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Review article

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The circular seabird economy is critical for oceans, islands and people

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Abstract

Nearly a third of seabird species are at risk of extinction, rendering them among the most threatened bird taxa globally. The decline in seabird populations has major ramifications for their associated ecosystems. An expansive literature covers seabird impacts on their breeding islands, and growing research expands understanding of the circular seabird economy — cross-ecosystem connections of seabirds from oceans to islands, and back to nearshore marine ecosystems, mainly driven by nutrient transfer. Amid the twin biodiversity and climate crises, maintaining and restoring the circular seabird economy is one way to achieve large-scale, cross-ecosystem impacts with simple and time-tested conservation methods. This Review summarizes researchers' understanding of the circular seabird economy and outlines goals for future research. Historically, research has focused on terrestrial impacts, with emerging research explicitly studying the cross-ecosystem impacts of seabirds. We identify substantial knowledge gaps, with research needed to understand how the circular seabird economy changes with space, time, across biomes and with island size. Emerging analytic and monitoring tools will help to propel this research forward. Many coastal communities, especially Indigenous people, rely on seabirds for their livelihoods and cultural connections, and so taking a people-centred approach incorporating Indigenous knowledge and perspectives is critical moving forward.

Sections

Introduction

Marine nutrients from sea to land

Seabird impacts on islands

Seabird impacts on adjacent marine ecosystems

Supporting circular seabird economies

Summary and future directions

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Introduction

Seabirds are top predators in marine ecosystems, consuming comparable amounts of primarily fish and squid to the commercial fishing industry's annual take[1–4]. Most seabirds spend the majority of their lives on the open ocean, but as obligate land breeders they come ashore to nest, predominantly on islands[5]. Seabirds are colonial and can nest in millions on a single island, although colonies typically range from hundreds to thousands of birds[6]. This movement of seabirds from oceans to land results in the movement of massive amounts of dietary-derived marine nutrients (carbon, nitrogen, phosphorus and calcium). These nutrients are deposited on islands via guano, eggshells, feathers and carcasses of chicks and adults, resulting in profound effects on island biodiversity and ecosystem functioning. Indeed, the impacts of seabirds on their breeding islands are so unique and consequential that they are often termed seabird islands[7]. However, the nutrient flow does not end on islands; the marine-derived nutrients eventually wash back into the ocean through runoff, groundwater seeps and, in the case of volatilized ammonia from guano, via wind. These nutrient inputs have important consequences for marine intertidal and nearshore environments, creating what has been previously termed the circular seabird economy[8]. The circular seabird economy is the process by which seabirds consume their prey in the ocean, transport nutrients to islands and then those nutrients are washed back out into the ocean, to be taken up by ocean organisms (Fig. 1). We argue this term provides a useful descriptor for the vast scale of seabird impacts in the many ecosystems that they link and helps those outside the disciplines of ecology and conservation to understand the importance of those links for the livelihoods of coastal communities dependent on seabird inputs.

Despite their importance for driving biodiversity on and around islands, and as top predators in oceans, seabirds are one of the most threatened taxa of birds, with nearly one-third listed as threatened, endangered or critically endangered[9]. Moreover, extinctions since European colonization have disproportionately occurred on islands[10], which are the primary nesting location for seabirds. Given that climate change threatens their breeding islands and negatively affects their food availability[9,11–13], seabirds sit at the nexus of both the biodiversity and climate crises. Because seabird impacts span large scales and multiple ecosystems, conserving and restoring their populations is one relatively simple way to maintain beneficial large-scale cross-ecosystem impacts. To understand how best to use seabird conservation to address the biodiversity crisis, and given emerging science that an intact seabird island, in turn, could be an important local resilience factor for island ecosystems facing climate change, it is first important to understand how the circular seabird economy works.

In this Review, we summarize research around the circular seabird economy (Fig. 1), describing the flow of nutrients and their ecological impacts. We highlight the effects of the circular seabird economy on ecosystems adjacent to seabird islands and identify threats to this balanced system, as well as describing relevant conservation efforts. We identify knowledge gaps pertaining to the circular seabird economy, and thus areas for prospective research, and end with what can propel this area of research into the future.

Marine nutrients from sea to land

Seabirds comprise ~3.5% of all avifauna and are defined as birds that are reliant on marine habitats for elements of their life cycles[14]. Body size can vary greatly (from 20-g least storm-petrels, *Halocyptena*

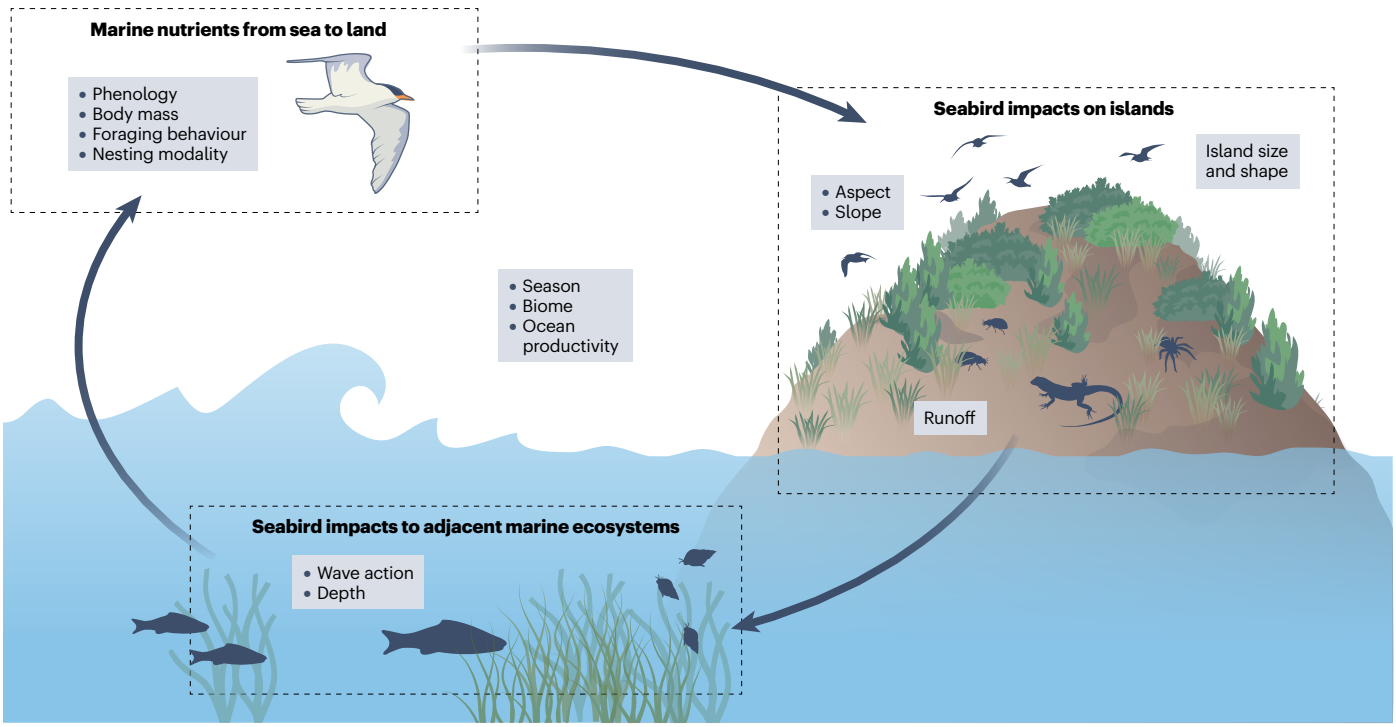


Fig. 1 | The seabird circular economy. Seabirds extract marine nutrients from the sea and deposit them on islands. These nutrients are assimilated directly in the terrestrial ecosystem and back into nearshore marine systems via runoff. This cycle is sensitive to biotic and abiotic factors that can vary with season, phenology and biogeography (Box 1).

