

Seabirds enhance coral reef productivity and functioning in the absence of invasive rats

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Biotic connectivity between ecosystems can provide major transport of organic matter and nutrients, influencing ecosystem structure and productivity¹, yet the implications are poorly understood owing to human disruptions of natural flows². When abundant, seabirds feeding in the open ocean transport large quantities of nutrients onto islands, enhancing the productivity of island fauna and flora^{3,4}. Whether leaching of these nutrients back into the sea influences the productivity, structure and functioning of adjacent coral reef ecosystems is not known. Here we address this question using a rare natural experiment in the Chagos Archipelago, in which some islands are rat-infested and others are rat-free. We found that seabird densities and nitrogen deposition rates are 760 and 251 times higher, respectively, on islands where humans have not introduced rats. Consequently, rat-free islands had substantially higher nitrogen stable isotope ($\delta^{15}\text{N}$) values in soils and shrubs, reflecting pelagic nutrient sources. These higher values of $\delta^{15}\text{N}$ were also apparent in macroalgae, filter-feeding sponges, turf algae and fish on adjacent coral reefs. Herbivorous damselfish on reefs adjacent to the rat-free islands grew faster, and fish communities had higher biomass across trophic feeding groups, with 48% greater overall biomass. Rates of two critical ecosystem functions, grazing and bioerosion, were 3.2 and 3.8 times higher, respectively, adjacent to rat-free islands. Collectively, these results reveal how rat introductions disrupt nutrient flows among pelagic, island and coral reef ecosystems. Thus, rat eradication on oceanic islands should be a high conservation priority as it is likely to benefit terrestrial ecosystems and enhance coral reef productivity and functioning by restoring seabird-derived nutrient subsidies from large areas of ocean.

The flow of organic matter and nutrients among ecosystems is a major determinant of productivity, composition and functioning. Animals, such as moose⁵, salmon⁶ and sea turtles⁷, can connect ecosystems by vectoring organic matter and nutrients between them. However, the magnitude and implications of these natural dynamics are poorly understood in contemporary ecosystems in which humans have disrupted connectivity by creating barriers such as dams, removing biomass and introducing predators^{2,8}. Seabirds are globally important drivers of nutrient cycling⁹, transferring nutrients from their pelagic feeding grounds to islands on which they roost and breed^{1,10}. This input of nutrient-rich guano increases plant biomass, alters species compositions of island plants, and enhances the abundance of many types of biota^{3,4}. Nutrients can leach from guano to adjacent marine systems, which may bolster plankton densities and influence feeding behaviour of manta rays^{11,12}. However, the effects of seabird-transported nutrients on the productivity, structure, and function of highly diverse coral reefs are currently unknown. Understanding natural nutrient connectivity is particularly important, yet challenging, because invasive predators such as rats and foxes have decimated seabird populations within 90% of the world's temperate and tropical island groups⁸.

Here we isolate the effects of seabird-derived nutrients on adjacent coral reefs using a rare, large-scale natural experiment in which some

islands in a remote coral reef archipelago are rat-infested, whereas others are rat-free. The northern atolls of the Chagos Archipelago, located in the central Indian Ocean, have been uninhabited by people for over 40 years, are protected from fishing, and host some of the world's most pristine marine environments¹³. Black rats (*Rattus rattus*) are thought to have been introduced to the archipelago in the late 18th and early 19th centuries, but owing to patterns of human habitation and movement, are not present on all islands. We use this unique scenario and a mixed-methods approach to investigate nutrient flux between oceanic, island, and coral reef ecosystems.

We studied six rat-free and six rat-infested islands, selected to be otherwise similar in terms of size, location and environment. Rats are known to predate upon bird eggs, chicks, and occasionally adults, decimating populations where they have been introduced⁸. Mean seabird density, averaged across a six-year period (Methods 'Seabird surveys'), on rat-free islands was 760 times greater than on rat-infested islands (Fig. 1a; 1,243 birds per ha rat-free, 1.6 birds per ha rat-infested). Owing to the high seabird densities on some islands, the Chagos Archipelago has ten Important Bird and Biodiversity Areas¹⁴. The biomass of 14 bird species within six families varied among islands, with terns and noddies contributing the most biomass, and boobies, shearwaters and frigate birds only common on some islands. Biomass of all species was greatest on rat-free islands (Fig. 1b).

We used species-specific abundance, body size-scaled defecation rate, nitrogen content of guano¹⁵, and mean residence times on the islands to estimate mean nitrogen input by the seabirds (Methods 'Seabird surveys'). The nitrogen input by seabirds per hectare of island was 251 times greater on rat-free islands than on rat-infested islands (Fig. 1c; 190 kg ha⁻¹yr⁻¹ rat-free, 0.8 kg ha⁻¹yr⁻¹ rat-infested). The nutrient input onto rat-free islands is comparable to nitrogen inputs by seabirds at the isolated Palmyra atoll in the Pacific Ocean¹⁵. We did not calculate nutrient input from rats as they are recycling nutrients already present on the islands. By contrast, the majority of the seabirds feed in the open ocean, substantial distances from reefs (Extended Data Table 1). By foraging offshore, seabirds feed from food webs supported by net primary production that is estimated to be 2–5 orders of magnitude higher than net primary production on adjacent coral reefs (Methods and Extended Data Fig. 1). Their capacity to access these oceanic prey resources leads to substantial deposition of oceanic nitrogen that would otherwise be unavailable on rat-free islands.

We used the abundance of nitrogen and stable isotopes (reported as δ values for the ratio of $^{15}\text{N}:^{14}\text{N}$ ($\delta^{15}\text{N}$)) to understand the uptake of nutrients on islands and in adjacent coral reef ecosystems (Methods 'Isotope sampling' and Fig. 2). Total nitrogen and $\delta^{15}\text{N}$ were strongly and positively correlated ($r = 0.96$), meaning that they show similar patterns in our samples. Soils on rat-free islands were enriched in ^{15}N , with $\delta^{15}\text{N}$ being 3.8 times higher than on rat-infested islands and comparable to reported values for seabird guano¹⁶ (Fig. 2b). Substantially greater $\delta^{15}\text{N}$ was also evident in new growth leaves of a coastal plant

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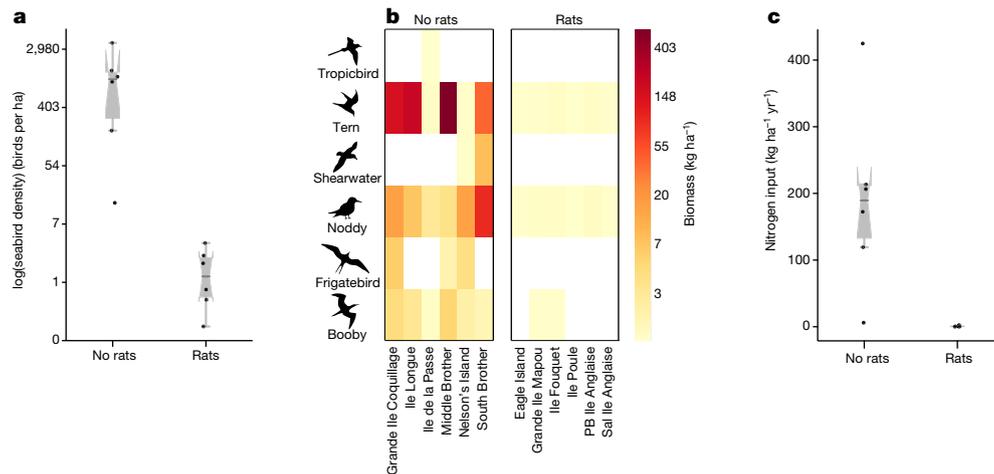


Fig. 1 | Seabird densities, biomass and nitrogen input to islands with and without rats in the Chagos Archipelago. **a**, Seabird density on rat-free ($n = 6$) and rat-infested ($n = 6$) islands. **b**, Heat maps of seabird biomass per family, on each island. Tropicbird: *Phaethon lepturus*; tern: *Thalasseus bergii*, *Sterna sumatrana*, *Sterna dougallii*, *Onychoprion fuscatus*, *Onychoprion anaethetus*, *Gygis alba*; shearwater: *Puffinus bailloni nicolae*, *Ardenna pacifica*; noddy: *Anous tenuirostris*, *Anous stolidus*; frigatebird: *Fregata* spp.; booby: *Sula sula*, *Sula leucogaster*.

