Influence of seabird nutrient input on intertidal ecology in the Farne Islands, Northumberland

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Declarations

I hereby declare that this dissertation is my own work and has not been submitted in substantially the same form for the award of a higher degree elsewhere. No sections of the dissertation have been published for a higher degree elsewhere.

Samuel Healing: Influence of seabird nutrient input on intertidal ecology in the Farne Islands, Northumberland

Abstract

Seabirds are keystone species, providing inter-habitat connectivity by transporting vast quantities of nutrients from their pelagic feeding grounds to terrestrial and marine ecosystems, dictating community structure and dynamics, and providing multiple ecosystem services. This flow of nutrients is being disrupted by human activities, such as invasive species, and seabirds are now one of the most threatened bird groups. Whether seabird nutrients are cycling through nearshore, temperate systems, in particular in the United Kingdom (UK), impacting biodiversity and productivity, and how these inputs may vary temporally, remains unknown. The impact of nutrient subsidies to the Farne Islands, Northumberland, areas of high seabird densities during breeding season, was compared to nearby low seabird density areas on the Northumberland coast. Seabird densities and nitrogen inputs of up to 2334 and 1054 times higher, respectively, on seabird islands resulted in both substantially enriched nitrogen stable isotope ($\delta^{15}N$) values and higher total nitrogen content in terrestrial and intertidal organisms, including soil, terrestrial plants, lichen, barnacles, and limpets, and just higher $\delta^{15}N$ values in macroalgae and turf algae. Temporal variation was also detected, though, surprisingly, nitrogen loads were higher during early breeding season. Some support was found for increased biodiversity in intertidal areas of seabird islands, in higher densities of intertidal predators and marginally greater algal species richness, though diversity differences were small overall. A marginal difference in limpet size was found, whilst on plots artificially cleared to simulate a disturbance event, barnacles were unexpectedly found to recolonise faster on mainland sites, which was likely caused by the mainland's increased exposure level. These findings provide evidence that seabirds are cycling pelagic nutrients into terrestrial and intertidal ecosystems on UK islands, though support for seabird nutrient input increasing biodiversity and productivity was mixed. Given the threats to seabirds globally, these findings promote seabird conservation, including the removal of invasive species, such as rat eradication programmes.

Chapter 1: General introduction

Seabirds often nest at high densities, supplying vast quantities of nutrients across ecosystems, influencing community structure and dynamics to the extent that they have been described as keystone species (Mulder *et al.*, 2011). Indeed, global quantities of the total nitrogen and phosphorous supplied by seabirds have been estimated to be approximately 600 and 100 million kg per year (Otero *et al.*, 2018). Nutrient subsidies enter many ecosystems, influencing productivity, functioning, diversity, biomass, and community dynamics, boosting food availability and quality, and providing ecosystem resilience (Polis *et al.*, 1997; Lundberg & Moberg, 2003; Loreau & Holt, 2004; Benkwitt *et al.*, 2019). Yet, compared to top-down control of marine ecosystems by seabirds, studies on bottom-up effects of seabirds to nearshore ecosystems remains understudied (Kazama, 2019). Some research has been performed in temperate systems globally (e.g., Mulder *et al.*, 2009; Jones, 2010; Gagnon *et al.*, 2013), but research in the United Kingdom and Crown Dependencies (hereafter referred to as UK) remains extremely limited. The current work aims to determine whether seabird nutrients are moving through terrestrial and intertidal ecosystems, and whether those nutrients are differing temporally, or influencing biodiversity and productivity, to improve understanding of both temperate and UK nearshore systems.

The role of nitrogen and stable isotopes

Nitrogen and phosphorous are limiting nutrients across many ecosystems. Seabirds transport both nitrogen and phosphorous from the open ocean to coastlines and islands, predominantly through guano, but also in the form of marine prey items that drop on the colony, whole or in stomach oils, lost feathers, abandoned or destroyed eggs, and individuals that die on land (Smith *et al.*, 2011). These allochthonous nutrients influence productivity, functioning, diversity, biomass, and community dynamics, boosting food availability and quality, and providing ecosystem resilience (Polis *et al.*, 1997; Lundberg & Moberg, 2003; Loreau & Holt, 2004; Benkwitt *et al.*, 2019).

Along with carbon, nitrogen is commonly used in stable isotope analysis, where the ratio of ^{15}N to ^{14}N, expressed as $\delta^{15}N$, is compared. Stable nitrogen isotope analysis provides trophic level estimates: greater $\delta^{15}N$ ratio is present in

predator diets, such as seabirds, due to their diets of fish, squids, and other high trophic level species (Hobson & Welch, 1992). In the context of seabird nutrient input, stable nitrogen isotope analysis is used to trace seabird-derived subsidies in food webs, therefore providing evidence of the flow of seabird nutrients from the open ocean to island and coastal ecosystems.

Effects of seabirds across ecosystems

Terrestrial systems: plant and soil chemical characteristics
Globally, there are approximately one billion seabird individuals (De La Peña-Lastra, 2021), which have been estimated to excrete fluxes of 591 Gg nitrogen year^{-1} and 99 Gg phosphorous year^{-1}. Indeed, the magnitude of the flows between marine and terrestrial environments by breeding seabirds is of the same order of magnitude for nitrogen as global scale phenomenon including lightening, nitrogen fixation by rice cultivation, and inputs to the ocean via groundwater. For phosphorous, the flows between marine and terrestrial environments by breeding seabirds is of a similar order of magnitude such as those occurring between oceanic waters and atmosphere, and those produced by fishing activities and (Otero *et al.*, 2018).

A review on plant and soil chemical characteristics was performed by Mulder *et al.* (2011a), with emergent trends found across 98 islands in eight systems globally. Relationships were identified between seabird density and soil chemistry, leaf chemistry, leaf growth form, and plant life history responses. Seabird density drove changes in most soil chemistry variables, with similar relationships evident across all systems: a marginal positive relationship between soil % nitrogen and seabird density; significant positive relationships between % phosphorous, % carbon, and nitrogen stable isotope ratio of δ^{15}N and seabird density; significant negative relationships between pH and seabird density. Both positive relationships and no relationship have both been found between seabird densities and both leaf chemistry and δ^{15}N. The relationship between leaf chemistry and nest density was found to increase linearly, stabilising at moderately high densities of seabirds, suggesting a limit at which plants may reach nitrogen saturation.

Terrestrial systems: plant communities

A literature review on the impacts of seabirds on plant communities has been performed by Ellis *et al.* (2011), which included the effects of seabird physical disturbance and seed dispersal as well as the alteration to soil conditions, all of which shape or modify plant stature, growth rates, nutrient status, and community composition. Response variables were plant species richness; relative abundance of plant growth forms; abundance of particular plant taxa; and proportion of non-native plant species. Further, Ellis (2005) review of seabird's impact on plant and soil chemical characteristics included the response variables plant biomass and community composition. Relationships with clear magnitudes and directions were observed only in species richness and the abundance of particular plant taxa. Suggested reasons for these relationships include system-specific conditions such as climate and latitude gradients that impact moisture levels (e.g., arid conditions resulting in guano causing toxicity; Hutchinson, 1950; Wait *et al.*, 2005). Other investigated response variables were island size (Hogg *et al.*, 1989); species-specific vegetation preference (e.g., ground-nesting birds choosing islands with fewer shrubs or trees; Ellis *et al.*, 2011); the nutrient status of recipient system (e.g., Wedin David & Tilman, 1996); and species-specific nesting behaviours, ranging from high-density (> 1 nest m^{-2}) cormorants (*Phalacrocorax carbo*; Ellis *et al.*, 2006) to low-density (3 nests ha^{-1}) wandering albatross (*Diomedea exulans*; Joly *et al.*, 1987).

Plant species richness was found to decrease with seabird density on islands in four island systems: Stockholm Archipelago (Kolb & Palmborg, unpublished data); Gulf of Maine (Mittelhauser, unpublished data); Northeast New Zealand islands (Fukami *et al.*, 2007; Bellingham *et al.*, 2010); and Gulf of California islands (Wait *et al.*, 2005). These results suggest that the physical disturbance and nutrient input from seabirds eliminated plant species that were intolerant of these conditions; the toxicity of elevated nutrients to slow-growing plant species promoted the growth of fast-growing species, thereby reducing species richness. Indeed, plant species on seabird islands have been found to be characterised by high relative growth-rates, abundant seed production, persistent soil seed banks, and tolerance or dependence on high nutrient levels and physical disturbance (Grime, 2001). Ellis (2005) reported species richness to be highest in areas of intermediate seabird presence, as whilst seabirds

increased nutrient availability to plants, the increased physical disturbance, including nesting, burrowing, trampling, and plant uprooting, caused an overall decrease to species richness when seabird numbers were extreme.

Plant biomass varies in the presence of seabirds. In wet years, seabirds can increase plant biomass by 11.8-fold (Anderson & Polis, 1999), whereas in dry years, seabird presence can cause a reduction in plant biomass (Sanchez-Pinero & Polis, 2000), as can extremely high seabird abundance (Smith, 1978; Joly *et al.*, 1987). Increased vegetation cover was observed on Baccalieu Island, Newfoundland and Labrador, Canada, due to Leach's Storm Petrels (*Hydrobates leucorhous*). Here, seabirds acted as ecosystem engineers by markedly modifying island vegetation cover and composition. Vegetation cover increased from approximately 23% to approximately 58% between 1940 and 2017, in part coinciding with seabird colony growth until around 1980 (Duda *et al.*, 2020).

Changes to plant community composition have been found to vary under the influence of seabird nutrients. Both an increase to cosmopolitan over native plant species (Hogg & Morton, 1983; Hogg *et al.*, 1989; Vidal *et al.*, 2003), and the converse (Dean *et al.,* 1994; Kamijo & Yoshinobu, 1995) have been observed, with nest density and species-specific nesting behaviours suggested as stronger drivers of magnitude and direction of causation (Ellis, 2005). Overall, despite the prohibitive effects of physical disturbance associated with extreme seabird abundance, Ellis (2005) found the increased nutrient availability to have a positive impact upon plant and soil ecological responses. A more recent study also found $\delta^{15}N$ values in terrestrial plants to be highest inside seabird colonies, and decreasing with increasing distance from the colonies (Pascoe *et al.*, 2022).

Seabirds have also been shown to be drivers of terrestrial ecosystem shift. A 14,000-year multiproxy record found that the Falkland Islands underwent changes in terrestrial plant community structure, composition, and function following seabird colony establishment. Driven by the newly introduced marine-derived subsidies, the region shifted from low levels of grass and a heathland of ferns and dwarf shrubs to coastal grasslands (Groff *et al.*, 2020).

Terrestrial systems: island consumers

Island seabird nutrient consumers can be considered direct consumers of seabirds, such as ectoparasites, scavengers, and the predators of those groups, or indirect consumers of species that have assimilated seabird nutrients, such as herbivores, detritivores, and the predators of those groups (Kolb *et al.*, 2011). Seabirds subsidising consumer diets has been explored through changes in the carbon stable isotope ratio of ^{13}C:^{12}C content (expressed as δ^{13}C) and δ^{15}N, as changes to both δ^{13}C and δ^{15}N can be used to trace seabird-derived subsidies in island food webs, therefore providing evidence of the flow of seabird nutrients. All consumers across six systems, including arthropods (e.g., Polis & Hurd, 1996), reptiles, and mammals (e.g., Bancroft, 2004), were more enriched in δ^{15}N on islands with seabirds than those without. Numerical responses were examined to provide information on population- and community-scale effects of seabird nutrients, with higher abundances of consumers on seabird islands observed across the majority of taxa, trophic levels, latitudes, and ecosystems.

Improvements to body condition, survival, and behavioural responses due to seabird nutrient input were also observed in species such as the dibbler, an endangered marsupial (*Parantechinus apicalis*; Wolfe *et al.*, 2004); however, confounding variables resulted in inconsistent observations in other studies. Changes to consumer species richness and community composition remains understudied. Examples include increases to species richness in invertebrates on wandering albatross island colonies (*Diomedea exulans*; Joly *et al.*, 1987) and spiders on mixed-seabird colonies (Towns *et al.*, 2009). However, seabird nutrients had no influence on beetle species richness on yellow-legged gull island colonies (*Larus michahellis*; Orgeas *et al.*, 2003), nor in nematodes and gastropods on mixed-seabird colonies (Towns *et al.*, 2009). In spiders on islands around Tasmania, though, the influence of seabird nutrients is highly localised, with high δ^{15}N inside seabird colonies, and decreasing with increasing distance from the colonies (Pascoe *et al.*, 2022). The variation observed in consumers across systems suggests that communities are regulated by numerous variables, including the structure and heterogeneity of food webs and top-down effects as well as bottom-up effects of seabirds (Hairston *et al.*, 1960; Hunter & Price, 1992; Fagan, 1997).

Seabird nutrients that enter terrestrial systems are not necessarily taken up by all consumers. For example, on Malpelo Island, Colombia, crickets, millipedes, and Hymenoptera in seabird colonies had $\delta^{15}N$ values consistent with autochthonous terrestrial species, whilst lizards, crabs, Isopoda, Araneae, Lumbricullidae, and *Odontomachus* sp. had $\delta^{15}N$ values that were up to twice as isotopically enriched, consistent with those enriched by seabird nutrients (Estupiñán-Montaño *et al.*, 2022). Indeed, patterns of spatial seabird isotopic influence can be complex, as seen on the Abrolhos Archipelago, Southwest Atlantic Ocean, a small tropical island system (Linhares & Bugoni, 2022). Here, whilst seabirds affected all trophic levels, including consumers grasshoppers, tarantulas, and lizards, consumers obtained allochthonous resources from subsidised terrestrial organisms from outside the colony, with lower $\delta^{15}N$ consistently found in consumers inside the colony. This may be explained by intensed nitrogen fractionation occurring following guano deposition in soils (Mizutani & Wada, 1988), and a reduced use of terrestrial resources from within seabird colonies.

Freshwater systems

Young *et al.* (2011) performed a literature review on the effects of seabird- and waterbird-derived nutrients on aquatic systems, finding a total of 27 studies on freshwater systems. The effects upon nutrient concentrations were examined in 13 studies, with all showing increased nutrient budgets due to birds. Birds were found to account for 28-40% of nitrogen budgets, and 17-95% of phosphorous budgets (Manny *et al.*, 1994; Post *et al.*, 1998; Kitchell *et al.*, 1999; Boros *et al.*, 2008). Increased concentrations of total nitrogen, total phosphorous, and dissolved organic carbon by approximately three times, ten times, and five times, respectively, have also been found at sites influenced by seabirds in a more recent study (Duda *et al.*, 2021). Whilst most studies found evidence of systems strongly dependent on birds for nutrients, there were also instances where nutrient subsidies were associated with foraging or nesting activity, causing them to be local and temporary (Marion *et al.*, 2004; Hahn *et al.*, 2008). Moreover, a study in Florida, United States, examined 46 lakes, finding that birds contributed only 2.4% of the total annual phosphorous load (Hoyer & Canfield, 1994), whilst

in Kis-Balaton, a very large lake in Hungary, effects were also found to be very small (Gere *et al.*, 2006).