microsoma, to 30–38-kg emperor penguins, *Aptenodytes forsteri*[5]) as well as foraging range (for example, <5 km in incubating Canadian roseate terns, *Sterna dougallii*, and >6,800 km in great shearwaters, *Ardenna gravis*, incubating eggs within the South Atlantic Ocean; Fig. 2). During their breeding seasons, seabirds are central place foragers, sometimes travelling vast distances from their nesting and roosting sites to feed, on trips that can last from hours to days, regularly crossing the terrestrial–marine boundary[15].

Seabirds feed most prevalently on pelagic marine organisms, particularly krill, squid and fish[2]. Globally, seabirds extract around 50–96 million tonnes of prey annually from marine ecosystems[1–4], securing energy for their basal metabolic processes, movement, growth, moult and reproduction. Seabird energy expenditure, and therefore their energetic requirements, increases with body mass[16], and large-bodied species, such as albatrosses and penguins (particularly the genus *Aptenodytes*), require substantial quantities of prey to balance their energetic budgets (Fig. 2). Seabird energetics also vary spatiotemporally, contributing to seasonal pulses in subsequent nutrient subsidies, with energy expenditure generally increasing throughout the breeding season as adults care for their developing offspring[16]. Outside the breeding season, moult is an energetically costly period, during which many seabirds also return to land[17], thereby depositing marine-derived nutrients that were assimilated into feather tissue from elsewhere in their ranges.

The breeding, life history and foraging behaviour of seabirds mean they function as biological pumps, consuming prey within their oceanic feeding grounds to meet their energetic requirements and then transferring large quantities of nutrients to their terrestrial roosting and breeding grounds[18,19]. The concentrations and quantities of nutrients that seabirds deposit at their colonies are influenced by factors such as body size, rate of energetic expenditure and foraging ecology[17], which can also vary by individual, sex, age and location[20] (Fig. 2). The protein-rich marine prey species of seabirds result in the transfer of two key elements: nitrogen and phosphorus[21]. Globally, seabirds transfer ~3.8×10^3 Gg nitrogen and 0.63×10^3 Gg phosphorus per year from the ocean to land[22]. This nutrient flux is comparable in magnitude to other major global flows of nitrogen and phosphorus, such as non-anthropogenic oceanic inputs of nitrogen via groundwater and riverine inorganic phosphorus fluxes to the ocean[22]. Guano represents the main form of nutrient input at colonies, and once deposited, some of the nitrogen is emitted to the atmosphere as ammonia gas[23], particularly in hot and humid environments[24]. In addition to nitrogen and phosphorus, seabird-derived nutrients contain a suite of elements such as zinc, copper, manganese, nickel, cadmium, lead and iron[25–27]. Although most inputs from seabirds are biotic or part of natural geochemical cycling, anthropogenic pollution means that seabirds also transport plastic and other contaminants to their breeding colonies[28]. Nutrient inputs via guano deposition can be substantial, with an estimated 591 Gg nitrogen, 99 Gg phosphorus, 39.3 Mg cadmium and 27.2 Mg lead being deposited annually at breeding colonies, demonstrating that seabirds are important components of numerous global biogeochemical cycles[19,22]. The fate of deposited nutrients includes being taken up into island food webs via plants and consumers, especially detritivores[29–31], transported back into the marine environment through runoff[8,29,30], into groundwater[31,32] and, in the case of volatilized ammonia, transported into nearby ecosystems via wind[24,33,34].

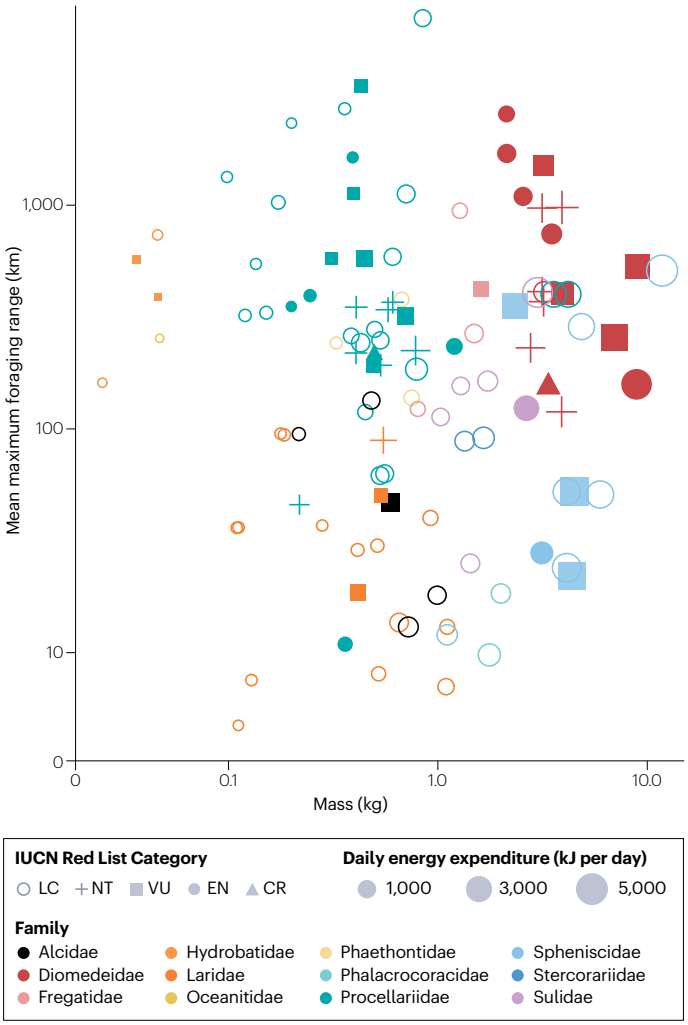


Fig. 2 | Seabird mass and foraging range. The relationship between mean bird mass (kg) and foraging range for breeding adult seabird species (km). Species are categorized by International Union for Conservation of Nature (IUCN) Red List conservation status (symbols), daily energy expenditure (kJ per day; point size) and taxonomic family (colour). Data on mean bird mass are from ref. 180. Data on mean seabird foraging ranges were collated for breeding adult seabirds where data exist within ref. 181 via Google Scholar searches ($n = 110$ seabird species). Where means were not available, medians were used. Daily energy expenditure was calculated via the Seabird FMR Calculator in ref. 16. See Supplementary information for further information and complete data sources. IUCN Red List categories: least concern (LC), near threatened (NT), vulnerable (VU), endangered (EN) and critically endangered (CR).