PB, Peros Banhos atoll; Sal, Salomon atoll. **c**, Nitrogen input by seabirds per hectare for rat-free ($n = 6$) and rat-infested ($n = 6$) islands. **a**, **c**, Notched box plots, in which the horizontal line is the median, box height depicts the interquartile range, whiskers represent 95% quantiles, and diagonal notches illustrate approximate 95% confidence intervals around the median. Estimated net rat effects (median and 95% highest posterior density intervals) are: **a**, 456 [22, 6393] birds per ha; **b**, 195 [184, 207] kg ha⁻¹ (total biomass) and **c**, 148 [81, 211] kg ha⁻¹yr⁻¹.

(*Scaevola taccada*) on rat-free islands (Fig. 2c), indicating uptake of oceanic-derived nutrients by island vegetation.

Nitrogen is expected to leach off islands to nearshore marine environments through rainfall and coastal advection¹¹. On the reef flat (approximately 1 m deep and 100 m from the shore) filter-feeding sponges (*Spheciospongia* sp.; Fig. 1d) and macroalgae (*Halimeda* sp.; Fig. 1e) had substantially higher $\delta^{15}\text{N}$ values near rat-free islands, although differences were smaller than observed for island soils and vegetation. This is consistent with findings of higher $\delta^{15}\text{N}$ values in corals closer to seabird colonies in New Caledonia¹⁷. On the reef crest (approximately 3 m deep and 230 ± 55 m (mean \pm s.d.) from island shorelines) $\delta^{15}\text{N}$ was substantially higher in turf algae and the muscle of herbivorous damselfish (*Plectroglyphidodon lacrymatus*) adjacent to rat-free islands (Fig. 2f, g). While recognizing the influence of trophic fractionation on $\delta^{15}\text{N}$ signatures, the relative depletion of the heavy isotope ^{15}N from the soils on rat-free islands across to the reef crests,

compared to the relatively stable values for rat-infested islands, provides strong evidence of seabird-vectored nutrient enrichment propagating out onto adjacent coral reefs. The diminishing effect sizes from the islands out to the reef crest probably reflect a range of processes, including uptake and conversion of nitrogen by micro- and macroorganisms across the reef flat¹⁸.

Comparison of damselfish growth on reef crests (using growth bands in otoliths; Methods ‘Fish growth’) demonstrated that individuals adjacent to rat-free islands were growing significantly faster towards their maximum expected size ($K_r - K = -0.10 [-0.18, -0.04]$ (95% highest posterior density intervals), net rat effect), and were larger for a given age than individuals on reefs adjacent to rat-infested islands (Fig. 3). This is the first evidence, to our knowledge, for seabird-vectored nutrient subsidies propagating through the food web to accelerate the growth of a marine vertebrate. Given the diversity and high biomass of fishes that feed on benthic algae on coral reefs¹⁹, this finding is likely to

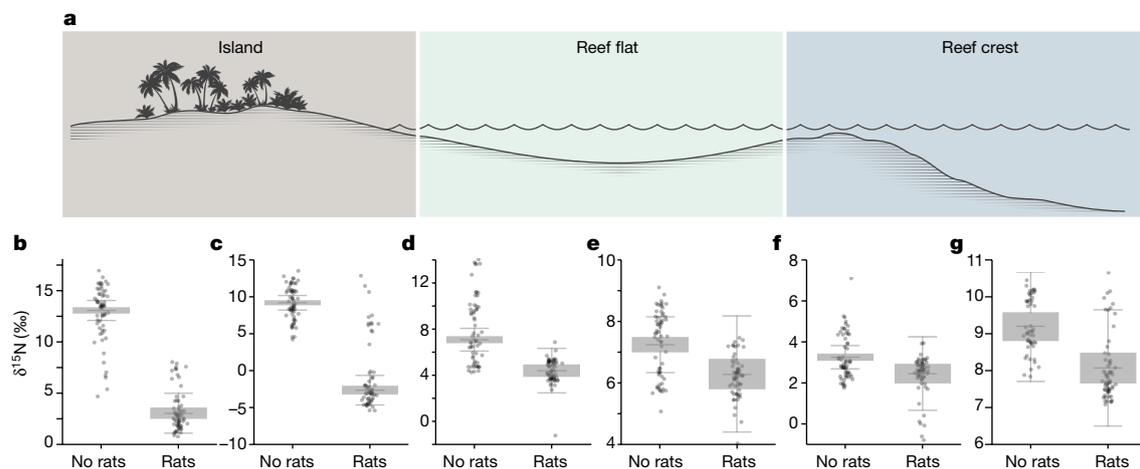


Fig. 2 | Nitrogen isotope signals from islands to reefs in the presence and absence of invasive rats. **a**, Schematic of study system. **b–g**, $\delta^{15}\text{N}$ values for soil (b) and new growth leaves (*S. taccada*) on islands (c), filter feeding sponges (*Spheciospongia* sp.) (d) and macroalgae (*Halimeda* sp.) on reef flats (e), and turf algae (f) and dorsal muscle tissue of damselfish (*P. lacrymatus*) on reef crests (g). For all groups 120 samples were collected, except for g, for which 110 samples were collected (Methods

‘Isotope sampling’). **b–g**, For box plots, the horizontal line is the median, box height depicts first and third quartiles and whiskers represent the 95th percentile. Net rat effect (median [95% highest posterior density]) and the probability of the effect being less than zero ($P(\text{neg})$) estimates are: **b**, $-9.9 [-11.3, -8.4]$, $P(\text{neg}) > 0.99$; **c**, $-11.8 [-13.2, -10.2]$, $P(\text{neg}) > 0.99$; **d**, $-1.0 [-2.3, 0.5]$, $P(\text{neg}) = 0.92$; **e**, $-2.7 [-4.1, -1.23]$, $P(\text{neg}) > 0.99$; **f**, $-0.8 [-2.23, 0.6]$, $P(\text{neg}) = 0.90$; **g**, $-1.1 [-2.5, 0.3]$, $P(\text{neg}) = 0.94$.