The effects of seabird nutrient inputs on primary producers in freshwater systems also generally increased in magnitude due to birds. Of the nine studies that looked at primary producers, five found increases in chlorophyll-*a* in phytoplankton of up to ten-fold (Oliver & Schoenberg, 1989; Kitchell *et al.*, 1999; Izaguirre *et al.*, 2004; Blais *et al.*, 2005; Keatley *et al.*, 2008), whilst one concluded an independent measure of higher primary production was due to increased bird-derived nutrient concentrations (Manny *et al.*, 1994). Two others were experimental studies, finding added guano had a limited (Pettigrew *et al.*, 1997) or no (Unckless & Makarewicz, 2007) response of chlorophyll-*a* in phytoplankton. The study of the 46 lakes in Florida similarly found no correlation between bird abundance and primary producers (Hoyer & Canfield, 1994).

The effects of consumers in freshwater systems is less studied compared to those on primary producers. Oliver & Schoenberg (1989) found increased planktivorous fish abundance due to bird nutrient input; Harding *et al.* (2004) found elevated $\delta^{15}N$ in aquatic invertebrates; Payne & Moore (2006) found elevated $\delta^{13}C$ and $\delta^{15}N$ in grazers (snails) and carnivores (freshwater fish). In contrast, experimentally adding waterbird guano to prairie wetlands produced little response in microinvertebrates (Pettigrew *et al.*, 1997).

Overall, seabirds and waterbirds have been found to increase nutrient concentrations, primary production, consumer abundance, $\delta^{13}C$ and $\delta^{15}N$. However, seasonable and local variability exists, which is largely attributed to bird abundance, water body size, and water flow patterns (Oliver & Schoenberg, 1989; Pettigrew *et al.*, 1997; Blais *et al.*, 2005). Modelling-based approaches supported seabirds and water birds providing large nutrient inputs (Hahn *et al.*, 2007; Hahn *et al.*, 2008). Indeed, evidence suggests that small water bodies, where nutrients do not settle or rapidly dissipate, are the most likely to be affected by bird nutrients (Portnoy & Soukup, 1990; Manny *et al.*, 1994; Marion *et al.*, 2004). However, the field remains understudied. More research is required to draw generalising conclusions, and to determine how the impact of bird-derived nutrients varies across recipient ecosystems.

Marine systems: overview

The benefits of increased seabird nutrients in terrestrial systems are often mediated by physical disturbance of the environment or can even result in toxicity in non-adapted plant species (de Graaf *et al.*, 1998; Stulen *et al.*, 1998; van den Berg *et al.*, 2005). Marine ecosystems will not undergo such disturbance of the environment, as the constant movement of ocean waves, tides, and currents are likely to reduce dilute the dominant source of seabird nutrient, guano, reducing the likelihood of eutrophication or pollution, which has been observed in freshwater systems (e.g., Benton *et al.*, 1983; Blais *et al.*, 2005). These factors suggest that marine ecosystems may experience the positive effects associated with seabird presence while being less subject to the negative effects sometimes observed in terrestrial and freshwater systems. However, the general trend of decreasing influence of bird nutrients with increased water body size and flow patterns in freshwater systems suggests that in marine systems seabird nutrient input may be reduced by the ocean's vast water body sizes and generally faster nutrient dissipation caused by waves, tides, and currents. Indeed, the presence of $\delta^{15}N$ in organisms has repeatedly been observed decreasing with increasing distance from seabird colonies in saltwater systems (Jones, 2010; McCauley *et al.*, 2012; Lorrain *et al.*, 2017; Savage, 2019; Benkwitt *et al.*, 2021a).

Marine systems: nutrient concentrations

Young *et al.* (2011) systematically reviewed the literature on the bottom-up effect of seabird nutrients to marine ecosystems published prior to 2010, finding a total of 34 studies. The effects of seabirds on nutrient concentrations in marine systems were examined in 15 studies, with 12 finding guano to cause an increase in nutrients (e.g., Littler *et al.*, 1991; Palomo *et al.*, 1999). However, greater variability was observed in saltwater systems compared to freshwater. Causation was accredited to already-abundant nutrients due to anthropogenic inputs, as well as well-mixed or vertically-mixed oceans (Bedard *et al.*, 1980; Tatur, 2002), with the use of stable isotope analysis hailed as helping determine the role of guano in the Bedard *et al.* (1980) study. Three instances that Young *et al.* (2011) describe as guano causing eutrophic conditions were observed, all within the intertidal zone (Bosman *et al.*, 1986; Bosman & Hockey, 1988; Powell *et al.*,

1989), though none of the authors of the individual studies describe the conditions as eutrophic.

Marine systems: primary producers

Young *et al.* (2011) argue that measuring water column nutrient concentrations may not quantify nutrient input from birds, due to settlement into the sediment and nutrients being taken up by primary producers. Consequently, Young *et al.* (2011) report 14 studies that looked at the effects of seabird- and shorebird-derived nutrients on marine producers as a better representation of the influence of nutrient input from birds. Almost all of these 14 studies found birds to have a direct positive impact on primary producer abundance, including macroalgae, phytoplankton (Methratta, 2004), lichens (Wootton, 1992), and seagrass (Powell *et al.*, 1989). The only instance of decreased algal abundance occurred in enclosed rock pools along the Baltic Sea shores near Stockholm, Sweden, where the ammonia concentrations likely had a toxic effect on the algae (Ganning & Wulff, 1969). Young *et al.* (2011) suggest that isotopic analyses of primary producers and their consumers may provide the greatest insights to seabird nutrient cycling. Five isotopic studies had been published prior to 2010. Comparing the effects in areas near to seabird colonies against areas away from seabirds, two found higher $\delta^{15}N$ & $\delta^{13}C$ signatures in algae (Mizutani & Wada, 1988; Wainwright *et al.*, 1998); two found elevated $\delta^{15}N$ status in algae (Wada *et al.*, 1981; Kolb *et al.*, 2010); and one found elevated $\delta^{15}N$ status in macroalgae at one site, but similar $\delta^{15}N$ status in macroalgae at a second site (Schmidt *et al.*, 2004).

More recently, high $\delta^{15}N$ values have been observed zooxanthellae, macroalgae, and turf algae (Lorrain *et al.*, 2017; Graham *et al.*, 2018; Savage, 2019). Further, in Svalbard, $\delta^{15}N$ values were over four times higher in marine algae from seabird-impacted sites compared to control sites (Finne *et al.*, 2022). Recovery of seabird populations following mammal eradication programmes looked at the impacts of macroalgae on islands with three invasion histories: never invaded by mammalian predators, eradicated over 30 years ago, and eradicated two years ago (Rankin & Jones, 2021). Macroalgal diversity was greatest at never-invaded islands, followed by islands where mammals were eradicated 30 years ago, with diversity lowest at islands where mammals were

eradicated two years earlier. δ¹⁵N values were also compared, with the highest δ¹⁵N, of up to around 20% higher, found on never-invaded islands, followed by islands that were where mammals were eradicated two years earlier, with the lowest δ¹⁵N values found on islands where mammals were eradicated 30 years earlier. A possible explanation may be discrepancies in island sizes, and presence of streams, estuaries, and sheltered bays.

Marine systems: consumers

The effects of seabirds and shorebirds on consumers in marine systems are more complex, as whilst nutrient subsidies can result in bottom-up interactions, birds predate upon marine consumers, and so also exert top-down interactions. Young *et al.* (2011) report 18 studies that looked at the effects of seabird- and shorebird-derived nutrients on consumers in marine systems, eight of which investigated the ecological responses of consumers to seabird nutrients, with all eight reporting ecological positive responses to bird nutrients. Responses included increases in abundances of mussels (Marsh, 1986), polychaetes (Bosman & Hockey, 1986), crustaceans (Zelickman & Golovkin, 1972), and limpets (Bosman & Hockey, 1988), as well as increases in the density of emergent midges (Kolb *et al.*, 2010) and increased crab burrows (Palomo *et al.*, 1999). Multi-trophic level impacts were investigated in some studies, such as higher mangrove growth rates resulting in increased terrestrial insect herbivory (Onuf *et al.*, 1977), or increased phytoplankton biomass, though macroalgal and macroinvertebrate diversity was found to decrease on high seabird density locations (Methratta, 2004). Impacts on the top-down effects of birds were observed in a number of studies, including invasive rat populations decimating bird densities, resulting in increased intertidal consumer abundance due to the decreased predation by birds, shifting community structure from one that was algal-dominated to one that was sessile invertebrate-dominated (Kurle *et al.*, 2008). The top-down influence of birds on the abundance of limpets was also investigated, with a decreased (Frank, 1982) and mixed response (Wootton, 1992) to bird abundance observed, as well as birds reducing urchin abundance, altering algal cover and taxonomic richness (Wootton, 1995).

Since the literature review by Young *et al.* (2011), a number of studies have looked at the influence of seabird nutrient input on marine consumers,

discussed in the section below (marine systems: stable isotope analysis). The Finne *et al.* (2022) study also looked at consumers, finding elevated $\delta^{15}N$ signals in Amphipods of 8.4‰ at seabird-impacted sites compared to 7.0‰ at control sites.

Marine systems: stable isotope analysis

Overall, Young *et al.* (2011) found seabird nutrients to produce positive ecological responses in marine systems, though there are cases where no effect was found (Bedard *et al.*, 1980), or eutrophication (e.g., Bosman *et al.*, 1986; Bosman & Hockey, 1988). However, it is suggested that such studies might have been reported differently had stable isotope analysis been possible at the time. Furthermore, Young *et al.* (2011) close their review by calling for future research to include investigations on the nearshore communities and the use of $\delta^{15}N$ as a reliable tracer of seabird nutrient input into marine systems.

A follow-up literature review to Young *et al.* (2011) on the bottom-up effects of seabird nutrients to marine ecosystems was performed by Kazama (2019) on studies published between 2011 and 2018, in which stable isotope analysis was again promoted as a method of tracking the flow of seabird derived nutrients through the environment and the effects on the ecosystem in open aquatic systems. Resultantly, much of the focus of the review by Kazama (2019) is on studies that measured $\delta^{15}N$ to track the flow of nutrients. Eight studies were found that met this criterion (including their own unpublished research), whilst a further three studies have been published between 2018 and 2022 (Table 1).

Table 1 Studies examining bottom-up effects of nutrients supplied by seabirds in open marine systems using stable isotope analysis since 2011. Note: * denotes studies published since 2018; POM: particulate organic matter; SOM: sedimentary organic matter.

Study	Location	Organisms or material responding to seabird nutrients	Observed effects (near seabird colony relative to areas far from colony)
McCauley *et al.* (2012)	Palmyra, Central Pacific	Soil, tree leaves, sponges, clams, zooplankton, manta rays	High abundance: zooplankton, manta rays High $\delta^{15}N$: soil, tree leaves, sponges, zooplankton, clams
Gagnon *et al.* (2013)	Baltic Sea, Finland	Macroalgae, periphyton, isopods, gastropods	High $\delta^{15}N$: all organisms Change in herbivore feeding habits
Zmudczyńska-Skarbek *et al.* (2015)	Svalbard, Norway	Kelp, terrestrial plants, urchin, crabs	High $\delta^{15}N$: crab, terrestrial plants High N content: kelp, terrestrial plants Low $\delta^{15}N$, N content: urchins
Honig & Mahoney (2016)	Hawaii, USA	Macroalgae	High $\delta^{15}N$
Lorrain *et al.* (2017)	Hawaii, USA	Coral, zooxanthellae	High $\delta^{15}N$: all organisms (within 100 m from shore)
Zmudczyńska-Skarbek & Balazy (2017)	Svalbard, Norway	POM, SOM, gastropods (*Buccinum sp.* and *Magarites helicinus*)	High $\delta^{15}N$: POM, SOM, *Buccinum sp.* No $\delta^{15}N$ difference: *Magarites helicinus*
Graham *et al.* (2018)	Chagos Archipelago, Indian Ocean	Macroalgae, turf algae, sponges, damselfish	High $\delta^{15}N$: all organisms Increased biomass and rapid growth: damselfish
Kazama (unpublished data)	Rishiri Island, Japan	POM, macroalgae, seagrass, kelp, gastropods, mussels	High $\delta^{15}N$ and N content: all organisms
	Kabishima, Japan	POM, macroalgae, seagrass, kelp, gastropods, mussels, crabs	No effects observed
	East Sand, Oregon, USA	Turf algae, macroalgae, gastropods, mussels, shrimps, catfish	High $\delta^{15}N$: turf algae, macroalgae No $\delta^{15}N$ difference: gastropods, mussels, shrimps, catfish
Savage (2019)*	Namena, Kubulau, Fiji	Coral, zooxanthellae	High $\delta^{15}N$: zooxanthellae Increased growth rate: coral
Benkwitt *et al.* (2021b)*	Chagos Archipelago, Indian Ocean	Parrotfish	Increased growth rate and mean body size Decreased size-based fecundity No $\delta^{15}N$ difference
Benkwitt *et al.* (2021a)*	Chagos Archipelago and Scattered Islands, Indian Ocean	Soil, terrestrial plants, macroalgae, damselfish	Increased probability of high $\delta^{15}N$: all organisms Increased growth rate (near never rat invaded islands): damselfish

			No effect to growth rate (near recently rat eradicated islands): damselfish
Linhares & Bugoni (2022)*	Abrolhos Archipelago, Southwest Atlantic Ocean	Soil, terrestrial plants, grasshoppers, tarantulas, lizards, coral	Low δ^{15}N: soil, terrestrial plants, grasshoppers, tarantulas, lizards Mixed δ^{15}N: coral High N content: terrestrial plants No N content difference: soil
Finne *et al.* (2022)*	Alkhornet, Svalbard	Water samples, filamentous stream algae, macroalgae, amphipods	High nitrate, nitrite, phosphate: water samples High δ^{15}N: all biota

Eleven of the thirteen studies (Table 1) investigated the effects of seabird nutrients to primary producers. Enriched $\delta^{15}N$ ratios were found in each study with the exception of Linhares & Bugoni (2022), although whilst Zmudczyńska-Skarbek et al. (2015) observed a higher $\delta^{15}N$ ratio in terrestrial plants, they also observed no $\delta^{15}N$ difference in kelp, and Kazama (unpublished data) also observed no $\delta^{15}N$ differences in one of their three sites (Kabishima, Japan). Nitrogen content in primary producers was also higher in kelp, terrestrial plants, macroalgae, and seagrass (Zmudczyńska-Skarbek et al., 2015; Linhares & Bugoni, 2022; Kazama, unpublished data).

Positive bottom-up effects of seabird nutrients on consumers were observed in eight of the eleven studies (Table 1), with the exceptions being gastropods in Kabishima, Japan Kazama (unpublished data). The exceptions to higher $\delta^{15}N$ in the presence of seabirds were one of Kazama's (unpublished data) three sites (East Sand, Oregon, USA), where no $\delta^{15}N$ difference was found in gastropods, mussels, or crabs, mixed $\delta^{15}N$ values in corals (Linhares & Bugoni, 2022), mixed $\delta^{15}N$ results across different species observed by Zmudczyńska-Skarbek et al. (2015), who found high $\delta^{15}N$ content in crabs, but low $\delta^{15}N$ content in urchins, and Zmudczyńska-Skarbek & Balazy (2017), who found high $\delta^{15}N$ in *Buccinum sp.*, but no $\delta^{15}N$ difference in *Magarites helicinus*. Changes to abundances were investigated in one study, where seabird nutrients were found in zooplankton and manta rays (McCauley et al., 2012). Finally, following nutrient enrichment from seabird colonies, increased consumption of periphyton by grazers over filamentous algae was observed in the isopod *Idotea balthica* and the gastropod *Theodoxus fluviatilis*, implying a dietary preference in the herbivores (Gagnon et al., 2013).