Seabird impacts on islands

The quantity of nitrogen and phosphorus deposition to seabird islands varies by seabird body size, energy requirements, population size, life history and phenology. Typically, seabirds with larger populations, larger-bodied species and longer nesting periods (or year-round roosts) contribute larger amounts than others[35–39]. Quantities taken up into island food webs and washed back into the ocean vary according to island abiotic factors such as island size, soil type, slope, precipitation regime and terrestrial nutrient status along the scale of oligotrophic to eutrophic[8,40,41] (Box 1) and presence of other biotic sources of marine-derived nutrients such as beach wrack, pinnipeds and intertidal invertebrates[41]. For example, impacts in arid ecosystems are positively

Box 1 | Sources of variation in impacts for islands and marine links

Environmental and ecological factors affecting both seabird distribution and behaviour, as well as the input and residency time of seabird-derived nutrients in nearshore marine habitats, can influence the contribution, distribution and impact of nutrient flows across the land–sea interface.

Seabird ecology

Seabird-derived nutrient flows to marine habitats are ultimately governed by guano deposition that is linked with seabird diet and breeding behaviours. The nutrient composition and quantity of guano can be dictated by species-specific feeding and nesting preferences, seabird body size, colony size and density and breeding season[121]. Guano deposition on islands and in nearshore marine habitat can therefore be concentrated in areas in and around colonies[55,120], might be temporally or seasonally limited[38], and could vary with seabird diversity and community composition[37]. Additionally, these natural nutrient flows can be disrupted by the presence of island invaders, whereby invasive vegetation restricts breeding habitat[44,182] and invasive predators eat seabirds (reviewed elsewhere[183–185]).

Island dynamics

The physical characteristics of islands, such as their total area, topography, elevation, slope and watershed size, further affect seabird nesting and roosting patterns and the cross-ecosystem flow of nutrients (Fig. 1). Given that nutrients can enter marine habitats through watershed or surface runoff and through percolation and submarine groundwater discharge[186,187], these island dynamics, coupled with variations in annual or seasonal precipitation, become key factors in determining the concentrations and patterns of nutrient distribution in nearshore marine ecosystems. For example, high islands typically have larger watersheds than low-lying islands or atolls, such that the primary vector for nutrient input into nearshore habitat can differ between runoff or stream outflow and submarine groundwater discharge, respectively[188].

Windscapes

Global and local wind patterns have ubiquitous influence on both seabird behaviour and nearshore marine hydrodynamics that can cause further variability in nutrient dynamics across the land–sea interface. Prevailing winds such as the easterly trade winds in the tropics, doldrums near the Equator and mid-latitude westerlies can affect large-scale migratory patterns and seabird distribution, as well as flight, foraging and breeding behaviours (reviewed elsewhere[189]). High winds and storms might also disrupt guano deposition by creating inaccessible nesting grounds[190]. Both prevailing winds and storms also increase wave exposure that more readily impacts windward compared with leeward sides of islands, perhaps increasing the presence of internal waves[191,192] and decreasing the residency time of nutrients in nearshore waters[193].

Seascapes

Other physical features of the nearshore marine habitat can influence the dissipation of nutrients and their residency times, and ultimately the degree of impact, or size of impact zone, of seabird-derived nutrients on marine ecosystems. Differences have been observed in the bioaccumulation of seabird-derived nutrients into algal, coral or fish tissue among varying distances from shore[29,112,122], reef habitats and depth[40,194] and at distance from active seabird colonies[115]. Biogeophysical modelling of seabird nutrient fluxes to marine systems has further identified variables such as seafloor curvature and water flow as crucial to local nutrient-delivery patterns[195].

Biomes

Each biome has unique seabird diversity, ecology, island dynamics, windscapes and seascapes, driving marked differences in the circular seabird economy between biomes. Seabird-derived nutrient impacts tend to be stronger in the oligotrophic systems of polar, desert and tropical ecosystems versus relatively eutrophic temperate systems[7,196]. Precipitation is a driving force of variation in seabird-derived nutrient impacts, with higher precipitation yielding stronger seabird-derived nutrient impacts across different biomes[40,197]. The degree of guano volatilization varies across biomes and will affect transfer to nearshore ecosystems; for example, in the hot, humid tropics, most guano quickly volatilizes into ammonia rather than flowing into ecosystems through soil deposition[22,24,198].

correlated with rainfall[42], and impacts on temperate islands are stronger in the rainy season[8,40]. Because the impacts of nitrogen and phosphorus deposition vary according to precipitation and nutrient context, they also vary by biome (Table 1 and Box 1), with stronger impacts seen in relatively nutrient-poor polar regions versus nutrient-rich temperate regions[26,43], and the relatively few studies available suggesting substantial impacts in nutrient-poor tropical systems[37,44,45].

Seabird-derived inputs can alleviate terrestrial nutrient limitation, enhancing primary productivity and carbon sequestration, although effects vary with vegetation types, climates and along longitudinal gradients. On tropical and subtropical islands, early successional vegetation can respond markedly to seabird influence[46], whereas mature, densely forested systems exhibit weaker responses[47,48]. Effects on primary production are modulated by rainfall, with positive effects on plant cover and biomass under sufficient rainfall[49] but toxic effects of seabird guano prevailing under dry conditions, often lowering plant cover[50]. In nutrient-limited Arctic systems, seabirds can increase carbon stocks[51], plant cover[52] and plant biomass[43,53]. Plant biomass increases coincide with compositional shifts towards plant species and traits adapted to uptake of seabird guano. Guano deposition can trigger transitions from woody to grass-dominated vegetation in tropical[54], temperate[55] and Arctic systems[52,56], often reducing species richness[57,58]. Under high guano loads, monodominant vegetation stands can form on tropical atoll islands (such as *Pisonia* forests)[59,60], as well as in Arctic systems[56]. Seabirds facilitate seed dispersal, actively driving compositional shifts in plant community composition[61–63]. Elevated terrestrial plant biomass can change herbivory rates, although plant trait-related factors govern general response strengths and directions[64].