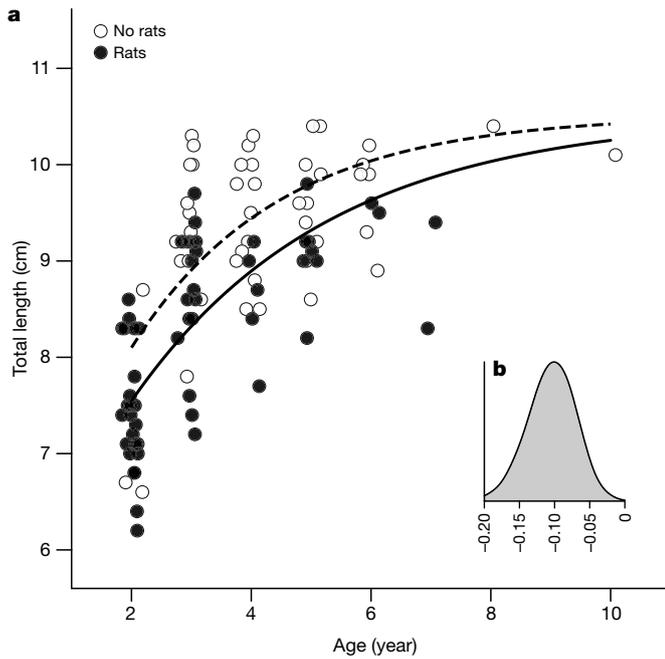


Fig. 3 | Growth of herbivorous damselfish on coral reefs adjacent to islands with and without rats. **a**, Age-by-length curves for *P. lacrymatus* on rat-free (open circles) and rat-infested (closed circles) islands. **b**, Effect-size posterior density for the difference between the growth parameter, K (Yr^{-1}), on rat-free compared to rat-infested islands. $n = 48$ and $n = 58$ biologically independent samples for rat-free and rat-infested islands, respectively.

indicate higher fish production adjacent to seabird-dominated islands with repercussions for the production of their predators.

To assess the influence of seabird colonies on reef-fish biomass production, we surveyed fish communities along the reef crests of the islands (Methods ‘Fish biomass and function’). Total biomass of the reef-fish community was 48% greater adjacent to rat-free islands.

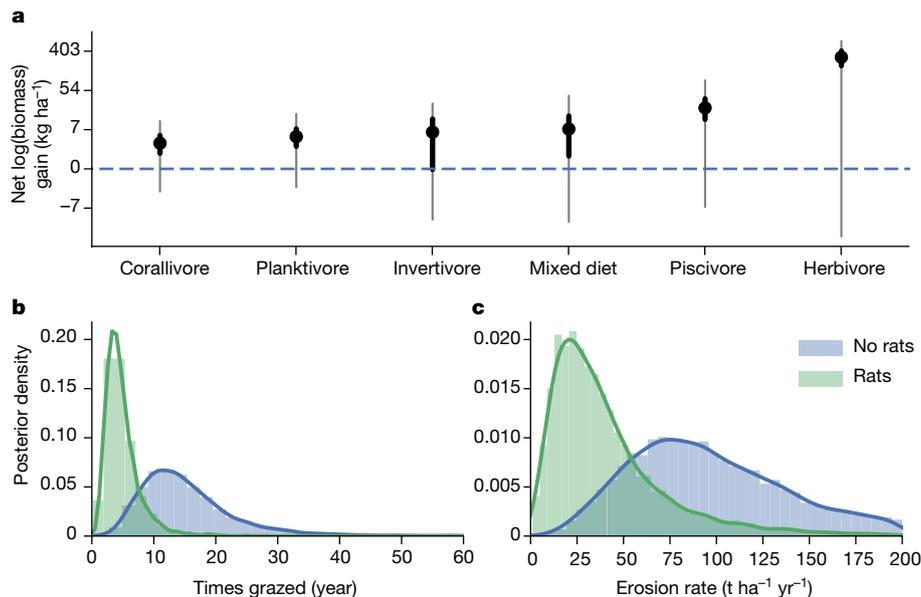


Fig. 4 | Biomass and functioning of reef-fish communities adjacent to islands with and without rats. **a**, Effect-size plots from a hierarchical Bayesian analysis of fish biomass for different feeding groups between rat-free and rat-infested islands. $n = 24$ biologically independent surveys for rat-free and rat-infested islands. Circles represent means and black and grey bars represent 50% and 95% uncertainty intervals, respectively

Assigning the 123 species of reef fish recorded into feeding groups, we found biomass to be greater for all feeding groups of fish on reefs adjacent to rat-free islands, with herbivore biomass having the largest effect size (93% of posterior distribution above zero; Fig. 4a). These results are consistent with seabird-vectored nutrients subsidising the entire ecosystem.

Herbivorous fish are functionally important on coral reefs, maintaining a healthy balance between corals and algae, and clearing space for coral settlement²⁰. Parrotfishes are among the most abundant and important herbivorous groups, providing unique grazing and bioerosion functions. We estimated grazing and bioerosion rates of parrotfishes for each island using density data, along with species- and body size-specific information on consumption rates²¹ (Methods ‘Fish biomass and function’). Reef crests adjacent to rat-free islands are fully grazed nine times a year, compared to 2.8 times for rat-infested islands (median values; Fig. 4b; $\text{grazing}_{\text{rats}} - \text{grazing}_{\text{no rats}} = -1.18 [-2.24, -0.11]$, net rat effect). Although variable, median bioerosion rates were 94 tonnes $\text{ha}^{-1} \text{yr}^{-1}$ adjacent to rat-free islands, 3.8 times higher than the 24.5 tonnes $\text{ha}^{-1} \text{yr}^{-1}$ adjacent to rat-infested islands (Fig. 4c; $\text{erosion}_{\text{rats}} - \text{erosion}_{\text{no rats}} = -1.06 [-2.77, 0.53]$, net rat effect). Bioerosion is critical for breaking down dead reef corals between major disturbance events to provide stable substratum for new coral growth and recovery²⁰, and for providing sand to maintain island growth in low lying atolls²². While some bioeroding parrotfishes can take bites from corals, coral cover was not lower on rat-free islands (coral cover rat-free = $26.3\% \pm 5.2$ (mean \pm s.e.m.); rat-infested = 28.2 ± 5.5). These data are consistent with seabirds on rat-free islands enhancing key ecosystem functions on coral reefs.

Following our surveys, coral reefs of the Chagos Archipelago lost approximately 75% coral cover in the 2016 El Niño-driven mass coral-bleaching event²³. It is possible that corals surrounding rat-free islands will show greater resilience to this event than corals adjacent to rat-infested islands, for two key reasons. First, in contrast to nutrient inputs from anthropogenic sources, nutrient delivery from biological sources, such as fish and seabirds, is rich in phosphorus^{3,24} and this has been shown to enhance coral thermo-tolerance²⁵ and coral calcification rates²⁴. Second, greater grazing rates, as observed on reefs adjacent to rat-free islands, is a key determinant of reef recovery²⁶.

Here, we show that seabird nutrient subsidies stimulate coral reef ecosystems, reflecting natural productivity and functioning in the absence of introduced rats. Oceanic coral reefs, such as those in the Chagos Archipelago, are highly productive ecosystems in an oligotrophic environment, the mechanisms of which have intrigued scientists for decades²⁷. Seabird-vectored nutrient subsidies are clearly a major pathway through which this productivity is supported, and such subsidies should be considered in the design and analyses of coral reef surveys adjacent to oceanic islands.

Rat eradication has been successful on 580 islands worldwide, and although success rates are slightly lower for tropical islands (89%) compared to temperate (96.5%), new techniques and guidelines are expected to close this gap²⁸. As eradication of rats from islands can lead to immigration and positive growth rates of seabird populations²⁹, rat removal should be a conservation priority for coral reef islands. The return of seabirds would benefit not only the island ecosystem, but also adjacent nearshore marine ecosystems. In a time of unprecedented threats to coral reefs from climate change³⁰, enhancing productivity and key ecosystem functions will give reefs the best possible chance to resist and recover from future disturbances.