Publications since 2011 reveal that the bottom-up effects of seabird nutrients almost always positively influenced marine ecosystem primary producers and consumers, predominantly through enriched $\delta^{15}N$ ratios. The instances where a positive effect was not observed may be explained by the nutrient status of the existing system: in oligotrophic conditions, nutrients will enhance productivity (Savage, 2019); in otherwise balanced systems or those subject to anthropogenic inputs, seabird nutrients may have no effect, or even be a source of eutrophication. Four studies located across five locations reported evidence of either no effect or a negative response in target species (Table 1),

with two of those studies taking place in Svalbard, Norway (Zmudczyńska-Skarbek *et al.*, 2015; Zmudczyńska-Skarbek & Balazy, 2017). In Svalbard, the Siberian and North American rivers are sources of relatively high nutrient input (Dunton *et al.*, 2006; Thomas *et al.*, 2008; Fichot *et al.*, 2013) and intense nutrient influx takes places due to vertical mixing (Sakshaug, 2004; Hunt & Megrey, 2005; Wassmann *et al.*, 2006; Bluhm & Gradinger, 2008), which may explain the lack of positive effect of seabird nutrients. Further, the island of East Sand, Oregon, is located in the estuary of the Columbia River, so is also likely to have an elevated nutrient compared to open ocean systems. Uncertainty on the location of Kabishima, Japan (Kazama, unpublished data) prevents inferences on the nutrient status of the local water system.

The islands of the United Kingdom and Crown Dependencies
Research on the bottom-up effects of seabird nutrients in marine systems in the islands of the UK is extremely limited. Studies in the UK have generally concentrated on the impact of seabird nutrients on terrestrial communities, where positive effects of seabird nutrient input were found in stimulated soil microbial biomass and bacteria abundance relative to fungi, as well as enriched $\delta^{15}N$ in soil, vegetation, and nematodes (Wright *et al.*, 2010; Callaham Jr. *et al.*, 2012).

The UK is of international importance for breeding assemblages of seabirds and waders, with many islands designated as Special Protection Areas under EU legislation (Stanbury *et al.*, 2017). To date, the influence of seabird nutrient input on the intertidal rocky shore in the UK remains largely unknown. Given the seabird presence in the UK, the importance of seabird nutrient input to numerous ecosystems, and the extinction threats to seabirds (see section below), it is important that the influence of seabirds upon marine systems be established in the UK.

Threats to seabirds
Whilst seabirds are important to terrestrial and marine ecosystems, they are one of the most threatened bird groups (Croxall *et al.*, 2012), with almost half of all seabird species threatened with extinction (IUCN, 2022). The current threats to seabirds include anthropogenic activities, principally commercial fishing, pollution, habitat degradation, human disturbance, and human-introduced invasive predators (Croxall *et al.*, 2012). Indeed, invasive predators have

decimated seabird populations within 90% of the world's temperate and tropical island groups (Jones *et al.*, 2008). These threats put not only seabirds at risk, but all ecosystems that are dependent on the nutrient input of these keystone species.

Invasive alien vertebrates threaten global island biodiversity (Glen *et al.*, 2013; Jones *et al.*, 2016), with seabirds one of the groups most at risk (Jones *et al.*, 2008). As a result, eradication programmes are becoming an increasingly important conservation technique. Invasive rats, in particular, have decimated seabird populations, feeding on nesting birds, chicks, and eggs, and are some of the largest contributors to seabird extinction and endangerment worldwide (Jones *et al.*, 2008). The UK's seabird populations are no exception to this danger, and half of all successful invasive alien invertebrate eradications on inhabited islands have occurred within the UK (Stanbury *et al.*, 2017). Successful programmes within the UK include the eradication of brown rats (*Rattus norvegicus)* on St. Agnes and Gugh, Isles of Scilly (Bell *et al.*, 2019), and other islands including Ramsay Island, Pembrokeshire, and Staple, Farne Islands, whilst black rats (*Rattus rattus*) have been eradicated on islands including Eynhallow, Orkney Islands, and Lundy, Bristol Channel (DIISE, 2022). These threats to already endangered- and extinction-threatened UK seabirds further highlight the conservation value in determining the importance of seabirds for UK marine, nearshore, and terrestrial ecology.

General introduction conclusion
The influence of the bottom-up effects of allochthonous seabird nutrient input on nearshore systems in the UK is currently unknown, and it is critically important that it be established to determine seabird importance, and to assist with conservation strategies. The international importance of the UK's breeding assemblages of seabirds and waders and the extinction threats, in particular those posed by invasive alien invertebrates, make the need to determine the value of seabirds to other ecosystems all the more valuable.

To test the impact of seabirds upon terrestrial and intertidal systems, high seabird density sites, the Farne Islands, Northumberland were compared to low seabird density sites, along Northumberland mainland coast. The study's aim was to determine whether seabird nutrient input was cycling through terrestrial

and intertidal environments, and if those nutrients differed temporally. The biological impact of seabird nutrients were also compared between high and low seabird sites, by comparing intertidal algal and macrofauna biodiversity, as well as limpet growth rates and recolonisation rates of algae and sessile filter feeders.

Chapter 2: Influence of seabird nutrient input on intertidal ecology in the Farne Islands, Northumberland

2.1 Introduction

The vectoring of nutrients and organic matter via the movement of mobile consumers has long been recognised as a mechanism that links ecosystems (Hutchinson, 1950). Allochthonous nutrient subsidies support many ecosystems, influencing productivity, functioning, diversity, biomass, and community dynamics, boosting food availability and quality, and providing ecosystem resilience (Polis *et al.*, 1997; Lundberg & Moberg, 2003; Loreau & Holt, 2004; Benkwitt *et al.*, 2019). Seabirds are nutrient vectors, transporting nutrients from their pelagic ocean feeding grounds to coastlines and islands, where they provide enriched resources to both terrestrial and aquatic ecosystems, driving primary production, and resultant cascading bottom-up effects (Graham *et al.*, 2018; Benkwitt *et al.*, 2021a).

Allochthonous seabird nutrients come in various forms, including marine prey items that drop on the colony, whole or in stomach oils, lost feathers, abandoned or destroyed eggs, and individuals that die on land. But it is guano that makes up the greatest nutrient subsidy. For example, during a single Nazca booby (*Sula granti*) breeding season, guano made up 99% of an estimated 171.6 t of marine nutrients input to a terrestrial ecosystem on Malpelo Island, Colombia (López-Victoria *et al.*, 2009). Seabird guano is a mix of undigested food residue and waste metabolic products (Bird *et al.*, 2008). Guano is high in nutrients that are often limiting resources across many ecosystems: nitrogen and phosphorous. In seabird guano, nitrogen and phosphorous content by mass are typically 7-21% and 0.4-2.9%, respectively, with over 80% of nitrogen comprised of crystalline uric acid (Lindeboom, 1984; Staunton Smith & Johnson, 1995; Hartz & Johnstone, 2006; Young *et al.*, 2010). Comparing this to the input of rainfall to terrestrial environments, seabird guano has been found to increase nitrogen and phosphorous input by over 300 and 400 times, respectively (Furness, 1991). At local scales, these levels of nutrient input dictates the structure and dynamics of communities to the extent that seabirds have been described as keystone species (Mulder *et al.*, 2011b). At global scales, seabirds may link marine and

terrestrial environments, contributing to inter-habitat connectivity and providing multiple ecosystem services (Signa *et al.*, 2021).

Despite their importance, seabirds are one of the most threatened bird groups, with almost half of all seabird species threatened with extinction (IUCN, 2022). The threats to seabirds will not only impact bird populations, but the ecosystems that are dependent on the seabirds' nutrients that act to stabilise recipient communities and food webs (McCann *et al.*, 2005; Rooney *et al.*, 2006). Indeed, islands where seabirds have been lost to invasive predators have smaller and less complex food webs (Thoresen *et al.*, 2017). Declines in seabird populations are steep worldwide, with the potential loss of seabirds due to anthropogenic causes threatening ecosystem-wide nitrogen cycling at scales ranging from local to global (Riddick *et al.*, 2018; Grant *et al.*, 2022). The current anthropogenic threats to seabirds include commercial fishing, pollution, habitat degradation, human disturbance, climate change, and human-introduced invasive predators (Croxall *et al.*, 2012). For example, the presence of rats, and consequently absence of seabirds, disrupts the flow of nutrients from seabird colonies, resulting in lower biomass of reef fish and reduced rates of key ecosystem functions (Graham *et al.*, 2018). Indeed, invasive predators threaten global island biodiversity, with seabirds one of the groups most at risk, having decimated seabird populations within 90% of the world's temperate and tropical island groups (Jones, 2010; Glen *et al.*, 2013; Jones *et al.*, 2016). Invasive species eradication programmes are becoming an increasingly important conservation technique, with approximately half of all successful European invasive alien vertebrate eradications on inhabited islands having occurred within the UK, such as on Staple island of the Farne Islands, Northumberland (Stanbury *et al.*, 2017).

Whilst the functional role of seabird nutrient input on terrestrial habitats has received a great deal of attention, coastal marine environments remain understudied, and empirical studies investigating the effects of bottom-up nutrients supplied by seabirds on marine ecosystems remain relatively deficient (Kazama, 2019; Signa *et al.*, 2021; Grant *et al.*, 2022). Nutrient input from seabirds to marine systems is best measured by using stable isotope analysis to track nutrient flow through the ecosystem and up the trophic levels, such as in primary producers and their consumers (Young *et al.*, 2011; Kazama, 2019).

Some research that used stable isotope analysis has been performed in temperate marine systems, with nitrogen stable isotopes (reported as δ values for the ratio of ^{15}N:^{14}N ($δ^{15}N$)) consistently higher near seabirds in primary producers and invertebrates, showing seabird nutrients moving through ecosystems (Jones, 2010; Kolb *et al.*, 2010; Gagnon *et al.*, 2013; Rankin & Jones, 2021). However, whilst nitrogen stable isotopes have been promoted as powerful tool in understanding the impact of seabird nutrient input on ecosystems, it is also important to establish whether these allochthonous nutrients are impacting biodiversity and productivity. Such patterns have received some attention in tropical systems, such as the growth rates of coral, damselfish, and parrotfish, as well as the biomass of fish communities (Graham *et al.*, 2018; Savage, 2019; Benkwitt *et al.*, 2021b; Benkwitt *et al.*, 2021). However, whilst some research has been performed in temperate systems (e.g., Kurle *et al.*, 2008; Kurle *et al.*, 2021; Rankin & Jones, 2021), the temperate environment remains understudied. In addition, seabirds are seasonal breeders, and spend most of the year away from their breeding colonies, which may result in great seasonal fluctuation in nitrogen input (Pascoe *et al.*, 2022), yet studies into the temporal variation in bottom-up effects are rare (Kazama, 2019).

Research on seabird nutrient inputs to nearshore environments in the United Kingdom (UK) is extremely limited. The UK is of international importance for breeding assemblages of seabirds and waders, with many islands designated as Special Protection Areas under EU legislation (Stanbury *et al.*, 2017), whilst the UK's breeding seabirds excrete vast quantities of nutrients along its coastlines (Riddick *et al.*, 2012). Given the international importance of the UK's seabirds, the global threats to seabird populations, and the fact that cold-water systems make up a large proportion of global oceans, it is important to determine the influence of seabird nutrient input on UK nearshore marine systems for both regional and global understanding.

To test the impact of seabirds upon terrestrial and intertidal systems in the UK, areas of high seabird density were compared to areas of low seabird density. The Farne Islands, Northumberland, areas of extremely high seabird densities the during breeding season, with hundreds of thousands of birds visiting the area each year (National Trust, 2022a), were chosen as a case study site and compared to nearby, low seabird density areas along the Northumberland

mainland coast. It was hypothesised that seabird nutrient input would cycle through the terrestrial and intertidal environments on the Farne Islands, boosting biodiversity, and that seabird nutrient input would be greatest at late breeding season, after the seabird colonies had spent several months on the islands. It was also predicted that seabird nutrient input would increase productivity by increasing limpet size and biomass. For the recolonisation rates, it was predicted that the impact of seabird nutrient input would reach the marine environment, increasing the abundance of barnacles' food source, plankton and zooplankton. Seabird nutrient input was also predicted to increase the food availability of limpets' preferred food, cyanobacteria and diatoms (Jenkins & Hartnoll, 2001). However, another food source for limpets, macroalgae such as *Ascophyllum nodosum* or *Fucus vesiculosus*, favour low nutrient conditions (Kraufvelin *et al.*, 2010). Therefore, whilst barnacle recolonisation was hypothesised to be greater on the Farne Islands, limpet recolonisation was hypothesised to be similar on the mainland and the Farne Islands.

2.2 Methods

2.2.1 Study sites

The Farne Islands are an archipelago situated off the Northumberland coast, located in the North Sea (55º 63' N, 1º 63' W). The Farne Islands have National Nature Reserve (NNR), Special Protection Area (SPA), and Site of Special Scientific Interest (SSSI) designations and have been under the care of the National Trust since 1925. The three study islands were Inner Farne, Staple, and Brownsman. Staple island underwent successful brown rat (*Rattus norvegicus*) eradications in 2006 and 2009. Initial agreement was made with Natural England for three sites on the Farne Islands for all methods. Partial observational data was also collected at a fourth site and communicated to Natural England for inclusion in the analyses. The four study sites were situated across the three islands, with two sites on Inner Farne. The partial observational data was collected on the second Inner Farne site.

The four mainland sites were situated within two regions on Northumberland coast, which, compared to the Farne Islands, has a very sparse seabird population. Two sites were located at Blackrocks Point and Harkness Rocks, around Bamburgh lighthouse (55º 62' N, 1º 72' W). This region has both

Northumberland Coast (SSSI) and Bamburgh Coast and Hills (SSSI) designations. A further two sites were located at Greenhill Rocks and Monks House Rocks (55º 59' N, 1º 68' W), which has Northumberland Coast (SSSI) designation. As on the Farne Islands, the full methodologies were performed at three sites, and partial methodologies performed at a fourth site.

Mainland sites were chosen to minimise the impact of confounding variables: all seabird island and mainland sites in which methodologies were performed were of a comparable size; all sites had similar rocky shore headland habitats; the seabird islands and mainland sites were as geographically close to one another as possible; all sites had a low slope; the geology at all sites was categorised as 'Igneous rocks, contemporaneous and intrusive basalt' (BGS, 1896). Differences existed between the Farne Islands and the mainland, though. Much of the land surrounding the mainland sites is agricultural and could be a source of nutrient input due to runoff. Moreover, sources of nitrogen input exist at two sites close to the mainland sites: marine nitrate toxicity issues in the River Tweed (Jarvie *et al.*, 2002), and eutrophication at Lindisfarne National Nature Reserve, where sources of nitrogen include diffuse agricultural runoff, misconnections in public and private sewage treatment works, seasonal tourism pressures on dated sewage treatment facilities, offshore influence from the North Sea and the River Tweed, and natural nutrient recycling in local shallow intertidal inlets (NCC, 2020). Wave exposure levels were higher at all mainland sites compared to the Farne Islands. Three site visits occurred, during the early breeding season (4-8 May 2021), mid breeding season (29, 30 June; 1 July 2021), and late breeding season (25-31 August 2021).

2.2.2 Seabird surveys
Breeding seabird densities on the Farne Islands were counted annually from 2017-2021, with each seabird island surveyed individually (National Trust, 2022a). The methodologies were species specific: cormorants, shags, gulls, and terns were surveyed using the apparently occupied nests methodology (AON); puffins were surveyed using the apparently occupied burrow methodology (AOB); fulmars were surveyed using a combination of the apparently occupied site methodology (AOS) and the whole-colony census method; guillemots were surveyed using the whole colony count method (from boats); kittiwakes and

razorbills were surveyed using the AOS (Walsh *et al.*, 1995; Bibby, 2000). Repeated surveys were performed for all species to verify counts over breeding seasons.