Increased carbon stocks and guano loads alter soil composition, nutrient content and functioning across biomes and longitudinal gradients. Nitrogen and phosphorus generally increase, whereas soil pH decreases[49,51]. Increased microbial biomass can transition from nitrogen

to carbon limitation, thus accelerating leaf litter decomposition[65] and soil nutrient and carbon fluxes[66,67]. These indirect effects of seabirds on island soils, via elevated nutrient inputs and terrestrial primary production, are often paired with direct soil impacts of seabirds, such as biopedturbation. Seabird burrowing can increase or decrease soil water content, depending on geography, vegetation cover and detritus accumulation[57,58]. Trampling and burrowing can reduce seedling species richness and density[68,69], modify soil compaction[57] and accelerate erosion[49].

In general, seabirds are associated with greater animal species diversity and abundance on islands, and positive impacts for ecosystems[26,70–72]. Invertebrate and lizard community composition and species richness are altered through changes in habitat and predator dynamics where seabirds are present. For example, on Gulf of California islands, seabirds promote increased invertebrate consumer abundance and increased abundance for their corresponding spider and lizard predators[73]. Invertebrates and detritivores, which directly consume seabird tissues and guano, show the strongest abundance increases[74]. Seabird impacts on terrestrial biodiversity are greatest on smaller islands, where seabirds are a unique or primary source of nutrients and where terrestrial ecosystems have otherwise limited internal nutrient stocks relative to a highly productive marine ecosystem[73].

Given that breeding seabirds affect the abundance of island biota, it should be no surprise that those impacts yield unique food web interactions. For example, increased diversity and abundance of detritivores, ectoparasites and scavengers that feed directly from seabird carcasses can yield more nutrient resources for their prey[75]. Impacts on consumers are expected to vary with biomes such that nutrient-rich systems and/or drier biomes exhibit lower-magnitude impacts to food webs than nutrient-poor and/or wetter biomes (Box 1 and Table 1). In nutrient-rich temperate ecosystems, seabirds serve as prey for many native island species; for example, around 8% of the large endemic Phillip Island centipede's (*Cormocephalus coynei*) diet comprises black-winged petrel (*Pterodroma nigripennis*) chicks[76]. Likewise, seabird burrows provide habitat for other species, especially reptiles such as tuatara (*Sphenodon punctatus*), lizards and snakes[77–80]. In Arctic biomes, whole-ecosystem transformations occur when seabird-derived nutrients pulse through these otherwise nutrient-limited systems, the whole ecosystem transforms from tundra to grassland, with attendant impacts to island biota, as seen in the Aleutians[43,53,56]. Native deer mice (*Peromyscus maniculatus*) depredate Scripps's murrelet (*Synthliboramphus scrippsi*) chicks[81], and scores of native birds of prey and other seabirds consume nesting seabirds, eggs and chicks[82–85].

Seabird impacts on adjacent marine ecosystems

The influence of seabirds on the coastal ecosystems that fringe their islands is a more nascent field[26]. Identified links between seabirds and intertidal community effects date back to the 1980s[86,87], but more substantive research has only emerged in the past decade[40,88,89]. Linkages are typically close to islands, in shallow water ecosystems such as coral reefs, seagrasses, rocky shores and mangroves[90]. Most links between seabirds on islands and nearshore coastal ecosystems are through the transfer of nutrients. Nutrients including nitrogen and phosphorus, and other elements found in seabird guano such as iron, enter coastal ecosystems via runoff, through groundwater discharges, and via gas exchange[41]. The influence of these nutrient exchanges for ecosystem functions, food web structures and biodiversity can be substantial. The strength of nutrient signals and uptake by marine organisms are mediated by processes such as wave energy and oceanic nutrient influence[40,91] (Box 1).

Seabird nutrient beneficiary ecosystems are often different from the marine ecosystems where the majority of seabirds are feeding and sourcing energy to transfer back to islands[92]. Indeed, for most seabirds, which feed some distance away from islands (Fig. 1), the circular seabird economy might not be a closed feedback loop, with the source marine energy coming from different spatial scales and ecosystems than the marine habitats that ultimately benefit. Alternatively, for seabirds that feed closer to shore, the circular seabird economy could function more like a closed feedback loop with seabird prey benefiting from locally seabird-derived nutrients. Notably, even pelagic feeding seabirds can affect forage prey density within 150 km from their breeding colonies[93]. The contribution of fish from nearshore environments to the seabird diet can be quite minimal, despite these communities being the most affected by breeding seabird nutrients[92,94]. However, seabird-derived nutrients can benefit nearshore habitats such as seagrass meadows, which serve as nurseries for younger age classes of seabird to forage fish[94], potentially closing the feedback loop. For islands in dry environments, with little potential for runoff, the conduit for nutrient transfer to the sea is via wind transporting volatilized ammonia[19,21,95]. For seabirds breeding on inland islands far from the ocean, there is no nutrient transfer back to the ocean and thus no closed loop. Identifying what influences the extent to which the seabird circular economy is a closed loop is a key future target for this field.

Where seabirds are providing otherwise limiting nutrients, seabird inputs can enhance growth rates of individual marine organisms (Fig. 3). For example, guano addition stimulates primary production of phytoplankton from coastal and open ocean areas[96–98] and macroalgae in the rocky intertidal zone[99]. Primary producers from a range of marine ecosystems also have higher abundance, biomass and/or per cent cover near seabird colonies (such as polar phytoplankton, subtropical seagrasses and temperate intertidal macroalgae)[86,96,100]. Although less is known about seabird nutrient effects on higher trophic levels (reviewed elsewhere[101,102]), on coral reefs seabird nutrients increase coral growth[103–105], fish growth[29,88,106] and fish biomass[88]. However, effects on biomass and abundance can be variable both within and among trophic levels (Table 1 and Box 1), in part owing to species interactions such as competition and predation[107,108]. For example, macroalgal cover has been shown to increase, decrease and remain similar across reefs with varying seabird nutrient inputs, probably owing to

Table 1 | Relative strength of terrestrial impacts of seabirds across biomes

Climate zone	Plant diversity	Plant biomass	Animal diversity	Animal biomass	Food web
Arctic	−−	+++	?	?	?
Northern Hemisphere temperate	−−	++	++	++	++
Tropical	−−	+	+++	+	?
Southern Hemisphere temperate	−−	++	++	++	++
Sub-Antarctic	−−	+++	?	?	?

Impacts assessments are based on studies included in this Review, with strength of the impact denoted with positive (+) or negative (−) notation. Each impact varies by factors discussed in Box 1. Many remain understudied, as indicated by question marks (?).