Online content

Any Methods, including any statements of data availability and Nature Research reporting summaries, along with any additional references and Source Data files, are available in the online version of the paper at <https://doi.org/10.1038/s41586-018-0202-3>.

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Competing interests The authors declare no competing interests.

Additional information

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METHODS

Study sites. The Chagos Archipelago (British Indian Ocean Territory) is situated in the central Indian Ocean, due south of the Maldives (5° 50' S, 72° 00' E). The archipelago was first discovered in the early 16th century, but was not settled until the 18th century, after which rats were inadvertently introduced to some islands of the territory³¹. In the early 1970s the British government established a lease of the southernmost atoll (Diego Garcia) to the US Navy for a military base, and resettled the Chagossian people in Mauritius, Seychelles, and the UK. Since that time, the atolls of the northern archipelago have had very few direct human influences³², with exceptionally high reef-fish biomass³³, very low levels of water pollution³⁴, and there are currently ten designated (two more proposed) Important Bird and Biodiversity Areas¹⁴. However, invasive rats remain on a number of islands, creating a natural experiment to study the influence of rats on relatively undisturbed oceanic islands. In March–April 2015, we conducted research at 12 islands, across three atolls (Extended Data Table 2). Six of the islands were chosen as they are rat-free, whereas the other six are rat-infested.

Seabird surveys. Breeding-seabird densities on each island were counted annually from 2009–2015 using the apparently occupied nests methodology (AONs)^{35,36}. The entire coastline of each island was surveyed first and AONs were counted directly. Following the coastal survey, the interior of the island was searched. There were no breeding seabirds in the interior of Ile Poule, Grande Ile Mapou, Ile Fouquet, Eagle Island, and both Ile Anglaise islands. On islands for which the interior search revealed breeding seabirds, techniques to estimate AONs varied by family. Brown Booby (*S. leucogaster*) AONs were directly counted. Red-footed Booby (*S. sula*) AONs were counted directly except on Nelson's Island, and Grande Ile Coquillage. On these islands the total surface area of the breeding population was calculated using a handheld Global Positioning System (GPS) and random plots of the area were counted for AONs. Plot size and whereabouts was directed by accessibility, visibility and the vulnerability of the breeding population. The means of the AONs of the plots were multiplied by the number of plots possible in the mapped area to estimate total AONs. Breeding frigatebirds (*Fregata* sp.) on Nelson's Island and Grande Ile Coquillage were estimated using the same technique described above for the red-footed booby. No tropicbird (*P. lepturus*) nesting cavities were located, so tropicbird breeding numbers were estimated by counting aerial displaying pairs above islands or nest-prospecting adults in an appropriate habitat. Shearwaters (Procellariidae) nest in burrows, with the largest colony on South Brother island and some also on Nelson's Island. Burrows is a loose term that covers rock fissures, crevices, tree roots, coconut boles, and various underground holes. Island surface area with burrows was estimated and AONs estimated by multiplying from an average burrow density, taken from random 10 m² sample plots throughout the island. Burrows were assumed occupied when a bird or egg was seen in them, there were indications of use (for example, feathers, droppings), or they were heavily scented with shearwater musk. Burrows were assigned to either one of the shearwater species by identification of large chicks, eggs, or adults. For the species of arboreal-breeding noddy (*Anous spp.*), direct counts were impractical for the large colonies on South Brother and Nelson's Island, for which subsampling and multiplication to the total colony area was used. All ground-nesting tern species (Sternidae) with the exception of sooty tern (*O. fuscatus*) had AONs directly counted. To calculate the number of sooty tern AONs, the total colony area was mapped and random sample plots were counted for AONs to multiply up to the total area. Plot size was dictated by accessibility, visibility and to avoid disturbing dense aggregations of breeding birds, with numbers counted from outside the colony at random points around the perimeter. Although vegetation type, such as coconut versus native forests, can also affect bird densities¹⁵, much of the indigenous island vegetation has been lost in Chagos¹⁴, and we used absolute bird-count estimates per island for this study.

Total annual seabird abundance was calculated on the basis of number of AONs multiplied by the mean number of birds occupying those nests per species, and the period of the year that the birds are present on the islands. For most species, a conservative estimate of three birds per nest was used (two adults and one chick), but some, for example sooty terns (*O. fuscatus*) have one adult, or one adult and one chick present for periods of the year, and others (for example, red-footed booby (*S. sula*)) have a chick and one to two juvenile/immature birds present in the nest or sub-colony area. The period of year spent on the island varied by species, from year round for species such as the brown booby (*S. leucogaster*) and common white tern (*G. alba*), to 4 months for the roseate tern (*Sterna dougallii*). Biomass of bird species was estimated using the average mass of an individual of each species taken from the Handbook of the Birds of the World³⁷.

We estimated the total nitrogen input from guano per hectare per year of each island following previously published methods¹⁵:

$$NI_{ij} = \frac{N_g \times Dr_i \times Bd_{ij} \times Res_j}{IsArea_j}$$

where nitrogen input per hectare per year (NI) is estimated from the nitrogen content of guano (N_g), the defecation rate in g per species of bird (i) per day (Dr), the number of that species of bird (Bd) on the island (j), the number of days of the year that the species is resident on the island (Res), and the area of the island ($IsArea$). Nitrogen content of guano was held at 18.1% on the basis of guano samples from similar species in the Pacific¹⁵. The contribution of guano was based on the red-footed booby and scaled for other species on the basis of species biomass, assuming allometric relationships with body size¹⁵. We adjusted the Bd estimates to account for time off islands during feeding forays. Given uncertainties in foraging durations and whether birds would have full crops and bowels, it is hard to be completely precise in these calculations. We assigned the 14 species into three groups, which account for foraging excursions off island in a fairly conservative way.

Group 1: Tropical shearwater, wedge-tailed shearwater, white-tailed tropicbird, sooty tern, brown noddy, and frigatebirds. Foraging will vary during the breeding cycle, but often one adult is foraging and may be off the island overnight. We therefore assumed only one adult of the pair was on the island at any one time.

Group 2: Red-footed booby. One bird of the pair makes daylight foraging forays but returns overnight. Adult numbers were therefore halved only during daylight hours (12 h).

Group 3: Great crested tern, roseate tern, black-naped tern, common white tern, bridled tern, brown booby, lesser noddy. In Chagos, these species tend to make much shorter foraging forays (1–4 h depending on species), meaning defecation at sea will be minimal compared to land. We therefore did not make any adjustments to their numbers.

Seabird densities per hectare of rat-free versus rat-infested islands were plotted as notched box plots, in which the horizontal line is the median, box height depicts the interquartile range, and diagonal notches in the boxes illustrate the 95% confidence interval around the median³⁸. The biomass of families of birds per island were plotted as log-scale heat maps for rat-free and rat-infested islands. Nitrogen input for rat-free versus rat-infested islands was plotted as notched box plots of kg per hectare per year. We also developed a set of simple Bayesian models to estimate the net rat effects on log-scale bird numbers, log-scale total biomass, and nitrogen input between rat-free and rat-infested islands:

$$y_i \sim N(\mu_i, \sigma_i)$$

$$\mu_i = \beta_0 + \beta_1 \times \text{RAT}$$

$$\beta_{0,1} \sim N(0, 10)$$

$$\sigma_i \sim U(0, 10)$$

where y_i was the response variable, RAT was a dummy variable for rat-infested islands, and variances were estimated independently within treatments. The β_1 parameters are the rat effect sizes reported in the caption of Fig. 1 along with the proportion of β_1 posterior density below zero.