Non-breeding seabird densities on the mainland were counted annually from 2015-2019 as part of the British Trust Ornithology (BTO) Wetland Bird Survey (BTO, 2022; note: data from seabird surveys during 2020 and 2021 were excluded due to disruptions caused by COVID-19). All four mainland sites fall within a single BTO survey sector, 'Seahouses to Budle Point', location code 55453 (BTO, 2022). Therefore, a mean seabird density for the entire survey area was estimated, which all four mainland sites were located within. The mainland survey methodology was monthly total count surveys. The difference in methodologies between the Farne Islands and the mainland may cause the mainland surveys to be overestimates, with the JNCC approved methods adopted on the Farne Islands likely to produce a more representative reflection of seabird abundances (Walsh *et al.*, 1995). In the mainland survey data, monthly gaps in coverage exist due to disturbance, weather induced effects on numbers and distribution, or surveyor unavailability. In instances where there was no data for any given month, the mean of the completed months for that year was used. The mean number of months that had data available across the five years was 7.6.

Specific species included in the Farne Island and mainland surveys were seabirds: Atlantic puffins (*Fratercula arctica*); black-legged kittiwakes (*Rissa tridactyla*); common guillemots (*Uria aalge*); European shags (*Gulosus aristotelis*); great cormorants (*Phalacrocorax carbo*); northern fulmars (*Fulmarus glacialis*); razorbills (*Alca torda*), gulls: black-headed gulls (*Chroicocephalus ridibundus*); common gulls (*Larus canus*); European herring gulls (*Larus argentatus*); great black-backed gulls (*Larus marinus*); lesser black-backed gulls (*Larus fuscus*); little gulls (*Hydrocoloeus minutus*), and terns: Arctic terns (*Sterna paradisaea*); common terns (*Sterna hirundo*); little terns (*Sternula albifrons*); roseate terns (*Sterna dougallii*); sandwich terns (*Thalasseus sandvicensis*). Non-seabird species were excluded from counts as they do not feed at pelagic locations and do not contribute to allochthonous nutrient inputs.

2.2.3 Total nitrogen input from guano

Total nitrogen input from guano per hectare per year was estimated for each seabird island, Inner Farne, Staple, and Brownsman, and the mainland survey area using previously published methods (Young *et al.*, 2010; Graham *et al.*, 2018):

$$NI_{ij} = \frac{N_g \times Dr_i \times Bd_{ij} \times Res_{ij}}{Area_j}$$

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 site (*j*), the number of days of the year that the species is resident on the site (Res), and the area of the survey site (Area). Nitrogen content of guano was held at 15.46%, as mean of other seabird species (Lindeboom, 1984; Staunton Smith & Johnson, 1995; Young *et al.*, 2010). The Dr was based on the red-footed booby (*Sula sula*) and scaled for all species by species' biomass, assuming allometric relationships with body size (Young *et al.*, 2010). Res was a sum of each species' incubation period, fledging period, and post-fledging care (in days; Schreiber & Burger, 2001). In instances of data deficiency, the number of post-fledging care days of the most closely related bird species present in Northumberland was used (or a mean of closely related species, where multiple were present) with the exception of common guillemots. Here, post-fledging care was stated to be zero, as common guillemots provide post-fledging care to their chicks at sea (Dunn *et al.*, 2022).

      The mainland survey site and each seabird island's area was calculated in ArcGIS Pro (Esri, 2022; version 2.5.2). The mainland's transect area was provided by the BTO (2022) with their survey data; the Farne Islands were estimated using Operational Land Imager (OLI) Collection 2 Level-1, Landsat 8 satellite imagery (30 m spatial resolution; USGS, 2022). The seabird islands were estimated to be 7.3 ha, 5 ha, and 6.9 ha Inner Farne, Staple, and Brownsman, respectively; the mainland site was estimated to be 722 ha. Note, these areas refer to the size of the areas in which bird survey areas were undertaken, not the size of the site in which the methodologies were undertaken.

2.2.4 Isotope sampling

The abundance of nitrogen and stable isotopes (δ^{15}N) in terrestrial and intertidal samples were used to understand the uptake of nutrients through the food chains in terrestrial and intertidal ecosystems. Spatial variation was determined by comparing low seabird density sites (the mainland) and high seabird density islands (seabird islands). Temporal variation was determined by comparing early seabird breeding season to late seabird breeding. For these methods, three study sites on the seabird islands were compared to three study sites on the mainland.

Terrestrial samples included soil, terrestrial plants, and lichen. To collect topsoil, loose leaf litter and vegetation was cleared to expose the soil. New-growth leaves were taken from C3, non-legume plants: sea campion (*Silene maritima*), dock (*Rumex* spp.), nettles (*Urtica dioica*), fiddlenecks (*Amsinckia* spp.), small bugloss (*Anchusa arvensis*), common orache (*Atriplex patula*), or red goosefoot (*Chenopodium rubrum*). Lichens were common orange lichen (*Xanthoria parietina*), orange sea lichen (*Caloplaca marina*)*,* strap lichen (*Ramalina* spp*.*)*,* or black shields (*Tephromela atra var. atra*).

Intertidal samples included macroalgae, epiphytic algae, turf algae, barnacles, and limpets. For the intertidal primary producers, macroalgae species were egg wrack (*Ascophyllum nodosum*) bladder wrack (*Fucus vesiculosus*)*, or* serrated wrack (*Fucus serratus*); epiphytic algae species were red algae (*Polysiphonia lanosa*) or tiny wrack bush (*Elachista fucicola*); turf algae species were flat fern weeds (*Osmundea spp.*), tufted coral weeds (*Corallina spp.*)*,* Irish moss (*Chrondus crispus*), or grape pip weed (*Mastocarpus stellatus)*. For the intertidal consumers, molluscs were common limpets (*Patella vulgata*); barnacles were acorn barnacles (*Semibalanus balanoides*)*.* Five samples of each type were taken, a minimum of 5 m apart, with the exception of epiphytic algae (due to it being absent) on Brownsman during both early- and late-breeding season, and two mainland sites during late-breeding season (absent at one site; two samples taken at another).

All samples were dried in a drying oven for at 60ºC for 36 h, or until fully dry, and stored in plastic sample vials. Stable isotope analysis of nitrogen for all samples was carried out at Lancaster University, UK, using an Elementar Vario MICRO cube Elementar Analyser and analysed in an Isoprime 100 Isotope Ratio Mass Spectrometer, with international standards IAEA 600 and USGS 41.

Isotope ratios were calculated from 2 to 91 mg of each sample added to tin capsules. Total nitrogen content (%) was also estimated. Soil, lichen, macroalgae, epiphytic algae, turf algae, and barnacles were acid washed with hydrochloric acid to dissolve any calcareous matter or sediments that may have contaminated the samples. All samples from seabird islands and the mainland were treated the same. Accuracy based on internal standards was 0.2 per mil standard deviation, with selected samples run in duplicate or triplicate to ensure precision of readings.

2.2.5 Community composition

Intertidal community composition was estimated to compare biodiversity between low seabird density sites (the mainland) and high seabird density islands (seabird islands). Here, there were four study sites on seabird islands, and four on the mainland. All community surveys were performed during the early-breeding season visit (4-8 May 2021). Five replicate 0.5 m^2 quadrats were haphazardly positioned at each site, a minimum of 5 m apart, in the mid-shore intertidal zone. All algae and sessile filter feeder species were identified and percent cover determined; all vacant rocky surface percent cover was determined; all macrofauna was identified and counted, but were not considered to occupy ground space due to their mobile nature, so were not included as part of the percent cover estimates.

To determine the relative similarity of ecological community structure, species were classed into functional groups based on their ecology: macroalgae, turf algae, other herbivores, and predators (Table 1). To compare species diversity and taxonomic relatedness, diversity measures were performed on both algal and fauna taxa to determine species richness (total taxa), Shannon's diversity index (H'; Shannon, 1948), and Pielou's evenness index (J'; Pielou, 1966).

Table 1 | Ecological functional groups on low seabird density mainland sites and seabird islands.

Functional group	Common name	Scientific name
Macroalgae	Egg wrack	*Ascophyllum nodosum*
	Bladder wrack	*Fucus vesiculosus*
	Serrated wrack	*Fucus serratus*
Turf algae	Sea lettuce	*Ulva* spp.
	Green branched weeds	*Cladophera* spp.
	Irish moss	*Chrondus crispus*
	Flat fern weed	*Osmundea spp.*
	Grape pip weed	Mastocarpus stellatus
	Dumont's tubular weed	*Dumontia contorta*
	Banded pincer weeds	*Ceramium*
	Dulse	*Palmaria palmata*
	Black scour weed	*Ahnfeltia plicata*
	Siphon weeds	*Polysiphonieae* spp.
	Laver	*Porphrya* spp.
	Tufted coral weed	*Corallina caespitosa*
	Sand binder	*Rhodothamniella floridula*
	Bunny ears	*Lomentaria articulata*
Other herbivores	Common periwinkles	*Littorina littorea*
	Flat periwinkles	*Littorina obtusata*
	Chiton	*Acanthochitona crinite*
Predators	Dogwhelks	*Nucella lapillus*
	Beadlet anemones	*Actinia equina*
	Common shore crabs	*Carcinus maenas*

2.2.6 Limpet size, abundance, and biomass

The size distribution of 100 common limpet (*Patella vulgata*) individuals at each site were compared between the mainland and seabird islands. Here, four study sites were included on seabird islands and the mainland. Vernier callipers were used to measure limpets' longest shell length to an accuracy of 1 mm. At each site, limpets were measured, starting at the approximate location of the final community composition quadrat (section 2.2.5), working away from the quadrat location in concentric circle. All limpets encountered were measured until the sample size reached 100. Limpet abundance (count per 0.5 m^2) was determined using community analysis data (see section 2.5).

Limpet biomass was calculated at each site, because the quantity of algae grazed is more closely related to the biomass of limpets than the number present, using the following mass/length regression equation (Branch, 1971; Bosman & Hockey, 1988):

$$M = 1.9 \times 10^6 \ (L)^{3.5};$$
$$N = 100, r = 0.99, p < 0.001$$

where dry somatic and gonadal mass (M) is a factor of the length in mm (L). Limpet biomass was site specifically calculated using the size distribution of the 100 limpets measured at each respective site, with limpets within each quadrat assumed to show the same pattern of size as the 100 individuals measured. Biomass was then calculated as a factor of limpet length and abundance.

2.2.7 Recolonisation patterns

To determine re-colonisation rates following recent disturbance, plots were artificially cleared on the low seabird density mainland sites and the seabird islands. Five replicate 15 cm^2 plots were cleared of all algae, sessile filter feeders, and common limpets (*Patella vulgata*) at each study site (three study sites each on seabird islands and the mainland). Plots were a minimum of 5 m apart, in the mid-shore intertidal zone. Prior to plot clearance, percent cover of algal species and sessile filter feeders were determined, and all macrofauna identified and counted. The plots were cleared in May 2022, around the period of acorn barnacles settlement (Hawkins & Hartnoll, 1982), using paint scrapers and wire brushes, leaving a substratum of bare rock. The plots were checked at eight-

week intervals to determine algae and sessile filter feeder recolonisation levels (percent cover), and the number of all macrofauna present.

2.2.8 Statistical analysis

To test for differences in the responses of terrestrial and intertidal communities around high seabird density islands versus low seabird density mainland sites, a combination of univariate and multivariate statistics were used. Linear mixed models (LMMs) were used to analyse univariate responses, with site included as a random effect to account for spatial non-independence among samples. Likelihood ratio tests were used to determine the effect of seabird density (low versus high) on each response (Zuur *et al.*, 2009). Univariate analyses were not performed when there were extreme unequal variances between mainland and seabird island sites.

All univariate analyses were assessed for normality and homogeneity, with square root transformations used when those assumptions were not met. Individual species densities that required transformation were serrated wrack (untransformed data), dulse (untransformed data), mussels (untransformed data), common winkle (untransformed data). Functional groups that required transformation were 'turf algae' and 'other herbivores'. Limpet biomass also required transformation.

PERMANOVA tests were conducted to test for community differences (Anderson & Walsh, 2013). Indicator species analysis (IndVal; Dufrêne & Legendre, 1997) was performed on both percentage area and count data to help determine which species drove dissimilarities between the communities. Univariate tests were then performed on selected species on both the untransformed and presence-absence data.

A multivariate principal component analysis (PCA) was used on Bray-Curtis similarity matrices to analyse algae and sessile filter feeder percentage area data. A non-metric multidimensional scaling (NMDS) was used on Bray-Curtis similarity matrices to analyse macrofauna count data (Kruskal, 1964), as continuous data such as percent cover is suited to PCA, and count data (with associated high '0' values) is suited to NMDS (Graham *et al.*, 2007). Multivariate analyses were performed on untransformed data, to determine the contributions

of the dominant species, and presence-absence data, to determine the contribution of intermediate and rarer species.

To determine whether the presence of seabirds influenced recolonisation responses of barnacles (percent cover) and limpets (count), the effect of seabirds (high versus low seabird), time (prior to clearance of plots, zero weeks, eight weeks, and 16 weeks), and their interaction were analysed between seabird islands and the mainland. As above, site was included as a random effect to account for spatial non-independence among samples (Zuur *et al.*, 2009), and post-hoc tests with a Bonferroni correction performed to determine the drivers of differences (Holm, 1979).

All statistical analyses were conducted in R version 4.0.2 with associated packages ggplot2, dplyr, vegan, moments, ape, indicspecies, tidyverse, rstatix, lme4, and RColorBrewer (De Caceres & Legendre, 2009; Neuwirth, 2014; Bates *et al.*, 2015; Wickham, 2016; Wickham *et al.*, 2018; Paradis & Schliep, 2019; Oksanen *et al.*, 2020; Kassambara, 2021; Komsta & Novomestky, 2022; Wickham & Girlich, 2022).

2.3 Results

2.3.1 Seabird density and nitrogen input

Mean seabird density, averaged across a five-year period, was 1601, 2334, and 972 times greater for Inner Farne, Staple, and Brownsman, respectively, than on the mainland (Fig. 1a; mean ± standard error (SE); 3778.0 ± 125.1, 5509.3 ± 232.2, and 2334.3 ± 93.1 birds ha^{-1} for Inner Farne, Staple, and Brownsman, respectively; 2 ± 0.4 birds ha^{-1} for the mainland).