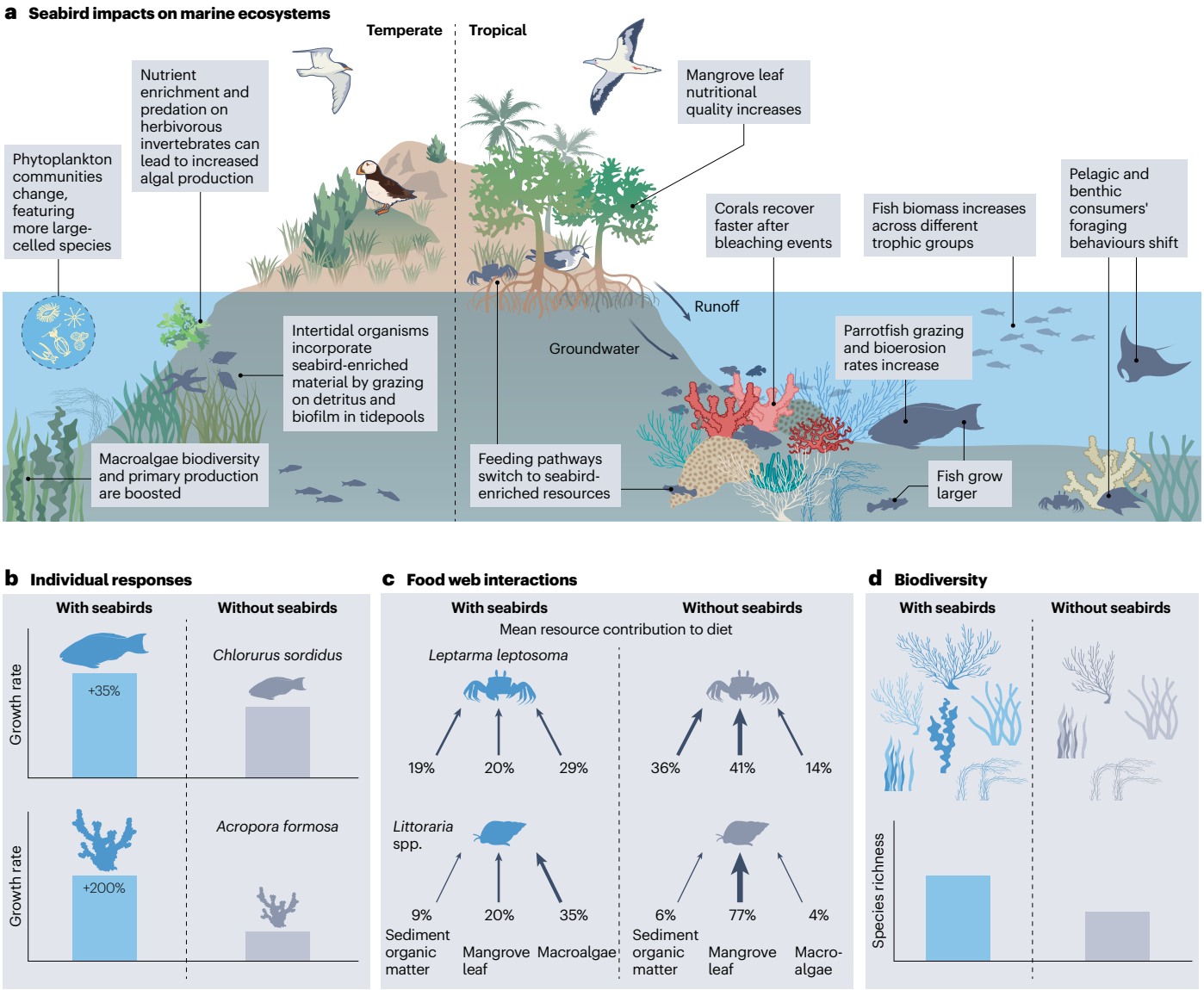


Fig. 3 | Seabird impacts on adjacent marine ecosystems. a, Impacts on temperate (left) and tropical (right) ecosystems. **b**, Coral and reef fish growth rates are boosted by seabird nutrients. **c**, Seabird presence reshapes food web interactions in a mangrove. **d**, Macroalgae diversity in a temperate intertidal system increases near seabird colonies. Data in part **b** are from refs. 88,103,104. Data in part **c** are from ref. 116. Data in part **d** are from ref. 33.

differences in available space and/or herbivory[109–112]. Similarly, even within a single system seabird nutrients can have different effects across species and trophic levels, resulting in altered community structure rather than a uniform increase in abundance or biomass across all organisms[30,107,113,114].

Seabird nutrient inputs enrich nearshore coastal food webs across multiple trophic levels[29,30,115–117] (Fig. 4). Like in terrestrial ecosystems, nutrient enrichment of primary producers in coastal and marine habitats, and their increase in biomass and abundance, can enhance herbivory rates. For example, in mangrove forests, seabird-derived nutrients boost mangrove productivity and improve leaf nutritional quality, leading to increased herbivory by folivorous insects[118]. On coral reefs, herbivorous parrotfish exhibit higher grazing rates on algae enriched by seabird-derived nutrients[88]. Seabird nutrient inputs also modify marine producer–consumer interactions by altering feeding pathways. In seabird-subsidized food webs, consumers can shift their resource use towards primary producers with higher concentrations of seabird-derived nitrogen. Such resource shifts have been observed across multiple ecosystems and taxa, including invertebrates in coastal ponds[119], mangroves[45] and nearshore waters[120,121], as well as cryptobenthic fishes inhabiting shallow coral reefs[106]. The hard coral *Pocillopora damicornis* adjusts its feeding strategy in response to seabird-derived nutrient availability, relying more on autotrophy when nutrient input is high, while shifting towards mixotrophy or heterotrophy when inputs are lower, depending on seasonal and site-specific

conditions[122] (Box 1). Additionally, seabird nutrient inputs can alter interactions by influencing consumer behaviour. For example, on coral reefs near seabird islands, damselfish feeding on turf algae enriched with seabird-derived nutrients show reduced foraging effort and smaller foraging territories while exhibiting more aggressive territory defence, compared with those on reefs near islands without seabirds[123].

In addition to species growth and food web interactions, seabird nutrient subsidies can also affect coastal biodiversity (Fig. 3). These impacts can differ in direction and intensity, with both positive and negative relationships identifiable in biodiversity and ecosystem function comparisons (such as biomass and productivity) across terrestrial and aquatic systems[124]. In coastal systems, guano enrichment can alter microbial[125] and phytoplankton[114] community structure and growth. The addition of nitrogen-rich guano in laboratory experiments resulted in an overall biomass increase and shifting species dominance[98]. Comparisons of natural seabird islands reveal slightly greater macroalgae species richness at high-density seabird islands[30] and seabird islands with the longest history of seabird presence relative to lower densities and shorter presence histories[40]. However, nearshore coral reefs show decreasing macroalgal richness, evenness and diversity with increasing seabird-derived nutrients[112]. Seagrass beds are more diverse with extensive coverage surrounding seabird islands compared with islands without seabirds[100]. Seabird nutrient subsidies do not alter biodiversity and ecosystem functioning relationships in coral reef fishes, but instead enhance ecosystem functions directly, and have marginal positive effects on biodiversity[89]. Biodiversity and ecosystem functioning relationships are highly dependent on the local ecosystem, trophic interactions and spatial scale[126–128]. Seabird nutrient subsidies could also influence biodiversity metrics differently based on biome (polar, temperate and tropical).