Primary production and potential prey biomass and production available to seabirds. Biomass, production, and size structure of consumers in the ocean surrounding the Chagos Islands were calculated from the primary production available to support them using a size-based model that characterizes some of the main factors affecting the rate and efficiency of energy processing in marine ecosystems³⁹. In brief, these factors are (i) temperature, which affects rates of metabolism and hence growth and mortality; (ii) the size of phytoplankton and the predator to prey body mass ratio, which determine the number of steps in a food chain; and (iii) trophic transfer efficiency, a measure of the energy conserved and lost at each step in the chain. In the model, size composition of the phytoplankton community is predicted from primary production and temperature using empirical relationships and, in turn, this size composition is used to estimate particle export ratios that influence transfer efficiency in the first steps of the food chain. The model is depth integrated and we made the simplifying assumption that all primary production occurs in the euphotic zone. We did not explicitly model production of benthic communities, but these would not be accessible to seabirds.

In the model, relationships between primary-consumer production and consumer production at any higher trophic level are determined by trophic transfer efficiency. Production at a given body mass or trophic level was converted to biomass and numbers at the same body mass or trophic level on the basis of the assumption that body size and temperature determined individual rates of production³⁹. The modelled size spectrum was discretized into units of 0.1 (log₁₀) for analysis.

The environmental data used to force the models consisted of annual mean estimates of depth-integrated primary production (g C m⁻² d⁻¹) and sea surface temperature (°C) as derived from monthly predictions for the years 2010–2012.

Chlorophyll and primary production were obtained from the Mercator Ocean Project (Global Biogeochemical Analysis Product, BIOMERIV1 monthly 0.5° degree resolution) (<http://www.mercator-ocean.fr/>; the data are copyright of Mercator Ocean, product and interpretations obtained from Mercator Ocean products, Mercator Ocean cannot be held responsible for the results nor for the use to which they are put, all rights reserved.). Monthly temperature data were obtained from the Mercator Ocean physical NEMO model (PSY3V3R1)⁴⁰. Inputs to the size-based models were allocated to a 0.5° grid that covered the sea area defined by the maximum foraging distance of the species of seabird, assumed to be a radius, such that foraging areas were circular around the islands (Extended Data Table 1). These distances are an approximation from the published literature, given that foraging ranges can vary geographically⁴¹. Cells were assigned a mixed layer depth (m) and total depth (m)^{42,43}. Mean biomass and production for organisms in body mass (wet weight) classes 0.1–9 g (smaller prey) and 1–50 g (larger prey) was estimated per unit area by grid cell, to approximate size ranges consumed by the seabird species on the basis of prey-size information in the literature and body-mass class^{44,45}. To address considerable uncertainty in model parameters, we ran 10,000 simulations for each biomass or production estimate in each grid cell, with parameter estimates in each simulation drawn randomly from appropriate distributions. When parameters were correlated, the parameter estimates were drawn from multivariate distributions³⁹. Model results, expressed as medians and percentiles, were calculated from the distribution of output values. Conversions from carbon to wet weight were based on published values^{39,46}. Estimates of nitrogen content in prey-size classes were based on an assumed C:N ratio of 3.4:1, which is a typical value for fish⁴⁷ and reflects the fall in the C:N ratio with trophic level in food webs that are supported by primary producers with C:N ratios typically averaging 6.6:1^{48,49}. Estimates of biomass and production per unit area were converted to estimates of total biomass or production in the foraging area of each bird species (Extended Data Table 1 and Extended Data Fig. 1).

While rates of gross primary production can be high on coral reefs, net primary production, although variable in space and time, is typically comparable with net primary production in the more productive areas of the tropical ocean^{50,51}. Given the area of reef surrounding the rat-free islands is approximately 1.02 km², whereas foraging areas are >105 km² for 14 of the 15 bird species using these islands, large numbers of seabirds can feed from oceanic food webs with much higher production than those on the reefs (Extended Data Fig. 1). Even the production estimates for prey in the size ranges eaten by the seabirds are typically three or more orders of magnitude higher than the expected primary production on this area of reef (0.0001 Tg C yr⁻¹, if mean on-reef primary production is assumed to be 0.3 g C m⁻² d⁻¹)⁵⁰. Given the numbers of seabirds and the extent of the prey resource they have the potential to access, the strong signal from guano-derived nitrogen on the reefs surrounding rat-free islands is unsurprising. While the model has a number of assumptions, the results do highlight that oceanic production in the foraging area is expected to be several orders of magnitude higher than production on the reefs surrounding the islands and therefore that the higher levels of connectivity that result from higher seabird abundance have the potential to transport relatively high quantities of nitrogen to the reef systems.

Isotope sampling. From each island, ten samples of topsoil (<5 cm from surface) were taken from just behind the coastal vegetation boundary. Loose leaf litter and other vegetation was cleared to expose the soil, and samples were taken a minimum of 10 m apart. Along the beach margin of each island, new-growth leaf samples were taken from ten *S. taccada* plants. On the reef flat on the lagoonal side of each island (1 m deep and approximately 100 m from shore) ten samples of filter-feeding sponges (*Sphaciospongia* sp.) and macroalgae (*Halimeda* sp.) were taken from individual colonies and thalli, respectively. On the reef crest of each island (~3 m deep and 230 ± 55 m from shore) ten turf-algal samples were taken from dead corals. Ten adult territorial herbivorous damselfish (*P. lacrymatus*) individuals were collected on the reef crest of each island in the same area the turf algae were collected. Fish were euthanized on ice. Fish samples could not be collected from Nelson's Island. A sample of dorsal white muscle was taken from each fish. All samples were dried in a drying oven at 60 °C for 24 h or until fully dry. Samples were powdered with a pestle and mortar and stored in sealed plastic sample vials.

Stable isotope analysis of nitrogen for all samples was carried out at the University of Windsor, Canada. Isotope ratios were calculated from 400 to 600 µg of each sample added to tin capsules and analysed with a continuous-flow isotope-ratio mass spectrometer (Finnigan MAT Deltaplus, Thermo Finnigan). Total nitrogen content (%) was also estimated. Stable isotope values for nitrogen are expressed as delta (δ) values for the ratio of ¹⁵N:¹⁴N. Turf, sponge, soil and macroalgae samples were acid washed with hydrochloric acid to dissolve any calcareous matter or sediments that may have contaminated the samples. Subsets of samples that were run with and without the acid wash had correlation coefficients between 0.9 (turf-algae) and 0.99 (soil), and all samples from rat-free and rat-infested islands were treated the same. The standard reference material was atmospheric nitrogen. Samples were run twice, with select samples run in triplicate

to ensure accuracy of readings. Accuracy was within 0.3‰ for soil and within 0.1‰ for other samples, on the basis of soil elemental microanalysis B2153 and USGS 40 internal standards, respectively.