Mean seabird nitrogen input, averaged across a five-year period, was 675, 1033, and 423 times greater for Inner Farne, Staple, and Brownsman, respectively, than on the mainland (Fig. 1b; mean ± SE; 688.3 ± 37.1, 1054.1 ± 57.1, and 431.7 ± 15.8 kg^{-1} ha^{-1} for Inner Farne, Staple, and Brownsman, respectively; 1.0 ± 0.3 kg^{-1} ha^{-1} for the mainland).
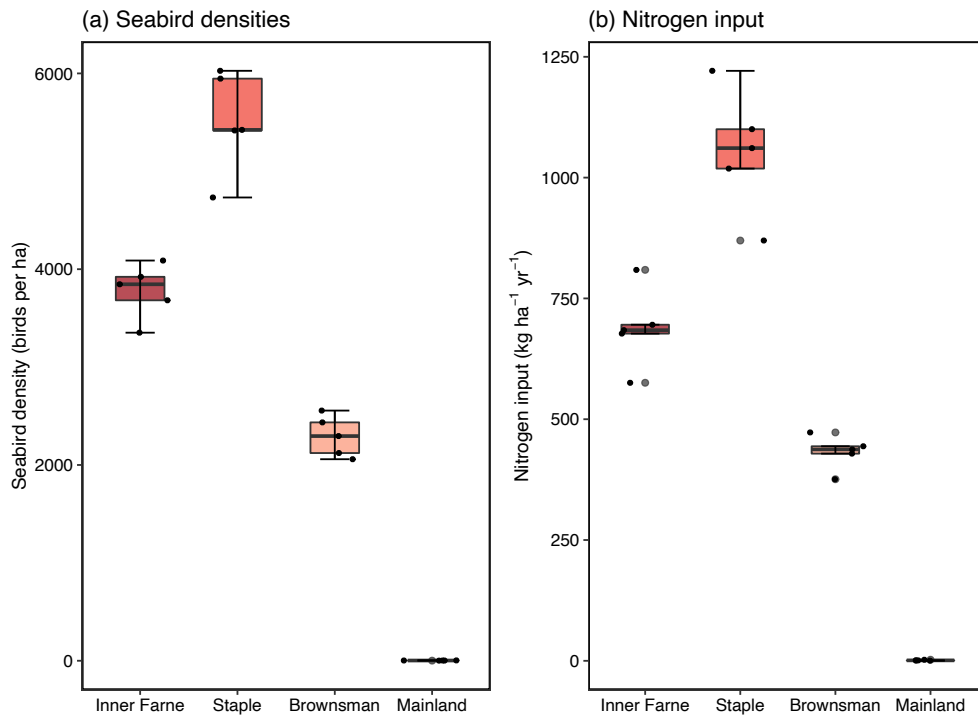
Figure 1 | Seabird densities and nitrogen input to seabird islands (Inner Farne, Staple, and Brownsman, the Farne Islands) and low seabird density mainland sites (Northumberland coast). (a) Seabird density on Inner Farne, Staple, and Brownsman and the mainland. (b) Nitrogen input by seabirds for Inner Farne, Staple, Brownsman, and the mainland. Values are mean (±SE, n = 5). Box limits represent the first and third quartiles (25% and 75% percentiles), middle line represents the median (50% percentile), and whiskers represent the smallest and largest observations less than or equal to 1.5 × inter-quartile range. Note differences in y-axes.

2.3.2 Stable isotope analysis

2.3.2.1 Early-breeding season nitrogen

Significantly enriched $\delta^{15}N$ was found on high seabird density islands compared to low seabird density mainland sites in soils, terrestrial plants, lichen, macroalgae, turf algae, barnacles, and limpets (Fig. 2; Table 1). The $\delta^{15}N$ were much higher for terrestrial samples soil, plants, and lichen, reflecting the direct guano signature. $\delta^{15}N$ values in the intertidal zone were comparatively lower than terrestrial samples, but a large effect size to the mainland demonstrates a strong seabird nutrient signature still exists. Soil, terrestrial plants, lichen, turf algae,

barnacles, and limpets also had significantly higher total nitrogen content on high seabird density islands (Fig. 3; Table 2).
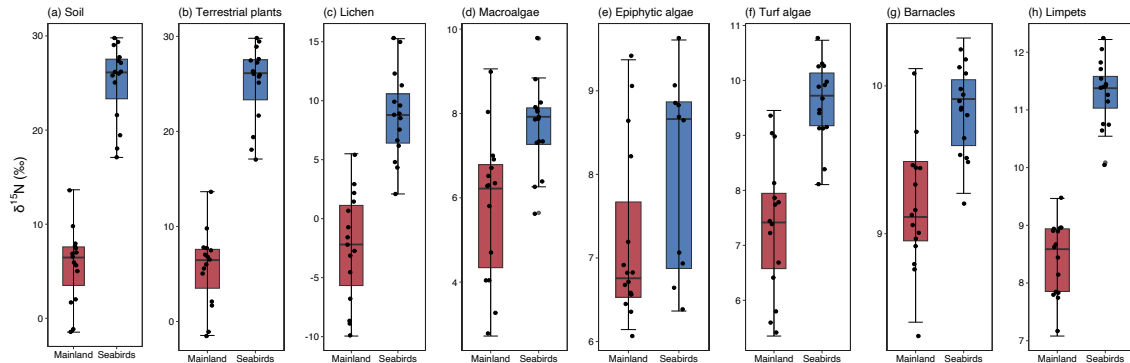

Figure 2 | Early-breeding season nitrogen isotope signals in terrestrial and intertidal areas on the low seabird density mainland sites and seabird islands. a-h, $\delta^{15}N$ values for (a) soil, (b) new growth leaves, (c) lichen, (d) macroalgae, (e) epiphytic algae, (f) turf algae, (g) barnacles, and (h) limpets. Values are mean (± SE, n = 15 for all sample types except for seabird island epiphytic algae, where n = 10 (see Methods section 2.4)). Box limits represent the first and third quartiles (25% and 75% percentiles), middle line represents the median (50% percentile), and whiskers represent the smallest and largest observations less than or equal to 1.5 × inter-quartile range.

Table 2 | Early breeding season nitrogen isotope values and total nitrogen content in terrestrial and intertidal areas on low seabird density mainland sites and seabird islands. Values are mean ± standard error (SE), n = 15 for all sample types except for mainland epiphytic algae, where n = 10 (see Methods section 2.4). **bold** p is significant (> 0.05).

| Sample type	δ^{15}N isotope values (‰)		χ^2	p	Total nitrogen content (%)		χ^2	p
	Mainland	Seabirds			Mainland	Seabirds		
Soil	5.4 ± 0.3	22.2 ± 0.6	22.56	**< 0.001**	0.4 ± 0.1	2.4 ± 0.3	8.51	**0.004**
Terrestrial plant	5.6 ± 1.0	25.1 ± 1.1	16.58	**< 0.001**	3.9 ± 0.3	5.0 ± 0.2	4.27	**0.039**
Lichen	-2.4 ± 1.2	8.7 ± 1.0	8.99	**0.003**	1.2 ± 0.2	3.2 ± 0.1	11.77	**< 0.001**
Macroalgae	5.8 ± 0.5	7.7 ± 0.3	9.67	**0.002**	2.2 ± 0.1	2.3 ± 0.1	1.66	0.197
Epiphytic algae	7.2 ± 1.0	8.1 ± 0.4	1.02	0.312	7.2 ± 0.3	7.5 ± 0.4	0.14	0.711
Turf algae	7.4 ± 0.3	9.6 ± 0.2	15.88	**< 0.001**	5.4 ± 0.4	6.4 ± 4.0	3.14	0.076
Barnacles	9.2 ± 0.1	9.9 ± 0.1	8.60	**0.003**	3.4 ± 0.5	7.8 ± 0.3	15.35	**< 0.001**
Limpets	8.4 ± 0.2	11.3 ± 0.1	23.41	**< 0.001**	6.2 ± 0.3	8.8 ± 0.3	13.50	**< 0.001**
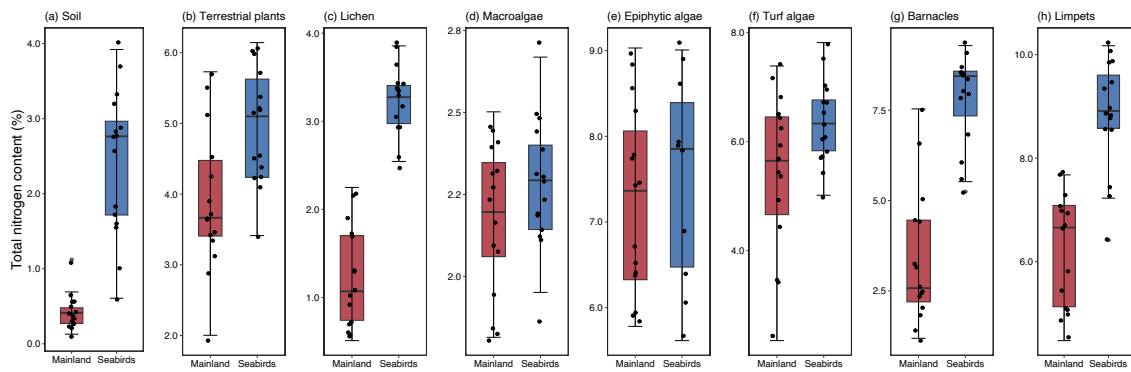
Figure 3 | Early breeding season total nitrogen content in terrestrial and intertidal areas on the low seabird density mainland sites and seabird islands. a-h, total nitrogen content for (a) soil, (b) new growth leaves, (c) lichen, (d) macroalgae, (e) epiphytic algae, (f) turf algae, (g) barnacles, and (h) limpets. Values are mean (± SE, n = 15 for all sample types except for mainland epiphytic algae, where n = 10 (see Methods section 2.4)). Box limits represent the first and third quartiles (25% and 75% percentiles), middle line represents the median (50% percentile), and whiskers represent the smallest and largest observations less than or equal to 1.5 × inter-quartile range.

2.3.2.2 Temporal nitrogen variation

δ^{15}N was significantly higher in early breeding season compared to late breeding season in terrestrial plants on low seabird density sites (Fig. 4a; mean ± SE; Chi-squared test; early breeding season = 5.6 ± 1.0 δ^{15}N ‰, late-breeding season = 3.4 ± 0.6 δ^{15}N ‰; df = 1, N = 15, χ^2 = 3.91, p = 0.048). No significant δ^{15}N temporal variation was found in terrestrial plants on seabird islands (Fig. 4a; mean ± SE; Chi-squared test; early breeding season = 25.1 ± 1.1 δ^{15}N ‰, late breeding season = 23.8 ± 2.1 δ^{15}N ‰; df = 1, N = 15, χ^2 = 0.53, p = 0.465). In macroalgae, no significant δ^{15}N temporal variation was found on the mainland (Fig. 4b; mean ± SE; Chi-squared test; early breeding season = 5.8 ± 0.5 δ^{15}N ‰, late breeding season = 6.7 ± 0.2 δ^{15}N ‰; df = 1, N = 15, χ^2 = 2.98, p = 0.084) or on seabird islands (Fig. 4b; mean ± SE; Chi-squared test; early breeding season 7.7 ± 0.3 δ^{15}N ‰, late breeding season 7.6 ± 0.1 δ^{15}N ‰; df = 1, N = 15, χ^2 = 0.03, p = 0.863).

Percent nitrogen was significantly higher in early breeding season compared to late breeding season in terrestrial plants on the mainland (Fig. 4c;

mean ± SE; Chi-squared test; early-breeding season = 3.9 ± 0.3% nitrogen, late-breeding season = 2.3 ± 0.2% nitrogen; df = 1, N = 15, χ^2 = 22.37, p < 0.001) and on high seabird density islands (Fig. 4c; mean ± SE; Chi-squared test; early-breeding season = 5.0 ± 0.2% nitrogen, late-breeding season 3.1 ± 0.2% nitrogen; df = 1, N = 15, χ^2 = 30.15, p < 0.001). In macroalgae, a significantly higher percent nitrogen was found in early breeding season compared to late breeding season on the mainland (Fig. 4d; mean ± SE; Chi-squared test; early-breeding season = 2.2 ± 0.1% nitrogen, late-breeding season = 1.1 ± 0.1% nitrogen; df = 1, N = 15, χ^2 = 61.29, p < 0.001) and on seabird islands (Fig. 4d; mean ± SE; Chi-squared test; early breeding season = 2.3 ± 0.1% nitrogen, late breeding season = 1.4 ± 0.1% nitrogen; df = 1, N = 15, χ^2 = 55.80, p < 0.001).
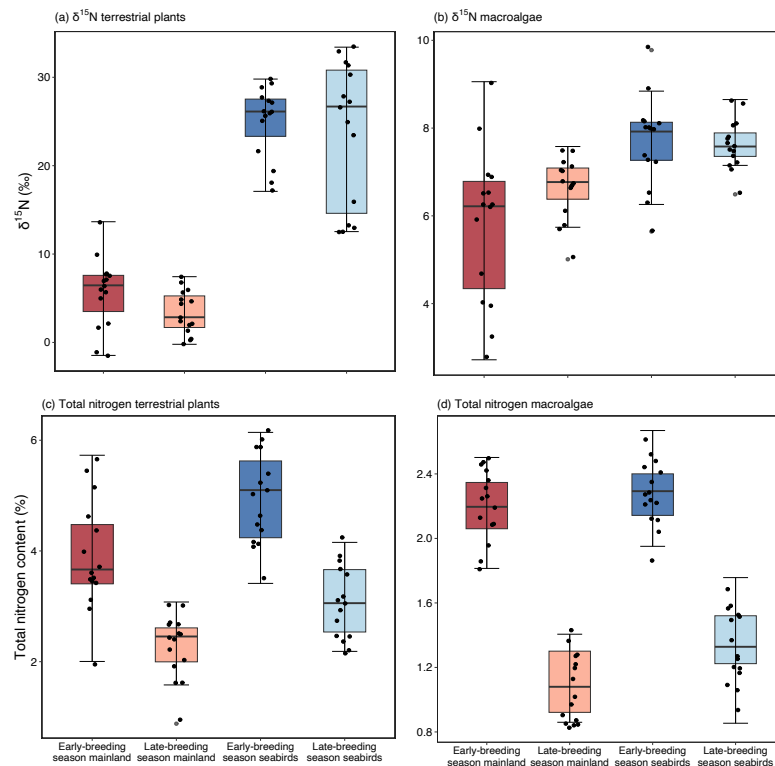

Figure 4 | Temporal variation in nitrogen isotope signals and total nitrogen content in terrestrial plants and macroalgae on low seabird density mainland sites and seabird islands. a-b, δ15N values for (a) terrestrial plants, and (b) macroalgae, **c-d**, total nitrogen content for (c) terrestrial plants, (d) macroalgae. Values are mean (± SE, n = 15). Box limits represent the first and third quartiles (25% and 75% percentiles), middle line represents the median (50% percentile), and whiskers represent the smallest and largest observations less than or equal to 1.5 × inter-quartile range.

2.3.3 Community analysis

2.3.3.1 Algae and sessile filter feeders

There was no difference in intertidal community structure (all algal types, sessile filter feeders, and vacant surfaces (rock and sand)) between low seabird density mainland and high seabird density islands both when using untransformed data to determine the contributions of the dominant species using a PCA ordination (Fig. 5a; PERMANOVA, F = 1.53, p = 0.352) and when analysing the presence-absence data to determine contributions of intermediate and rarer species (Fig. 5b; PERMANOVA, F = 2.05, p = 0.110).

When analysing the contributions of the dominant species (untransformed data), indicator species analysis (IndVal) found some species differed between the mainland and seabird islands communities, including serrated wrack (Fig. 5c; mean ± SE; Chi-squared test; mainland = 12.7 ± 5.9% per 0.5 m^2, seabirds = 2.6 ± 1.3% per 0.5 m^2; df = 1, N = 20, χ^2 = 0.95, p = 0.329), Irish moss (Fig. 5d; mean ± SE; not statistically analysed; mainland = 0.0 ± 0.0% per 0.5 m^2, seabirds = 0.5 ± 0.2% per 0.5 m^2), dulse (Fig. 5e; mean ± SE; Chi-squared test; mainland = 0.4 ± 0.2% per 0.5 m^2, seabirds = 1.9 ± 0.8% per 0.5 m^2; df = 1, N = 20, χ^2 = 0.73, p = 0.394), and pink encrusting algae (Fig. 5f; mean ± SE; Chi-squared test; mainland = 3.5 ± 1.4% per 0.5 m^2, seabirds = 6.5 ± 1.7% per 0.5 m^2; df = 1, N = 20, χ^2 = 1.14, p = 0.286).