Supporting circular seabird economies

The circular seabird economy faces multiple ongoing and interacting threats. However, there are innovative methods to help to restore seabirds and their linkages to islands and oceans and ensure that the circular seabird economy is resilient to ongoing threats. Global climate change is a particularly pressing threat to the circular seabird economy, because it affects seabirds directly through sea level rise and increased storm frequency on low-lying breeding islands and indirectly through modulating seabird prey availability. Seabirds themselves might confer adaptive capacity to the terrestrial and marine ecosystems they connect, which will be increasingly important in an increasingly uncertain future.

Current threats to future resilience

Past and on-going anthropogenic activities at sea and on land have led to seabird extinctions, extirpations from breeding islands and reduced abundance on land and sea[129], thus interrupting the seabird circular economy for many land–ocean systems. Comprehensive syntheses of threats to seabirds on land and at sea have classified threat timing, scope and severity by species and identified where knowledge gaps exist[9,129]. Invasive predators remain the key threat to nearly half of seabird species worldwide[9]. Seabirds killed in fisheries, or bycatch, are the second most important threat to albatrosses and petrels. Other threats include overfishing of prey species, climate change altering prey

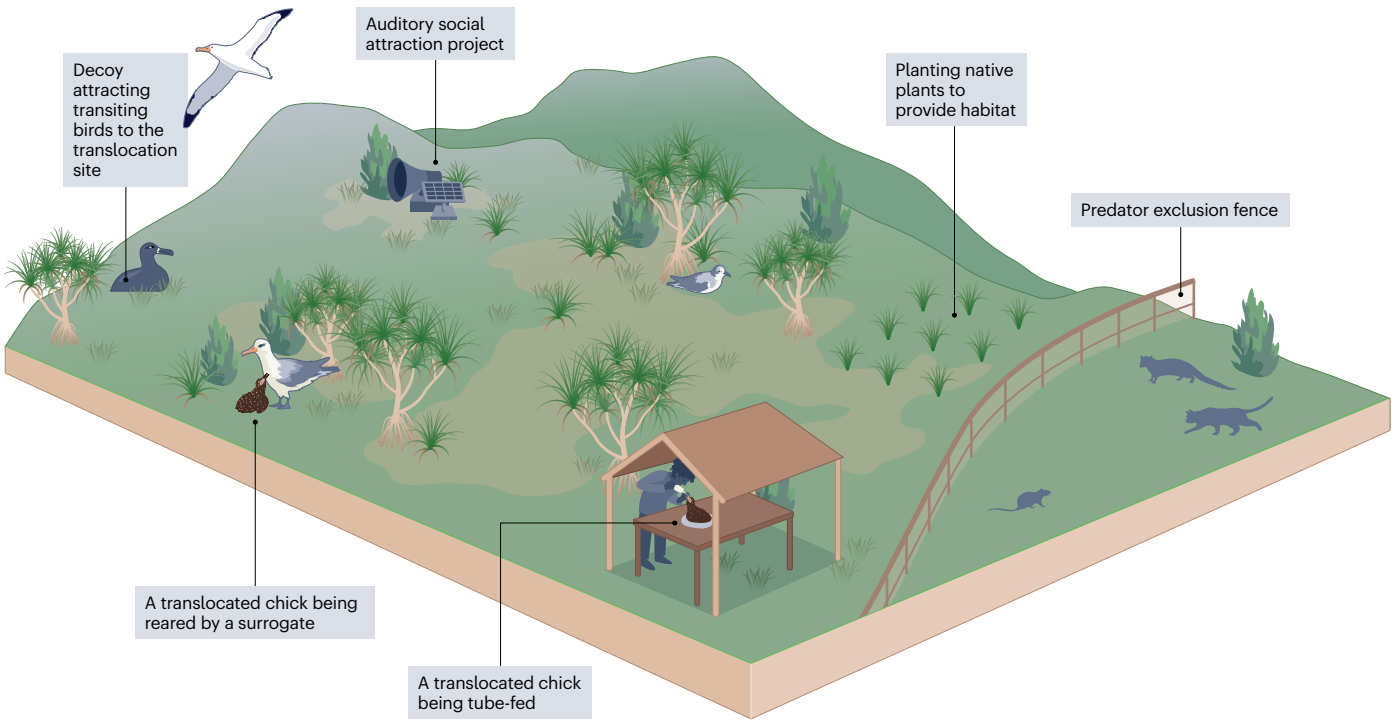


Fig. 4 | Seabird restoration methods. Predator exclusion fencing prevents invasive mammalian predators from accessing the newly established seabird colonies. Plantings of native plant species can provide habitat for seabirds to roost. Use of decoys can attract seabirds to suitable translocation sites. Auditory social attraction play-back systems with long-range speakers, a solar panel and battery can also be used for attracting seabirds to translocation sites. Finally, translocation interventions can support struggling populations, including tube feeding of chicks or establishment of interspecific surrogacy programmes.

distributions[130], direct harvesting of chicks and eggs[9], light pollution[131] and plastic pollution/ingestion[132–134]. The threats that seabirds face are increasing and intensifying, and novel threats are emerging, such as highly pathogenic diseases, pollution and offshore wind farm developments[135]. Although studies are increasingly investigating the cumulative and synergistic impacts of these multiple and dynamic threats to seabirds on land and at sea, understanding their complex interplay remains a considerable challenge[11].

Seabird restoration reconnects oceans and islands

Despite threats to seabirds, there are tools to ensure their future resilience by protecting existing colonies, increasing existing populations and establishing new colonies. Conserving existing colonies, establishing protected areas in and around those colonies and investing in biosecurity are common sense approaches. Removing invasive predators, either through eradication or predator-proof fencing, is often the first step to seabird recovery (Fig. 4) and has been shown to re-establish the circular seabird economy in many instances[29,136]. Once predators are removed, one way to kickstart seabird colonies is to restore native island vegetation so that seabirds have suitable nest-building materials, structural support for their burrows and nests and the improved ability to avoid avian predators[137,138] (Fig. 4).

Beyond restoring vegetation, by far the most common ways to increase extant populations or establish new colonies are through direct social attraction and/or translocation[95,139,140] (Fig. 4). Seabird social attraction uses visual, auditory, olfactory or a combination of these cues to entice target seabird species to (re)colonize and breed at a restoration site; this method has been used in over 800 restoration projects of at least 138 seabird species[95]. Many seabirds depend on social cues, such as the presence of other seabirds to select a nesting location[141–145], so social attraction often uses recorded vocalizations and decoys to attract new breeders[95,139,146]. Social attraction has been most successful on species with little natal philopatry and short generation times, such as gulls and terns, or when there are nearby source colonies[95,147]. A review of seabird restoration projects found that 83% of Laridae social attraction projects with known outcomes have resulted in successful breeding[148].

