doi.org/10.5281/zenodo.12622076

Randomization

Blinding

Did the study involve field work? Yes No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involvement
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology and archaeology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data
<input checked="" type="checkbox"/>	<input type="checkbox"/> Dual use research of concern
<input checked="" type="checkbox"/>	<input type="checkbox"/> Plants

Methods

n/a	Involvement
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging

Plants

Seed stocks

Novel plant genotypes

Authentication