δ¹⁵N values between rat-free and rat-infested island treatments were analysed using Bayesian hierarchical models, with the area of reef surrounding each island (RA; calculated using GIS) as a covariate, and samples nested within their specific atoll. Distance to shore from the reef crest (DS) was used as an additional covariate for the turf algae and fish muscle samples. Models were run using the PyMC3 package⁵² in Python (www.python.org), including a *t*-distribution with four degrees of freedom as:

$$\delta^{15}\text{N}_{oij} \sim t_4(\mu_{oij}, \sigma_o)$$

$$\mu_{oij} = \beta_{0i} + \beta_{1o} + \beta_{2o}\text{RA}_j + \beta_3\text{DS}_j$$

$$\beta_{0i} \sim N(\gamma_0, \sigma_\gamma)$$

$$\beta_{1,2,3}, \gamma_0 \sim N(0, 1,000)$$

$$\sigma_o, \sigma_\gamma \sim U(0, 100)$$

where each organism (*o*) had their own offset (β_o) relative to island-level (*i*) soil intercepts (β_i). Models were examined for convergence and fit by consideration of stability in posterior chains, Gelman–Rubin (\hat{R}) statistics, and the fit of the models with the data⁵³.

Fish growth. The total length of each damselfish (*P. lacrymatus*) sampled was carefully measured to the nearest mm. The paired sagittal otoliths (ear bones) were removed from each individual to estimate age⁵⁴. One otolith from each pair was weighed to the nearest 0.0001 g and affixed to a glass slide using thermoplastic glue with the primordium located just inside the edge of the slide and the sulcal ridge perpendicular to the slide edge. The otolith was ground to the slide edge using a 600-grit diamond lapping disc on a grinding wheel along the longitudinal axis. The otolith was then removed and re-affixed to a clean slide with the flat surface against the slide face and ground to produce a thin transverse section approximately 200 µm thick, encompassing the core material. Finally, the exposed section was covered in thermoplastic glue to improve clarity of microstructures. Sections were examined twice and age in years was estimated by counting annuli (alternating translucent and opaque bands) along a consistent axis on the ventral side of the sulcal ridge, using transmitted light on a stereo microscope.

Growth curves for the otoliths from the rat-free versus rat-infested islands were modelled using the three-parameter van Bertalanffy growth function, implemented in PyMC3 as:

$$\log(L_{t,i}) \sim N(\mu_i, \sigma_i)$$

$$\mu_i = \log(L_\infty - (L_\infty - L_0)e^{-(k_0+k_1)t_i})$$

$$k_0 \sim U(0.001, 1)$$

$$k_1 \sim N(0, 10)$$

$$L_0 \sim N(0, \min(L_t))$$

$$L_\infty \sim U(\max(L_t), \max(L_t) \times 2)$$

$$\sigma_i \sim U(0, 1,000)$$

Where L_t is the observed total length (cm) at age t (years), L_∞ is the estimated asymptotic length, K is the coefficient used to describe the curvature of growth towards L_∞ (here split into k_0 (no rats) and k_1 (rat offset)) and L_0 is the theoretical length at age zero⁵⁵. We specified uniform bounds for the L parameters on the basis of observed minimum ($\min(L) = 6.2$) and maximum ($\max(L) = 10.4$) fish lengths. Again, models were examined for convergence and fit by consideration of stability in posterior chains, \hat{R} statistics, and the fit of the models with the data.

Fish biomass and function. Underwater visual surveys were conducted along the reef crest of each island on the lagoonal side of each atoll. Four 30-m transects were laid along the reef crest at 3 m depth, separated by at least 10 m. Benthic cover of corals, algae, and other organisms were surveyed using the line intercept method, for which the substratum type under the transect tape was recorded along the entire 30-m length. The structural complexity of the reef was estimated visually on a six-point scale, ranging from no relief to exceptionally complex (>1 m high) relief with numerous caves and overhangs. This structural complexity measure captures landscape complexity, including the complexity provided by live corals, that of the underlying reef matrix and other geological features, and has been shown to correlate well to other measures of complexity, such as measures of reef height and the linear versus contour chain method⁵⁶. The density and individual sizes of

diurnally active, non-cryptic species of reef-associated fish were estimated along each transect. Larger, more active fish were surveyed on the first pass of each transect in a 5-m-wide belt, whereas the more territorial and abundant damselfish family (Pomacentridae) were surveyed on a second pass of the transect in a 2-m-wide belt. We converted data on fish counts to biomass with published length–weight relationships from FishBase (<http://www.fishbase.org>) and a previously published work⁵⁷. Fish were assigned to feeding groups on the basis of their dominant diets and feeding behaviour⁵⁸.

The grazing and erosion potential (that is, area of reef scraped and volume of carbonates removed, respectively) by parrotfishes at each site was calculated as the product of feeding rate, bite dimension (area or volume), and fish density (following previously published methods²¹). Size-specific feeding rates for each species were derived from best-fit regressions of bite rate (bites per min) and fish length (total length, cm) for each species. Bite rates were quantified at three locations (Lizard Island, northern Great Barrier Reef, northern Sumatra, Indonesia, and the central Red Sea) using focal feeding observations. An individual parrotfish was haphazardly selected, followed for a short period of acclimation (~1 min) during which the fish length (total length, TL) was estimated to the nearest centimetre. After the acclimation period each fish was followed for a minimum of 3 min during which the number of bites on different benthic substrata (primarily epilithic algal matrix and live corals) and observation time were recorded. Bite rates were then converted to bites per min. Observations were discontinued if the focal individual displayed a detectable response to the diver. All feeding observations were conducted from 9:00 to 15:00 with a minimum of 25 observations conducted per species per location.

The area (mm²) and volume (mm³) of material removed per bite by individual parrotfish was estimated from species-specific relationships between bite size and fish length. To estimate bite area an individual parrotfish was haphazardly selected, its total length was estimated and it was followed until it took a bite from the reef substratum. The dimensions of the bite (length and width) were then measured in situ using dial callipers. A minimum of 16 observations (mean = 34.3 observations) were made per species, with all observations performed at Lizard Island, northern GBR. Bite volumes of species were largely taken from the literature⁵⁹, and supplemented with in situ observations at Lizard Island for *Chlorurus microrhinos*. Where possible, species-specific bite rates and bite dimensions were used, when these were not available, values for closely related congeners were used.

Total biomass and biomass of each trophic feeding group of fish (BIO_{*ij*}) was modelled using Bayesian hierarchical models, with observations (*j*) nested within atolls (*i*) and including factors that could influence fish biomass as covariates; coral cover (HC) and reef structural complexity (SC). The general model was:

$$\log(\text{BIO}_{ij}) \sim N(\mu_{ji}, \sigma_0)$$

$$\mu_{ji} = \beta_{j0i} + \beta_1 \text{RAT} + \beta_2 \text{SC}_j + \beta_3 \text{HC}_j$$

$$\beta_{j0i} \sim N(\gamma_{j0}, \sigma_\gamma)$$

$$\beta_{1,2,3}, \gamma_{j0} \sim N(0, 1,000)$$

$$\sigma_0, \sigma_\gamma \sim U(0, 100)$$

with models examined for convergence and fit by consideration of stability in posterior chains, \hat{R} statistics and the fit of the models with the data.