Many seabirds such as shearwaters, petrels, storm-petrels and albatrosses exhibit strong natal philopatry, which restricts the colonization of new restoration sites, even if social attraction is used[95,139,140]. For such species, egg or chick translocations are the best way to establish new colonies or increase existing ones. Most translocations involve moving cohorts of chicks from their natal colony to the restoration site before the chicks have imprinted on their natal colony. Translocated chicks then imprint on the restoration site and, upon sexual maturity, return to the restoration site to breed[95]. Of the 851 reported seabird restoration efforts up to 2021, only 6% have included translocation[95], because of the high cost of translocations, the expertise needed to rear chicks and the lack of identified suitable habitat for colony creation[140]. The founding translocated chicks help to socially attract other conspecifics and species. Translocated seabirds might also use new marine foraging grounds based on their new fledge location, which re-establishes or newly establishes a circular seabird economy around the restoration site. Seabird restoration can unite people and communities and increase the cooperation among communities, land managers and conservation practitioners, which also increases the chances of long-term success for the newly founded colony[139,140,149].

Most research studies the efficacy of seabird social attraction and translocation itself[95,143], rather than the ecosystem-level impacts of seabird restoration. What little work that has been conducted suggests that seabird translocation results in positive ecosystem impacts, including increased seabird-derived nutrients in island food webs and arthropod diversity[150]. Ecosystems also show marked improvements of nutrient cycling, biodiversity and community composition when seabirds passively recover from invasive mammal removal[29,66,68,136,137,151,152]. However, full restoration of all components of the circular seabird economy could take decades or longer, owing to different recovery times of various island ecosystem constituents[153]. Specifically, invertebrates and faster-growing plants tend to respond fastest to seabird density increases, whereas seabird-derived nutrient cycling and flora–fauna community composition take longer to recover[153]. Because they respond most quickly to restoration attempts, gulls and terns might be conduits of faster ecosystem restoration than species that respond more slowly, such as petrels, shearwaters and albatrosses. More research on which seabird species can most effectively recover the circular seabird economy could help practitioners seeking whole-ecosystem responses.

Restoring seabirds for climate change resilience

Restoring seabird colonies and augmenting existing ones through seabird restoration can help to combat the biodiversity crisis by restoring the circular seabird economy, with all the attendant impacts to islands and oceans. However, seabirds sit at the nexus of both the biodiversity and climate crises, and thus also have the potential to contribute to ecosystem adaptations and resilience against climate change.

The impacts of climate change on seabirds have been extensively reviewed[9,12,13], but few direct attempts have been made to determine the impacts of seabirds on climate change resilience (though see refs. 47,104,111). However, the broad-scale and large-scale effects of seabirds on ecosystem functioning suggest likely interconnectedness. Focusing on the major resilience factors and adaptive capacities of ecosystems, and how these are influenced by the circular seabird economy, can guide future research on the interactions between the circular seabird economy and climate resilience[60]. Particularly relevant is the extent to which seabirds improve the adaptive capacity of terrestrial and marine systems to climate-induced shifts (such as temperature, water availability, storm surge, sea level rise and severe weather events), as well as their potential to mitigate climate change via effects on carbon sequestration.

Given that the impacts of both climate change and the circular seabird economy vary across biomes, the relevance of seabirds for climate resilience will certainly vary biogeographically. As described, seabirds have particularly strong effects on nutrient cycling in polar and subpolar regions, where there are limited other external nutrient subsidies[22,26]. In turn, seabirds have a major role in shaping vegetation and maintaining the functioning of terrestrial and marine communities and ecosystems near their colonies, increasing localized climate resilience when such systems are protected or restored. However, seabirds might also negatively affect climate resilience and mitigation in the short term, especially in ecosystems in which plant communities are in the process of recovery, as seabird burrowing can alter forest regeneration and composition, which accelerates erosion[68,69,154].

More is known about the effects of seabirds on climate resilience in the tropics, where low-lying atoll and reef islands are major seabird hotspots[155,156]. To withstand projected sea level rise, increased storm surges and severe rain events, these islands require deposition of reef-borne materials to maintain their adaptive growth capacity[148,157,158], and intact coral reefs that provide a physical barrier

against high-energy oceanic erosive forces[159,160]. Through their nutrient inputs, seabirds can enhance these resilience factors by contributing to increased coral growth and calcification rates[103–105], sediment generation rates from bio-eroding parrotfish[88] and mangrove ecosystem productivity[116]. Tropical coral reefs are themselves some of the most vulnerable ecosystems to climate change, as increasing marine heatwaves cause mass die-offs of reef-building corals[161]. Seabird nutrient inputs contribute directly to coral reef resilience by facilitating faster coral recovery following extreme marine heatwaves[104] and might also indirectly enhance resilience through their effects on other reef organisms (for example, crustose coralline algae and herbivorous fishes)[88,111].

There is now increasing recognition that conservation interventions, such as eradicating invasive predators on islands, could also benefit climate resilience via benefits to seabirds, as well as by other direct and indirect effects[162,163]. Likewise, native vegetation, seabirds and climate resilience are intricately interconnected — with seabirds preferring native vegetation and also benefiting it via nutrient inputs[44], and native vegetation influencing climate mitigation via carbon stocks and climate adaptive capacity via soil stability[164]. Such feedback between climate change impacts on seabirds, and seabird impacts on climate change resilience, suggests that holistic ecosystem restoration could be an avenue to provide mutualistic benefits.

Summary and future directions

In Hawai'i, early naturalist observations, palaeontological, genetic and isotopic evidence, demonstrate 'ua'u or Hawaiian petrel were once widespread across the archipelago, and foraged at a higher trophic level in the pelagic zone[165–167]. On atolls, where comparable historical evidence is often intractable, seabird diversity and abundance thrives where anthropogenic threats are minimal, indicating seabird impacts globally were previously more widespread[88,168]. Thus, historically, seabirds were vastly more abundant, and circular seabird economies connecting oceans and islands were larger in magnitude and complexity than they are today. Despite global seabird declines, this Review presents the large-scale, cross-ecosystem impacts seabirds have both in oceans and on their associated islands. Seabirds have top predator roles in oceans, transfer nutrients to islands, resulting in unique biogeochemistry and ecology, both on islands and in surrounding marine communities. Even though seabirds continue to face numerous threats, restoration efforts have been largely successful; further restoration can ensure that the circular seabird economy continues

Box 2 | Emerging approaches to explore the circular seabird economy

The impacts of the circular seabird economy are far-reaching. Identifying and measuring useful indicators of these impacts are subject to time and logistical constraints, availability of expertise and technological limitations. However, the introduction and novel application of methods, including energetic approaches, eco-acoustics, remote sensing and omics techniques, is continually improving data collection capabilities and growing scientists' mechanistic, spatial and temporal understanding of the circular seabird economy.