For intermediate and rarer species (presence-absence data), indicator species analysis (IndVal) found species differed between the mainland and seabird island communities including Cladophera (mean ± SE; Chi-squared test; mainland = 0.3% ± 0.1% per 0.5 m^2, seabirds = 0.6 ± 0.1% per 0.5 m^2; df = 1, N = 20, χ^2 = 0.95, p = 0.329), and false Irish moss (mean ± SE; Chi-squared test; mainland = 0.2 ± 0.1% per 0.5 m^2, seabirds = 0.3 ± 0.1% per 0.5 m^2; df = 1, N = 15, χ^2 = 0.43, p = 0.511).
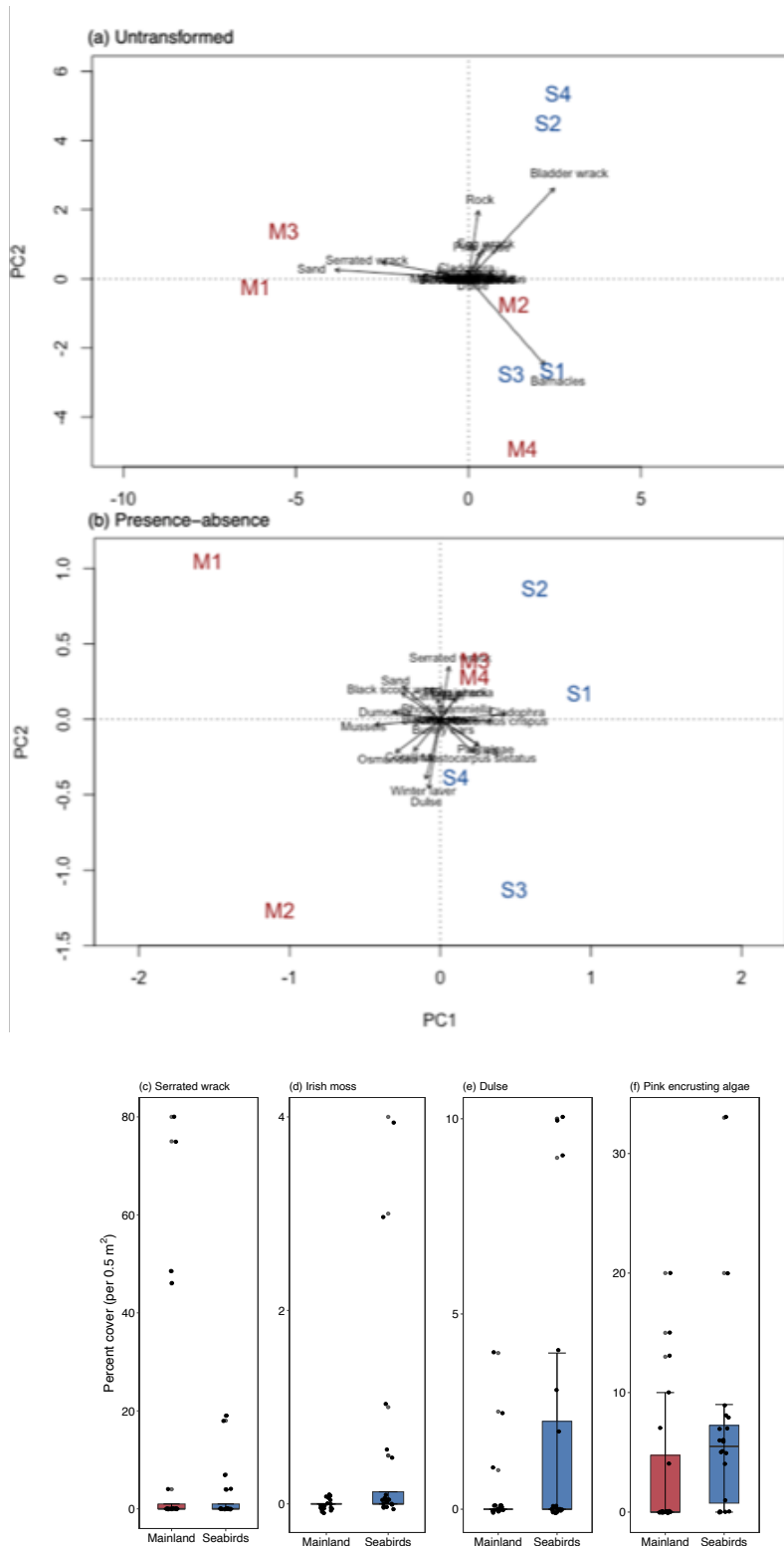
Figure 5 | Principal component analysis (PCA) biplots and boxplots comparing indicator species (those driving community dissimilarities) on low seabird density mainland sites and seabird islands. a-b, PCA for (a) raw, untransformed algae and sessile filter feeder percent cover data (highlights dominant species importance), and (b) presence-absence transformed data (highlights intermediate and rarer species importance). Mainland sites are displayed as M1-4, seabird sites are displayed as S1-4. **c-f**, algae and sessile filter feeder percent cover (untransformed data) for (c) serrated wrack, (d) Irish moss, (e) dulse, and (f) pink encrusting algae. Values are mean (± SE, n = 20). Box limits represent the first and third quartiles (25% and 75% percentiles), middle line represents the median (50% percentile), and whiskers represent the smallest and largest observations less than or equal to 1.5 × inter-quartile range.

2.3.3.2 Intertidal macrofauna

Significant variation was found when analysing the presence-absence low seabird density mainland and high seabird density islands communities to determine the contributions of intermediate and rarer intertidal macrofauna species using an NMDS ordination (Fig. 6b; PERMANOVA, F = 2.64, p = 0.026). The species that drove dissimilarities between the mainland and the seabird island communities was dogwhelks (mean ± SE; not statistically analysed; mainland = 0.0 ± 0.0 no. per 0.5 m^2, seabirds = 0.4 ± 0.1 no. per m^2).

However, no distinct variation was found when analysing the untransformed macrofauna to determine the contributions of the dominant species (Fig. 6a; PERMANOVA, F = 2.39, p = 0.113). The species that drove dissimilarities between the mainland and seabird island communities were dogwhelks (Fig. 6c; mean ± SE; not statistically analysed; mainland = 0.0 ± 0.0 no. per 0.5 m^2, seabirds = 1.1 ± 0.4 no. per 0.5 m^2) and common winkle (Fig. 6d; mean ± SE; Chi-squared test (square root transformed); mainland = 1.8 ± 1.0 no. per 0.5 m^2, seabirds = 0.4 ± 0.2 no. per 0.5 m^2; df = 1, N = 20, χ^2 = 0.77, p = 0.381).
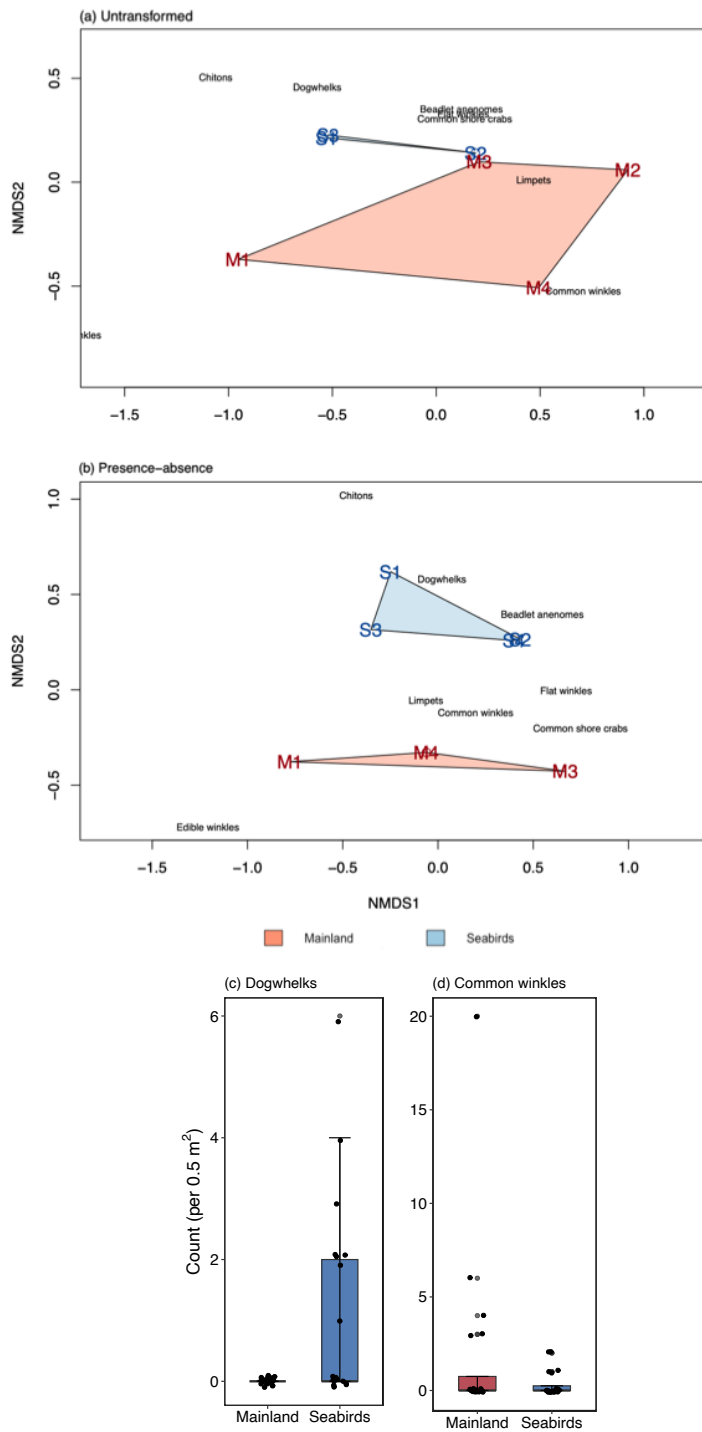
Figure 6 | Non-metric dimensional analysis (NMDS) biplots and boxplots comparing indicator species (those driving community dissimilarities) on the low seabird density mainland sites and seabird islands. a-b, NMDS for (a) untransformed data, and (b) presence-absence transformed data. Mainland sites are displayed as M1-4, seabird sites are displayed as S1-4. **c-d**, count (untransformed data) for (c) dogwhelks and (d) common winkles. Values are mean (± SE, n = 20). Box limits represent the first and third quartiles (25% and 75% percentiles), middle line represents the median (50% percentile), and whiskers represent the smallest and largest observations less than or equal to 1.5 × inter-quartile range.

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2.3.3.3 Functional groups

Intertidal predator densities were significantly higher at high seabird sites than low seabird sites (Fig. 7e; Chi-squared test; mean ± SE; mainland = 0.1 ± 0.1 no. per 0.5 m^2, seabirds = 1.3 ± 0.4 no. per 0.5 m^2; df = 1, N = 20, χ^2 = 7.22, p = 0.007). However, there were no significant differences in densities in macroalgae (Fig. 7a; Chi-squared test; mean ± SE; mainland = 48.9 ± 9.1% per 0.5 m^2, seabirds = 63.0 ± 6.7% per 0.5 m^2; df = 1, N = 15, χ^2 = 1.38, p = 0.240), turf algae (Fig. 7b; Chi-squared test (square root transformed); mean ± SE; mainland = 11.1 ± 3.2% per 0.5 m^2, seabirds = 14.3 ± 3.3% per 0.5 m^2; df = 1, N = 20, χ^2 = 0.28, p = 0.597), sessile filter feeders (Fig.7c; Chi-squared test; mean ± SE; mainland = 28.1 ± 6.6% per 0.5 m^2, seabirds = 31.6 ± 4.6% per 0.5 m^2; df = 1, N = 20, χ^2 = 0.06, p = 0.812), and other herbivores (Fig. 7d; Chi-squared test; mean ± SE; mainland = 3.4 ± 1.3 no. per 0.5 m^2, seabirds = 1.1 ± 0.3 no. per 0.5 m^2, df = 1, N = 20, χ^2 = 1.66, p = 0.198).
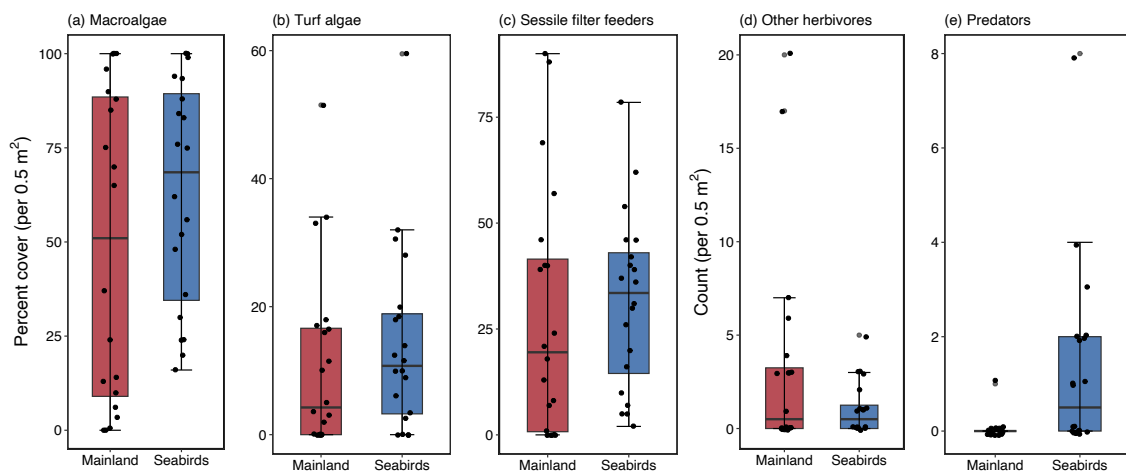

Figure 7 | Functional group classification differences between low seabird density mainland sites and seabird islands. a-c, Percent cover for (a) macroalgae (b) turf algae, and (c) sessile filter feeders. **d-e**, count for (d) other herbivores, and (e) predators. Values are mean (± SE, n = 20). Box limits represent the first and third quartiles (25% and 75% percentiles), middle line represents the median (50% percentile), and whiskers represent the smallest and largest observations less than or equal to 1.5 × inter-quartile range. Note differences in y-axes.

2.3.3.4 Diversity measures

There was a trend towards higher algal species richness on high density seabird islands compared to the low seabird density sites (Fig. 8a; Chi-squared test; mean ± SE; mainland = 4.8 ± 0.5 no. per 0.5 m^2, seabirds = 6.6 ± 0.5 no. per 0.5 m^2; df = 1, N = 20, χ^2 = 3.23, p = 0.072). However, there was no difference in the total number of fauna species (Fig. 8b; mean ± SE; Chi-squared test; mainland = 1.7 ± 0.2 no. per 0.5 m^2, seabirds = 2.0 ± 0.3 no. per 0.5 m^2; df = 1, N = 20, χ^2 = 0.55, p = 0.458).

No difference in Shannon's Diversity Index (H') between the communities was detected for algal species (Fig. 8c; mean ± SE; Chi-squared test; mainland = 0.6 ± 0.1 H', seabirds = 0.8 ± 0.1 H'; df = 1, N = 20, χ^2 = 0.41, p = 0.521) or fauna species (Fig. 8d; mean ± SE; Chi-squared test; mainland = 0.6 ± 0.1 H', seabirds = 0.6 ± 0.1 H'; df = 1, N = 20, χ^2 = 0.19, p = 0.661).