The two ecosystem functions, grazing and erosion potential (rounded to nearest whole number), were modelled with the same Bayesian hierarchical structure, but with an alternative Poisson (Pois) rate (XR) likelihood:

$$\text{XR}_{ji} \sim \text{Pois}(e^{\mu_{ji}})$$

$$\mu_{ji} = \beta_{j0i} + \beta_1 \text{RAT} + \beta_2 \text{SC}_j + \beta_3 \text{HC}_j$$

$$\beta_{j0i} \sim N(\gamma_{j0}, \sigma_\gamma)$$

$$\beta_{1,2,3}, \gamma_{j0} \sim N(0, 1,000)$$

$$\sigma_0, \sigma_\gamma \sim U(0, 100)$$

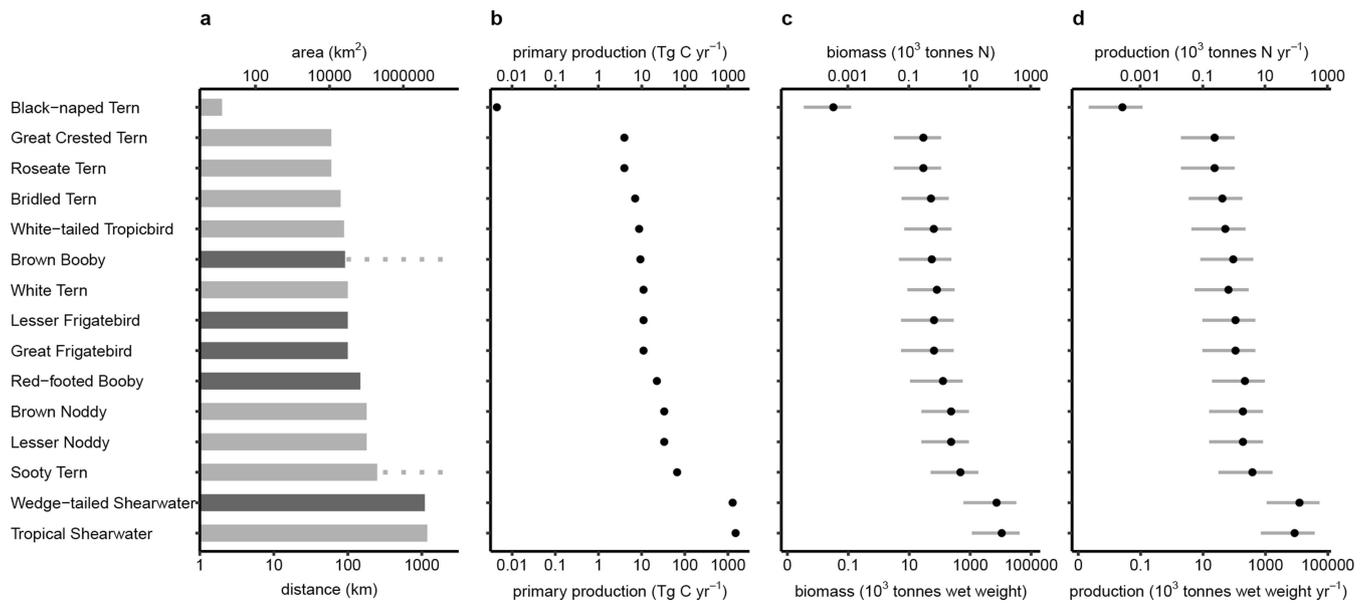
Reporting summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

Code availability. Code used for Figs. 1–4 in this paper are available from GitHub (<https://github.com/mamacneil/ChagosRats>).

Data availability. Data used for Figs. 1–4 in this paper are available from GitHub (<https://github.com/mamacneil/ChagosRats>).

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Extended Data Fig. 1 | Primary production and potential prey biomass and production in areas accessible to seabirds foraging around the Chagos Islands. **a**, Recorded foraging ranges for seabird species that feed on smaller prey (light tone, 0.1–9 g individual wet weight) or larger prey (dark tone, 1–50 g individual wet weight; broken lines indicate that greater ranges are expected for two of the species thus foraging area calculations assumed that the foraging range is the radius of the foraging

area). **b**, Primary production in the foraging area. **c**, Modelled biomass. **d**, Production of fauna in the foraging area. Median and 90% uncertainty intervals on the basis of 10,000 simulations to assess the effects of parameter uncertainty³⁹ on biomass or production estimates are shown. Biomass and production were estimated for fauna in the prey size ranges consumed by each bird species, and expressed as wet and nitrogen (N) weight, respectively.

Extended Data Table 1 | Species-specific foraging locations, foraging distances and foraging observations from Chagos

Species	Foraging location	Reported foraging distance in km	Chagos-specific foraging behaviour
Wedge-tailed Shearwater <i>Ardenna pacifica</i>	Pelagic	300-1100 (ref. 60)	Forages over open ocean normally well away from the islands. Often associates with other seabirds where sub-surface predators (e.g. tuna) are driving prey to the surface.
Tropical Shearwater <i>Puffinus bailloni</i>	Pelagic	379-1190 (ref. 61)	As <i>Ardenna pacifica</i> .
White-tailed Tropicbird <i>Phaethon lepturus</i>	Mainly pelagic	89 (ref. 62)	Solitary; forages over open ocean far away from land.
Lesser Frigatebird <i>Fregata ariel</i>	Pelagic	100 (ref. 63)	Normally pelagic, occasionally kleptoparasites other seabirds returning to colonies with food
Great Frigatebird <i>Fregata minor</i>	Pelagic	100 (ref. 64)	As <i>Fregata ariel</i>
Brown Booby <i>Sula leucogaster</i>	Inshore waters	>92 (ref. 64)	Usually seen foraging over submerged off-atoll banks. Presumably this is because there is very little "inshore waters" in the Chagos.
Red-footed Booby <i>Sula sula</i>	Pelagic	39-148 (ref. 65)	Forages over open ocean areas usually in association with tuna. At large prey balls, hundreds of red-footed boobys can be present, along with shearwaters, brown noddy, sooty terns and white terns.
Brown Noddy <i>Anous stolidus</i>	Pelagic	180 (ref. 66)	Forages over open ocean miles away from land. Often feeds in association with Red-footed Booby and on prey balls.
Lesser Noddy <i>Anous tenuirostris</i>	Pelagic	180 (ref. 66)	In the Chagos this species forages in flocks in atoll lagoons or over off-atoll banks. Usually associated with tuna.
White Tern <i>Gygis alba</i>	Semi-pelagic, including inshore waters	2-100 (ref. 67)	Normally found foraging within 5km of land. Targets large prey balls.
Sooty Tern <i>Onychoprion fuscata</i>	Pelagic	>250 (ref. 63)	Forages far and wide over open ocean.
Bridled Tern <i>Onychoprion anaethetus</i>	Semi-pelagic, including inshore waters	20-80 (ref. 68)	Usually seen foraging over off-atoll banks.
Roseate Tern <i>Sterna dougallii</i>	Semi-pelagic, including inshore waters	60 (ref. 66)	Very rare in the Chagos and its foraging habits are not known
Black-naped Tern <i>Sterna sumatrana</i>	Atoll lagoons, close inshore, but sometimes at sea.	2 (ref. 69)	Feeds around coral fringes of islands or in lagoons. Often associates with lesser noddy.
Great Crested Tern <i>Thalasseus bergii</i>	Atoll lagoons, close inshore, but sometimes at sea.	60 (ref. 66)	Another inshore species with similar foraging requirements as black-naped tern.

Data on forage distances are from previously published work⁶⁰⁻⁶⁹.