Energy requirements, which underpin all biological and ecological interactions, have been largely neglected in conservation biology despite being a well-established field. The application of ecological energetics allows exploration of the influence of resource availability and use on organismal metabolisms and species interactions in various ecosystems and compares disparate organisms using a common currency[199]. Indeed, energetic approaches have been used to evaluate the influence of land-use changes on species diversity and dynamics[200] and to project the influence of tropical island restoration for seabirds and coral reefs[194]. Given that seabird energetics are inextricably linked to nutrient flows between trophic levels and across ecosystems, the predictive capacity of ecological energetic modelling can contribute useful indicators of a healthy seabird economy and support informed island management practices.

Remote-sensing methodologies provide additional opportunities to measure indicators over greater spatial and temporal scales, with higher sampling frequency and resolution. Non-invasive tools such as camera traps, drones and radar are already used to record seabird biomass and abundances[201,202]. Satellite images and Earth observation data that use hyperspectral or multispectral sensors can help to determine both direct and indirect seabird impacts on islands and nearshore habitats (reviewed elsewhere[203]). For example, seabird guano has a distinct spectral signature that can be used to locate seabird colonies[204], and spectral, infrared, chlorophyll *a* or turbidity sensors can identify nutrients in marine habitats[205,206], vegetation canopies[207–210] and the atmosphere[211]. Coupled with machine-learning or artificial intelligence approaches[212], automated analyses of vast amounts of imagery and remote-sensing data can be performed while reducing data-accessibility barriers. With increased availability and lowered cost of tools such as recording devices and analytical software[213,214], eco-acoustic monitoring has proven effective in non-invasively recording seabird biodiversity[215,216], colony density[165] and population recovery following seabird restoration efforts[166]. Eco-acoustics can also support measurements of cross-ecosystem impacts, as they are known to provide proxies for marine biodiversity[167] and ecosystem recovery[217].

The use of omics tools that rely on DNA or RNA in environmental or biological samples enables the identification of species presence or absence, relative abundance and activity of entire land–sea assemblages within areas influenced by seabirds. For example, environmental DNA can be used to estimate seabird biodiversity[218], understand seabird diet[219] or analyse ancient sedimentary DNA to recover historic seabird baselines[220]. Researchers can also use environmental DNA to detect invasive predators that might threaten seabird populations[221,222], and explore shifts or variability in entire marine communities[223,224]. Similarly, 16S rRNA metabarcoding can reveal the impact of seabird nutrient subsidies on microbial community dynamics in island soils[225] and nearshore marine habitats[112], offering early biological indicators of broader ecological change[226]. Additional (meta)genomics and (meta)transcriptomics tools could further elucidate taxa and genes associated with seabird-derived nutrient uptake to help to identify indicator species that might support a more mechanistic approach to ecosystem monitoring[227].

to thrive in the face of large-scale ecosystem change. In an ideal world, the seabird restoration techniques discussed in this Review could be the conduit for repairing lost linkages between oceans and islands globally. Indeed, if seabird restoration reaches its fullest potential, all sparsely or uninhabited islands would be rich in seabirds and the benefits they provide.

To restore the circular seabird economy at scale, there are important knowledge gaps that should be addressed regarding the recovery of nutrient cycling and ecosystem function during seabird recovery. These gaps can be filled using traditional and emerging approaches (Box 2). Seabird-derived nutrients, such as nitrogen, have measurable declines with time since seabird colony abandonment[169]. Although these nutrients often increase in the decades following invasive species removal[136,170], a historical baseline of isotopic enrichment or nutrient availability to evaluate recovery is rarely available, though the use of nearby, relatively undisturbed islands can be useful recovery targets[136,150,171]. Additionally, it remains unclear when islands no longer function as seabird islands — that is, when terrestrial island systems are no longer driven by seabird-derived subsidies. Seabird-derived nutrients can be highly localized in terrestrial systems, declining with distance from colonies[172], and with island size[151]. Further research on potential island size thresholds beyond which seabirds do not dominate nutrient cycling, or ecosystem circumstances that may prevent reinstatement of the circular seabird economy, is necessary. Ideally, researching seabird nutrient dynamics and island size thresholds would be done at scale throughout various biomes, to improve understanding of how patterns change across different ecosystems. The technology to track seabird impacts at scale is emerging (Box 2), and as it expands, so too will researchers' ability to tackle knowledge gaps globally.

Cross-system and marine effects began to be systematically studied around a decade ago[36,173–175]. Accordingly, knowledge about seabird nutrient effects is patchy, and several critical habitats such as mangroves, reefs, oyster beds and seagrass beds are understudied even when seabird benefits have been established. The partial or total absence of replication for some of these systems further limits researchers' ability to reliably quantify and predict seabird effects and how these interact with local conditions and stressors. Likewise, cross-system studies integrating both terrestrial and marine habitats remain scarce, representing 5% of all seabird effect publications[26], offering a poor understanding of the timescales over which terrestrial and marine outcomes return following seabird restoration[153]. This scarcity is in spite of extensive evidence of strong ecological connectivity between islands, coastal areas and the surrounding nearshore marine habitats, especially for atolls[60].

Beyond habitats, this patchiness extends to marine organisms, with very little understanding of how seabird nutrients affect marine consumers[36]. Likewise, there is a paucity of work on how seasonal and temporal variability affects seabird nutrient delivery (but see ref. 172). Importantly, the lack of systematic and replicated documentation of seabird effects in marine environments, both with respect to nearshore impacts and the link between nearshore impacts and the pelagic ecosystems in which most seabirds forage (for example, ref. 93), directly undermines the potential of these studies for building knowledge, informing decision-makers and guiding conservation practices that target marine environments[168]. Although this Review has mostly focused on regional scale impacts, it is important to note that many seabirds move within large global marine flyways[176], suggesting nutrient and energy flows with land–sea impacts at a global scale similar to other mobile marine vertebrates (for example, ref. 177) that have rarely been studied for seabirds. Future research must address these spatial and temporal gaps by fostering a more integrated marine-terrestrial, and planetary, perspective.

Gaps in knowledge about seabirds and their interactions have complex implications, which are probably underestimated in dominant forms of science. Seabirds provide both direct and indirect benefits to people and have a central role in many Indigenous cultures and local communities around the world, particularly given that coastal and island communities rely on both subsistence and market economies for their livelihoods[149]. For example, 80% of Maldivian tuna fishers navigate and locate fishing grounds by following seabirds[178]. Seabirds provide provisioning, supportive and cultural services with sizeable historical connections to human sustenance and local economies in which communities mined seabird guano as a fertilizer for agriculture and harvested seabirds and their eggs for food[179]. The benefits of the circular seabird economy to people largely focus on the indirect impact that their supportive services (nutrient cycling, seed dispersal and ecosystem engineering) have to the ecosystems that people rely on — such as increased fish biomass[88], improved coastal ecosystem resilience[104] and carbon sequestration[163].

Moreover, dominant forms of science have eschewed Indigenous and traditional ecological knowledge, potentially placing conservation actions such as restricting seabird harvesting at odds with Indigenous resource management practices[149]. Future research into the benefits of the circular seabird economy should seek a more holistic, people-centred approach that integrates Indigenous ways of knowing, perspectives and cultural benefits.

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