No distinct variation in Pielou's Evenness Index (J') between the communities was detected for algal species (Fig. 8e; mean ± SE; Chi-squared test; mainland = 0.2 ± 0.0 J', seabirds = 0.2 ± 0.0 J'; df = 1, N = 20, χ^2 = 0.41, p = 0.521) and fauna species (Fig. 8f; mean ± SE; Chi-squared test; mainland = 0.2 ± 0.0 J', seabirds = 0.2 ± 0.0 J'; df = 1, N = 20, χ^2 = 0.19, p = 0.662).
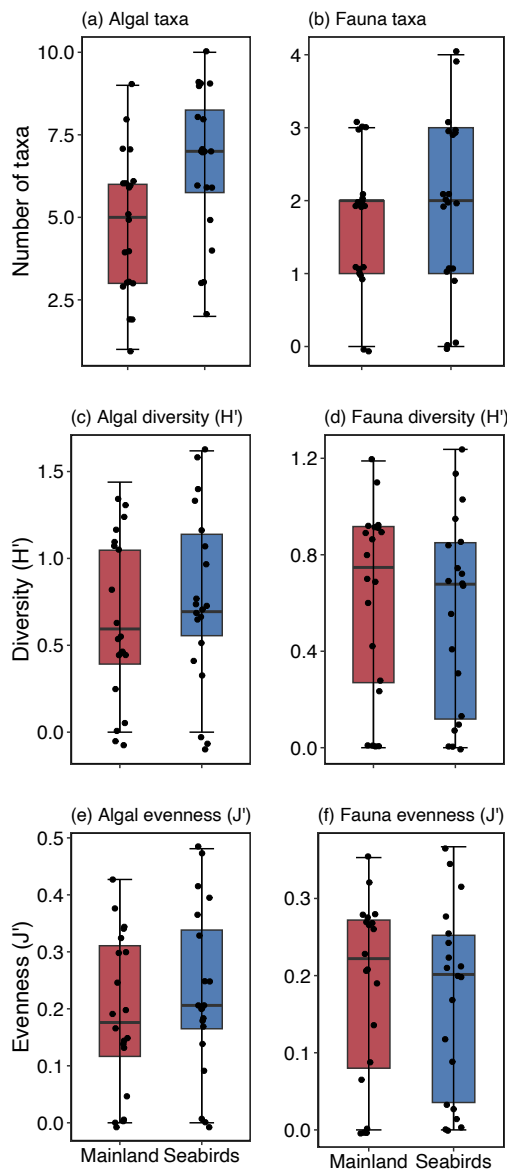
Figure 8 | Community diversity measures boxplots comparing low seabird density mainland sites and seabird islands. a-b, total number of taxa for (a) algal species, and (b) fauna species. **c-d**, Shannon's Diversity Index (H') for (c) algal species, and (d) fauna species. **e-f**, Pielou's Evenness Index (J') for (e) algal species, and (f) fauna species. Values are mean (± SE, n = 20). Box limits represent the first and third quartiles (25% and 75% percentiles), middle line represents the median (50% percentile), and whiskers represent the smallest and largest observations less than or equal to 1.5 × inter-quartile range. Note differences in y-axes.

2.3.4 Limpet size, abundance, and biomass

There was some indication of a difference in limpet length between the mainland and seabird islands, though high variation meant that this was not significant (Fig. 9a; Chi-squared test; mean ± SE, mainland = 29.7 ± 0.6 mm, seabirds = 35.8 ± 0.4 mm; $df = 1$, $N = 400$, $\chi^2 = 2.17$, $p = 0.141$). Limpet abundance was found to be higher on mainland sites compared to seabird islands, but again this was not significant (Fig. 9c; Chi-squared test; mean ± SE; mainland = 12.7 ± 3.6 no. per 0.5 m^2; seabirds = 5.0 ± 1.1 no. per 0.5 m^2; $df = 1$, $N = 20$, $\chi^2 = 2.83$, $p = 0.160$). No distinct variation in limpet biomass was detected between the mainland and seabird islands (Fig. 9b; Chi-squared test; mean ± SE; mainland = 4.8 ± 1.4 g per 0.5 m^2, seabirds = 3.1 ± 0.7 g per 0.5 m^2; $df = 1$, $N = 400$, $\chi^2 = 1.19$, $p = 0.275$).
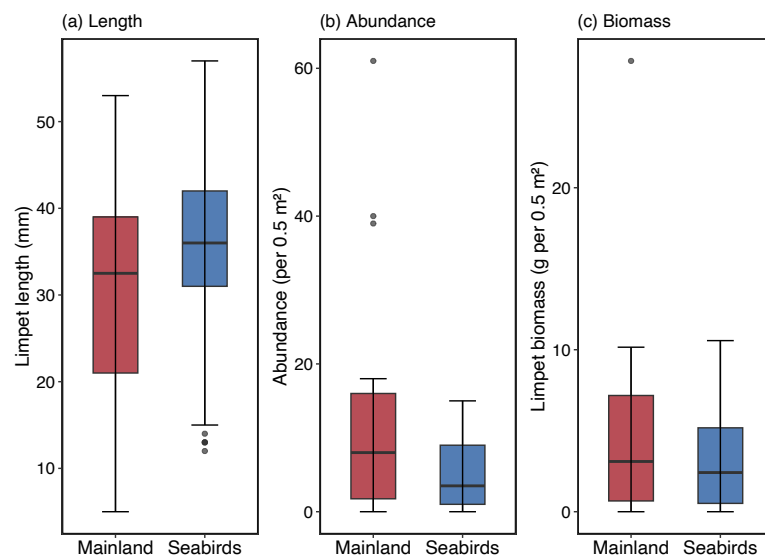

Figure 9 | Limpet distribution boxplots comparing low seabird density mainland sites and seabird islands. Distributions for (a) limpet length, (b) limpet abundance, and (c) limpet biomass. Values are mean (± SE, n = 400 for a; n = 20 for b and c). Box limits represent the first and third quartiles (25% and 75% percentiles), middle line represents the median (50% percentile), and whiskers represent the smallest and largest observations less than or equal to 1.5 × inter-quartile range. Note differences in y-axis.

2.3.5 Recolonisation patterns

Recolonisation rates of barnacles were higher at low seabird density sites than at high seabird density islands, and this effect did not vary by time (Fig. 10a; seabirds*time; Chi-squared test; *df* = 2, *N* = 15, χ^2 = 1.31, *p* = 0.520; seabirds; Chi-squared test; *df* = 2, *N* = 15, χ^2 = 4.38, *p* = 0.036). Barnacle abundance was significantly higher at sixteen weeks (Bonferroni; *F* = 10.240, *p* = 0.009), but there was no difference in abundance in pre-clearance plots (Bonferroni; *F* = 5.97, *p* = 0.063) or at 8 weeks post-clearance (Bonferroni; *F* = 4.86, *p* = 0.108).

Limpet recolonisation differed between mainland/seabirds and varied by time (Fig. 10b; seabirds*time; Chi-squared test; *df* = 2, *N* = 15, χ^2 = 5.98, *p* = 0.050). Limpet abundance was significantly higher at seabird sites at eight weeks (Bonferroni; *F* = 11.10, *p* = 0.006), but there was no difference in abundance in pre-clearance plots (Bonferroni; *F* = 2.38, *p* = 0.402) or at 16 weeks (Bonferroni; *F* = 0.35, *p* = 1.000).
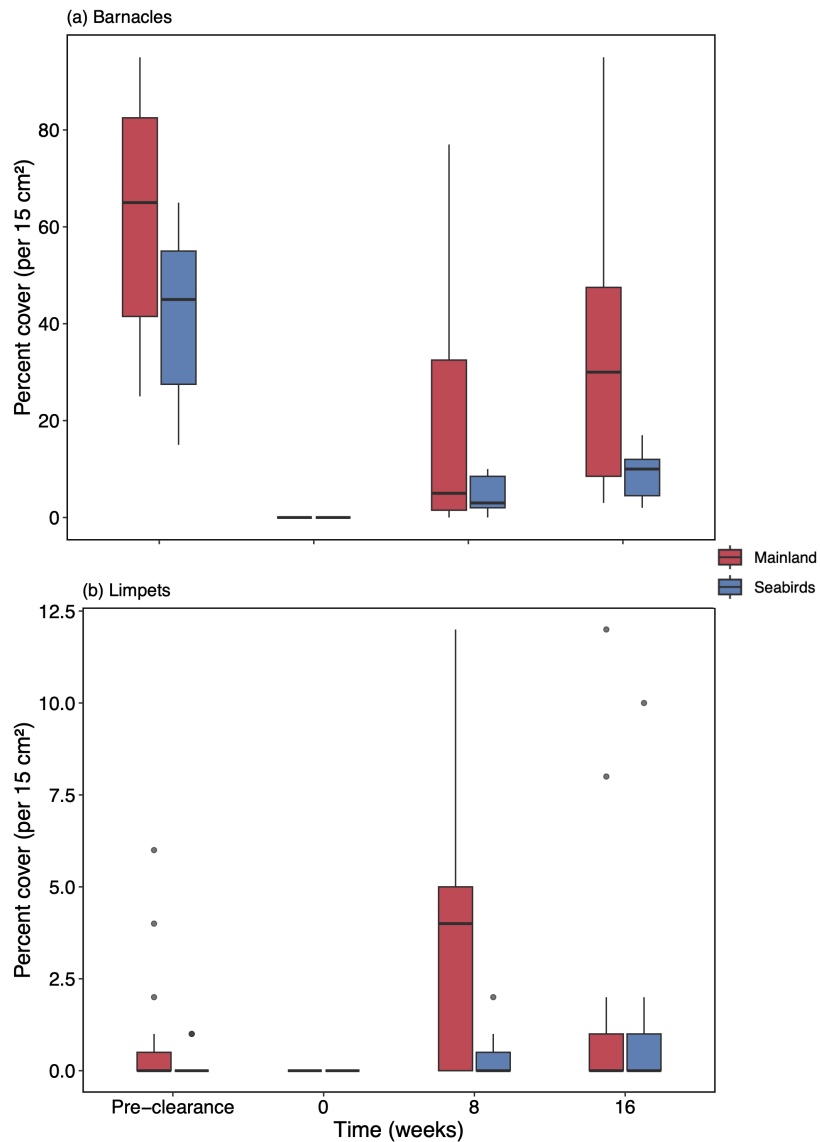
Figure 10 | Recolonisation rates of clearance for low seabird density mainland sites and seabird islands. Recolonisation rates from pre-clearance, zero weeks, eight weeks, and 16 weeks for mainland sites and seabird islands for (a) barnacles, and (b) limpets. Values are mean (± SE; n = 5). Box limits represent the first and third quartiles (25% and 75% percentiles), middle line represents the median (50% percentile), and whiskers represent the smallest and largest observations less than or equal to 1.5 × inter-quartile range.

2.4 Discussion

Summary of findings

Significantly enriched δ15N was found on high seabird density islands compared to low seabird density mainland sites for all sample types except epiphytic algae, as well as significantly greater nitrogen content on seabird islands in all sample types except macroalgae, epiphytic algae, and turf algae. Indicative support was found for higher algae species richness and limpet size due to seabird nutrient input. These findings provide evidence that that seabirds are cycling pelagic nutrient input through the terrestrial and intertidal environments. Some support was found of higher biodiversity on seabird islands, most notably when determining the contributions of intermediate and rarer intertidal macrofauna species, with the difference predominantly driven by predators. These findings show the cross-ecosystem link that seabirds provide, promoting seabird conservation in the UK and other temperate systems, including invasive mammal eradication programmes.

Seabird densities and nitrogen input

Higher densities of seabirds were found on the Farne Islands, Northumberland, compared Northumberland mainland by three orders of magnitude. By foraging in pelagic feeding grounds, seabirds were shown to be vectoring between two and three orders of magnitude greater nitrogen inputs to the seabird islands compared to the mainland.

Stable isotope analysis

Higher δ15N signals were found on seabird islands compared to low density seabird sites in terrestrial samples: soil, new-growth leaves, and lichen, as well as intertidal samples: macroalgae, turf algae, barnacles, and limpets. Significantly elevated nitrogen content was also found in soil, terrestrial plants, lichen, barnacles, and limpets, as well as marginally elevated turf algae nitrogen content. These findings support the hypothesis that seabird nutrient input is cycling through the terrestrial and intertidal environments. The higher densities of seabirds by three orders of magnitude were shown to be vectoring between two and three orders of magnitude greater pelagic derived nitrogen inputs to the seabird islands compared to low seabird density mainland sites. This greater nutrient input and subsequent greater δ15N signals and nitrogen content provide

evidence of a clear link by seabirds from pelagic to terrestrial and intertidal ecosystems, which can cause bottom-up interactions.

The proportion of seabird-derived nutrients decreases with increasing distance from seabird colonies in saltwater systems (Jones, 2010; McCauley *et al.*, 2012; Lorrain *et al.*, 2017; Savage, 2019; Benkwitt *et al.*, 2021a). Indeed, this pattern was generally observed in this study, with the samples closest to the seabird colonies, terrestrial plant, and soil, having the greatest $\delta^{15}N$ values on seabird islands, and macroalgae, epiphytic algae, and turf algae in intertidal areas having lower values. Interestingly, total nitrogen content generally increased with increasing distance from seabirds, which may suggest a nitrogen input from the marine environment is also occurring. Limpets had the third highest $\delta^{15}N$ values, which is likely explained by $\delta^{15}N$ values increasing with trophic levels, and microphagous limpets feeding on ^{15}N enriched diatoms and cyanobacteria, as well as organic material in the water column. Limpets also regulate the recruitment of macroalgae through consumption during early macroalgal stages (Jenkins & Hartnoll, 2001). However, the difference in $\delta^{15}N$ between macroalgae and limpet samples suggest that limpets on both the mainland and seabird islands are favouring other microscopic algae, as moving up one trophic level involves $\delta^{15}N$ increases of 2.2 to 3.4% (Zanden & Rasmussen, 2001; McCutchan Jr *et al.*, 2003), which is much greater than the difference in $\delta^{15}N$ values between limpets and both macroalgae and turf algae.

Contrary to the hypothesis, higher values of percent nitrogen were found during early breeding season compared to late breeding season. These findings contrast predictions that seabird nutrients would peak following breeding season, after high seabird densities had spent months at their breeding colonies, and would be at their lowest when the seabirds had been absent from the islands for months (Kazama, 2019). On the seabird islands, this might be explained by early breeding season being be the peak of seabird abundances, as well as seabirds spending increasingly more time at colonies on UK islands outside of breeding season (Dunn *et al.*, 2020). However, the same trend was observed on the mainland where no breeding colonies exist, and the seabirds are residents. Therefore, this reduction of nitrogen during spring and summer months could be related to plant use of nitrogen during these periods for growth. The general $\delta^{15}N$ trend of similar $\delta^{15}N$ values from May to August suggests the impacts of seabird

nutrient input are maintained and integrated all-year round. This finding is consistent with other research into temporal variation in seabird nutrients throughout breeding season (Pascoe *et al.*, 2022)*,* and seems probable given the huge quantities of nitrogen input during breeding season.

Community analysis

A notable difference was observed between seabird islands and the mainland, predominantly driven by higher densities of intertidal predators at high seabird sites. For example, dogwhelks comprised 81% of predators on seabird islands, yet were absent from mainland sites, so were likely the species driving community dissimilarities.