Extended Data Table 2 | Islands used in the study

Treatment	Atoll	Island	South	East	Island area (ha)
Rat-free	Peros Banhos	Ile Longue	5.270	71.867	25.5
Rat-free	Peros Banhos	Grande Ile Coquillage	5.372	71.969	28
Rat-free	Salomon	Ile de la Passe	5.304	72.251	26
Rat-free	Great Chagos Bank	Nelson's Island	5.682	72.313	81
Rat-free	Great Chagos Bank	Middle Brother	6.154	71.517	8
Rat-free	Great Chagos Bank	South Brother	6.172	71.544	23
Rat-infested	Peros Banhos	Ile Anglaise	5.439	71.757	12
Rat-infested	Peros Banhos	Ile Poule	5.414	71.755	108
Rat-infested	Peros Banhos	Grande Ile Mapou	5.266	71.753	19.5
Rat-infested	Salomon	Ile Fouquet	5.343	72.262	39.5
Rat-infested	Salomon	Ile Anglaise	5.327	72.223	75.5
Rat-infested	Great Chagos Bank	Eagle Island	6.187	71.338	243.5

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see [Authors & Referees](#) and the [Editorial Policy Checklist](#).

Statistical parameters

When statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main text, or Methods section).

n/a | Confirmed

- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
- An indication of whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided
Only common tests should be described solely by name; describe more complex techniques in the Methods section.
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistics including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
Give P values as exact values whenever suitable.
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated
- Clearly defined error bars
State explicitly what error bars represent (e.g. SD, SE, CI)

Our web collection on [statistics for biologists](#) may be useful.

Software and code

Policy information about [availability of computer code](#)

Data collection

No software was used for data collection

Data analysis

Python and PyMC3

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Data used for figures 1-4 in this paper are available through the GitHub links in the Methods.

Field-specific reporting

Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/authors/policies/ReportingSummary-flat.pdf](https://www.nature.com/authors/policies/ReportingSummary-flat.pdf)

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The study aimed to assess the influence of introduced rats on tropical islands on seabird densities, the nitrogen deposited on islands from seabirds, the signal of this nitrogen on the island and across the adjacent coral reef ecosystem, and how this influenced fish growth, biomass, and ecosystem function. This was achieved by contrasting 6 rat-infested islands to 6 rat-free islands, and using a combination of survey (count) data, stable isotope analyses and fish growth estimation.
Research sample	All seabirds present on the survey islands were counted, which included <i>Phaethon lepturus</i> , <i>Thalasseus bergii</i> , <i>Sterna sumatrana</i> , <i>Sterna dougallii</i> , <i>Onychoprion fuscatus</i> , <i>Onychoprion anaethetus</i> , <i>Gygis alba</i> , <i>Puffinus bailloni nicolae</i> , <i>Ardenna pacifica</i> , <i>Anous tenuirostris</i> , <i>Anous stolidus</i> , <i>Fregata</i> sp., <i>Sula sula</i> and <i>Sula leucogaster</i> . To capture nitrogen signals on islands we collected top soil and new growth leaf samples from a common coastal shrub (<i>Scaevola taccada</i>) which would be expected to uptake nitrogen from the soil. On the reef flat, we assessed nitrogen signals in filter feeding sponges (<i>Spherospongia</i> sp.) and macroalgae (<i>Halimeda</i> sp.), both of which should be reliant on available nitrogen. On the reef crest we assessed nitrogen signals in turf algae and herbivorous damselfish (<i>Plectroglyphidodon lacrymatus</i> - sex not determined, adult, mean age 3.6 years, with age range of 2-10 years), which again should reflect availability of nitrogen. The same species of damsel fish was used to assess fish growth. Underwater visual surveys of the reef fish community were conducted, excluding small (under 8cm), cryptic and nocturnal species which are typically poorly sampled using visual methods. Data on seabird foraging ranges, and fish grazing, were extracted from the peer reviewed literature.
Sampling strategy	The number of Islands (6 with rats, 6 rat free) was chosen prior to the research expedition to maximize replication with a balanced design in the time available. Total bird counts on each island were conducted. Isotope and fish otolith sample numbers (n=10 per item per island) were pre-chosen to enable sufficient replication across the items sampled. Reef fish underwater visual surveys (n=4 per island) followed standard replication numbers from other studies.
Data collection	Breeding seabird densities on each island were conducted by P Carr, using the apparently occupied nests methodology (AONs). Samples for isotope and fish growth analyses were collected haphazardly on the islands, (soil and leaves), reef flats (sponges and macroalgae) and reef crests (turf algae and damselfish) by N Graham and S Wilson. Fish community visual surveys were conducted by N Graham. Coral cover surveys were conducted by S Wilson. Modeling of primary and prey production available to seabirds was conducted by S Jennings.
Timing and spatial scale	The seabird surveys were conducted annually between 2009 and 2015. The research expedition for the 2015 seabird surveys and all other elements of the study took place from 15th March to 16th April 2015. Data collection was conducted on a 6 days on, 1 day off basis. Data were collected across 3 atolls of the Chagos Archipelago: Salomon, Peros Banhos, and the Great Chagos Bank.
Data exclusions	No data were excluded.
Reproducibility	A full description of the methodologies used is provided in the Methods, and the data and full code necessary to reproduce the findings are provided through the GitHub links in the Methods. Fish samples could not be collected from 1 rat-free island (relevant to fish muscle stable isotope (Fig. 2g) and growth analyses (Fig. 4). Otoliths could not be found in 4 individual fish (relevant to the growth analysis (Fig. 4). All other attempts at replication were successful.
Randomization	12 Islands of similar size, 6 rat-free and 6 rat-infested, were chosen haphazardly before the expedition. All samples for stable isotopes and otoliths were collected a minimum distance apart (e.g. 10m for soil samples) and haphazardly (e.g. first sponge found). Underwater visual survey transects were started at a random point directly out from the isotope sampling, and each transect was separated by a minimum of 10m.
Blinding	The bird surveys had been conducted for 6 years prior to this survey being conceived. The samplers (NAJG and SKW) of isotope and otolith samples and underwater visual surveys had never surveyed those sites in the past and thus blinding was applied as knowledge of species locations and compositions was not known. As group allocation was based on rat presence (and thus also birds), blinding of group allocation was not relevant or possible.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

Field work, collection and transport

Field conditions	Field (sea) conditions were calm.
Location	The study was conducted across 3 atolls of the Chagos Archipelago, Indian Ocean (5° 50' S, 72° 00' E)

Access and import/export

A research permit for the expedition to the Chagos Archipelago was issued on 13th March 2015 by the British Indian Ocean Territory Administration (BIOTA). Export permission for the samples used in isotope and growth analyses in this study was issued by BIOTA on 5th March 2015. Import permits were issued by the Australian Government Department of Agriculture (permit number IP15003863). Animal ethics for fish collection was approved by James Cook University (approval number A2166).

Disturbance

Only common plants and animals were used in the sampling for isotope analyses. All other data collection was observational.

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involvement	Included in study
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Unique biological materials
<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
<input type="checkbox"/>	<input checked="" type="checkbox"/>	Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Human research participants

Methods

n/a	Involvement	Included in study
<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

Animals and other organisms

Policy information about [studies involving animals](#); [ARRIVE guidelines](#) recommended for reporting animal research

Laboratory animals

The study did not involve laboratory animals.

Wild animals

110 individuals of *Plectroglyphidodon lacrymatus* (Jewel Damselfish) were collected and euthanized on ice. Sex was not determined. All individuals were adult. Mean age was 3.6 years (range 2-10 years). Muscle tissue samples and otoliths were extracted for isotope and growth analyses respectively. Animal ethics for fish collection was approved by James Cook University (approval number A2166). All other wild animal work was observational (visual counts of seabird and fish communities).

Field-collected samples

Field collected samples for isotope analyses were dried and powdered for analyses. Thin transverse sections of the fish otoliths were cut on a glass slide and age in years was estimated by counting annuli.