   Whilst seabird nutrient subsidies have been shown to result in bottom-up interactions in this study, this may in turn cause increased top-down interactions (Young *et al.*, 2011). Increased nutrients are predicated to increase algal biomass, increasing food available to herbivores, therefore increasing herbivore biomass, which in turn maintains algal abundance. Indeed, increased nutrient loading from seabirds increases primary producer biomass, resulting in increased algal herbivory to sufficiently maintain low primary producer levels following enrichment with seabird nitrogen (Methratta, 2004). This higher number of herbivores is likely to then increase the food resource available to predators, maintaining herbivore abundance. In the case of this study, it might be expected then that the greatest observable difference due to seabird nutrient input would exist in a greater predator abundance on the seabird islands compared to the mainland, which, indeed, is what was found. Indeed, the similar densities of macroalgae, turf algae, sessile filter feeders, and other herbivores indicate that the intertidal communities on seabird islands and the mainland are functionally similar. However, given that ten times the number of individual sites contained predators on seabird islands than the mainland, it is possible that seabird nutrient input are supporting an additional trophic level on the islands. This finding is inconsistent with research in Alaska that looked at community assembly, where increased seabird presence resulted in increased predation on intertidal invertebrates (Kurle *et al.*, 2021).

   Comparing species diversity and taxonomic relatedness, seabird islands had marginally greater algal species richness. However, there was no observed

difference in fauna species richness, or in community species diversity or evenness for either algal and fauna species. These findings suggest that the diversity effects are small, which is consistent with findings in benthic community differences in tropical systems (Benkwitt *et al.*, 2019). Drivers of ecological community diversity are highly complex, and seabird nutrient input is not the only factor influencing biodiversity, and it is possible confounding variables exist between the seabird islands and the mainland in this study. One major difference between the mainland and the seabird islands is that the mainland is generally more exposed than seabird islands, and exposed and sheltered communities can contain very different community patterns (Ballantine, 1961).

Community differences in intermediate and rarer algae and sessile filter feeder species were found to be marginally different, providing some support for greater biodiversity due to seabird nutrient input. No individual algae species or filter feeders were found to be statistically different between seabird islands and the mainland. However, the turf algae, Irish moss, was absent at all mainland sites, suggestive that a difference may exist. This provides some support that there is greater biodiversity on seabird islands due to diverse turf algae driving the dissimilarity, whereas mainland sites one and three were distinct from the others due to greater abundances of sand and lower diversity macroalgae. Indeed, turf algae thrive in the presence of mid-shore canopy forming macroalgae (Jenkins *et al.*, 1999; Jenkins *et al.*, 2004; Hawkins *et al.*, 2020), so given the elevated $\delta^{15}N$ ratios, it might be expected that greater abundances or productivity of turf algae exist on seabird islands.

Limpet size, abundance, and biomass
No statistical difference was detected in limpet size, abundance or biomass between seabird islands and the mainland. However, the effect size between the mainland and seabird islands was high, with mean limpet size 20% larger on seabird islands. The relationship between body size and population density within communities is central to explaining community resource use (Pagel *et al.*, 1991), and indeed, the quantity of algae grazed is more closely related to the biomass of limpets than their abundance (Branch, 1971; Bosman & Hockey, 1988). The results of this study suggest seabirds may be increasing limpet size, but that limpet abundance may be higher on the mainland, whilst the biomasses are

comparable. If indeed this is reflective of the seabird island and mainland communities, then it may suggest that limpet's food source, algae, is higher in quantity and/or quality because of the greater nitrogen loading caused by seabirds, which could be causing larger limpets on the seabird islands.

Shell growth in *P. vulgata* is rapid in their first two years, with growth rates between 0.4 and 2.0 mm/month. This rate then decreases over time, with a negative linear relationship existing between initial length and increment each year. By five years of age, they exhibit no measurable growth rate. Indeed, *P. vulgata* individuals five years and older are few, and form only negligible proportions of limpet populations. (Blackmore, 1969). Therefore, limpets attaining a larger size may suggest that their growth rates are more rapid (Branch, 1974; Balaparameswara Rao, 1976). If indeed seabird nutrient input is increasing limpet growth rate on the Farne Islands, then this is consistent with previous findings of faster limpet growth in the presence of seabirds (Bosman & Hockey, 1988). Mixed support for growth rate due to seabird nutrients has been found in damselfish and parrotfish (Graham *et al.*, 2018; Benkwitt *et al.*, 2019; Benkwitt *et al.*, 2021b). Enhanced growth rates have been observed in other organisms such as corals and fishes due to the bottom-up effects of allochthonous nutrients (Graham *et al.*, 2018; Savage, 2019; Benkwitt *et al.*, 2021a). The marginal differences observed in this study are indicative that a difference may exist in size, or potentially limpet growth rate, that this study was unable to detect statistically.

Explaining limpet abundance is a multi-disciplinary task, and not likely to be explained by higher nitrogen loadings alone. Limpet dispersal and connectivity varies between species and communities, and whilst limpets have the potential for long-distance dispersal, most larvae settle within much shorter distances (Ribeiro, 2008). Fully understanding limpet abundance on the Farne Islands and Northumberland coast would require further research.

Recolonisation patterns

Contrary to predictions, recolonisation rates were faster on the mainland than seabird islands for both barnacles and limpets. Barnacle abundance is dictated by both physical and biological settlement cues at a variety of spatial scales, and whilst every measure was taken to minimise the impact of confounding variables in the study, the mainland and seabird islands are inherently physically and biologically different, and it is likely that seabird nutrient input is not the dominant driver of demographic differences between the communities. Barnacle abundances increase with increasing wave exposure level, with the most sheltered shores absent of barnacles (Ballantine, 1961), and indeed, the three sites on the seabird islands are all sheltered from the prevailing UK west to south-westerly winds compared to the mainland. Other physical settlement cues and confounding variables include surface roughness and a lower vertical centre of gravity of surface (Le Tourneux & Bourget, 1988; Hills & Thomason, 1998). Furthermore, biological settlement cues will also impact community differences, including the presence of alga species, diatoms, abundance/fineness of detrital matter, microheterogeneity, food supply, and chlorophyll *a* concentration (Le Tourneux & Bourget, 1988; Hills & Thomason, 1998; Burrows *et al.*, 2010). Finally, marine nitrate toxicity issues exist in the River Tweed and there is eutrophication at Lindisfarne National Nature Reserve (Jarvie *et al.*, 2002), both of which and may be a source of increased nutrient input are close to the mainland study sites.

Greater limpet recolonisation was also observed on mainland sites than on seabird islands, with limpet abundance at week eight driving the difference. It is likely that limpets were more abundant on the recently disturbed plots as this disturbance increased the abundance of microphagous limpets' preferred food type within the plots, a microalgal film largely consisting of diatoms and cyanobacteria (Jenkins & Hartnoll, 2001). The majority of limpets within the plots were adults, rather than new recruits, which may be influenced by the slightly higher densities of limpets on the mainland. In order to determine the long-term patterns of limpet recolonisation, a longer recolonisation study would need to be performed. This is also true of algal recolonisation, with only 10% of plots showing visible abundances of algae after 16 weeks, all of which were negligible quantities of encrusting algae. The high numbers of limpets, particularly at eight weeks, may

explain the absence of turf and macroalgae species, due to limpet herbivory. It is also possible that the observed increase in barnacles recolonisation was in part driven by the increased limpet recolonisation, as has been observed in other empirical research (Benedetti-Cecchi, 2000).

Seals

As well as being seabird breeding grounds, there are also seal residents on the Farne Islands, predominantly grey seals (*Halichoerus grypus*), who use the islands as rookeries during their own breeding season, from October to January. Foraging distance in grey seals from the Farne Islands has been observed to vary from short trips to known haul-out sites (mean distance 39.8 km) to long and distant travel (2100 km; McConnell *et al.*, 1999). Therefore, it is possible that the seals are also providing an allochthonous source of nutrients to the Farne Islands. Furthermore, seal biomass exceeds that of seabird biomass on two of the three study islands (National Trust, 2022b). However, whilst seal biomass may exceed that of seabirds across the three islands, seabird abundance is approximately fifty times higher than seal abundance (Webber *et al.*, 2015; National Trust, 2022a; National Trust, 2022b).

In terms of seal proximity to the sites on the seabird islands, none of the study sites were seal rookeries, and the seabird colonies were closer to each study site. Seabirds also travel across the islands frequently, whereas the seals tend to haul out in one spot. With this in mind, the particularly high $\delta^{15}N$ in the terrestrial samples suggest that it is the seabirds, not the seals, that are the dominant cause of increased nitrogen loads to the terrestrial environments, at least. Moreover, it is possible that it is only the females who are feeding at pelagic locations, as male grey seals often eat at benthic locations (Tucker *et al.*, 2007), which may be sourced close enough to the islands to not be an allochthonous source.

Caveats and future research

Low seabird density sites were chosen to be as similar as possible to the seabird islands, but a more direct comparison would be between high and low seabird density Farne Islands. This would reduce the impact of confounding variables that may exist between the Farne Islands and Northumberland mainland coast, such wave exposure or the marine nitrate toxicity and eutrophication issues.

However, the mainland and seabird islands were as similar as was possible (e.g., same habitat, proximity between mainland and seabird sites), so the findings of this study should not have been strongly influenced by confounding variables. All study sites being located on the Farne Islands would also make wave exposure/shelter levels more comparable, improving recolonisation study set-up.

The site locations on the seabird islands were also not directly below the greatest assemblages of birds. Cliff nesting species puffins and guillemots made up the greatest seabird abundances (National Trust, 2022a), where there is no intertidal zone. Further, there were locations of intertidal zone that were closer to the seabird nests and burrows than those used in this study. As the proportion of seabird-derived nutrients decreases with increasing distance from seabirds (Benkwitt *et al.*, 2021a), it is possible greater differences would have been observed if the sites on the seabird islands were closer to where the greatest assemblages of congregate. Further research could also include studying the impact to marine areas directly below the greatest assemblages of seabirds, in the ocean.

Staple island, the island found to contain the highest seabird densities and subject to the greatest nitrogen input, underwent brown rat (*Rattus norvegicus*) eradications in 2006 and 2009 (DIISE, 2022). Positive seabird population growth, facilitated by immigration, particularly in the presence of gulls and terns, usually follows mammal eradications (Brooke *et al.*, 2018), and indeed, Staple was shown to support the greatest seabird presence, including gulls and terns, and nutrient input of the three seabird islands. However, the full return of cross-ecosystem seabird nutrient subsidises and all their demographic benefits may take multiple decades (Benkwitt *et al.*, 2021a). Moreover, mixed evidence exists of islands' recovery rates following rat eradications, ranging from a full recovery within 11 years to having not begun after 13 years (Jones, 2010; Kurle *et al.*, 2021). Therefore, the increased seabird presence and nutrient loading may not yet be reflected in Staple's biodiversity or productivity.

Further future research could include processing the remaining late breeding season isotope samples to gain a fuller understanding of temporal variation. Increasing the timescales of the recolonisation experiments would allow further barnacles and limpet observations, as well as giving algae time to recolonise. A more extensive community analysis might also produce a more

representative reflection of the communities. Given that limpet biomass is better correlated with algae consumption than limpet abundance, calculating the biomass of predators and other herbivores is worth consideration, as is extending the scope of surveys to include other habitats in the region, such as rock pools.

Whilst support exists that seabirds, not seals, are the dominant source of nutrients entering the Farne Islands, predominantly in enriched terrestrial nitrogen isotope values, the input of seal nutrient input remains undetermined. Establishing seal defecation rates and scat nitrogen content would help quantify seal nutrient input to the Farne Islands. Carbon isotope analysis could be performed to determine foraging locations. Precisely establishing breeding ground locations would help better understand seal nutrient contribution to the terrestrial and intertidal ecosystems. Further, there are islands close to Lindisfarne that may be home to high abundances of seals, but limited seabird populations, which could be useful for comparing impacts of seabirds and seals.

Final conclusions

Strong evidence was found of seabird nutrients moving through terrestrial and intertidal ecosystems, through elevated $\delta^{15}N$ signals and total nitrogen content. This study provides a clear link by seabirds from pelagic to terrestrial and intertidal habitats, causing bottom-up interactions, suggesting seabirds may be acting as keystone species to both terrestrial and intertidal ecosystems, highlighting and promoting the importance of seabird conservation in the UK, and potentially global temperate systems.

Some support was also found for higher biodiversity in the presence of seabirds, and that seabird nutrient input may enhance limpet size. However, the lack of statistical support for higher biodiversity, limpet size, and recolonisation patterns suggest further research would be needed to understand the impact of seabirds to the Farne Islands more fully, and a greater understanding of seals' impact would help differentiate between seabirds' and seals' impact. This research could assist and guide future conservation management in areas where seabirds are present by supporting the recommendation of concentrating on seabird conservation to maximise resource use. Furthermore, the findings support the use of rat eradication programmes in the UK and other temperate

systems, to stop rats from destroying seabird populations, which are subsidising terrestrial and intertidal ecosystems.

Chapter 3: General discussion

Key findings

Empirical studies examining the bottom-up effects of nutrients supplied by seabirds to marine and nearshore systems using stable isotope analysis have typically found increased $\delta^{15}N$ signals across an array of sample and species types in the presence of seabirds. High $\delta^{15}N$ has been observed in soil, tree leaves, terrestrial plants, macroalgae, turf algae, periphyton, particulate organic matter (POM), sedimentary organic matter (SOM), gastropods, crabs, isopods, sponges, seagrass, kelp, zooplankton, clams, zooxanthellae, mussels, and damselfish (McCauley *et al.*, 2012; Gagnon *et al.*, 2013; Zmudczyńska-Skarbek *et al.*, 2015; Honig & Mahoney, 2016; Lorrain *et al.*, 2017; Zmudczyńska-Skarbek & Balazy, 2017; Graham *et al.*, 2018; Kazama, 2019; Savage, 2019; Benkwitt *et al.*, 2021b; Benkwitt *et al.*, 2021). Within these studies, whilst the overarching trend was increased $\delta^{15}N$ signals in the presence of seabirds, there have also been instances where no $\delta^{15}N$ difference was observed between high and low seabird density sites in gastropods, seagrass, kelp, POM, coral, mussels, crabs, and parrotfish (Zmudczyńska-Skarbek & Balazy, 2017; Kazama, 2019; Savage, 2019; Benkwitt *et al.*, 2021b), or even instances of low $\delta^{15}N$ in urchins in the presence of seabirds (Zmudczyńska-Skarbek *et al.*, 2015).

The findings of the present study, on the Farne Island archipelago, are in keeping with the trends observed in other studies that used stable isotope analysis to study the effects of seabird nutrient input. A general trend of substantially higher $\delta^{15}N$ values was found in the presence of seabird nutrients in soil, terrestrial plants, lichen, macroalgae, turf algae, barnacles, and limpets, with epiphytic algae the only sample type that did not record a statistical difference. A similar pattern was also observed in total nitrogen content, with macroalgae, epiphytic algae, and turf algae the only sample types that were not found to be substantially different in the presence of seabirds. In terms of biological outputs, a marginally greater biodiversity was found on seabird islands, whilst productivity did not differ between high and low seabird sites, and barnacles and limpets were found to recolonise faster on sites with low seabird densities.

Implications

The trends of increased nitrogen isotope values at locations with high seabird densities observed in this study and others reflect what can often be observed throughout ecology: allochthonous nutrients can be traced moving through ecosystems, but the effects are not always universal, and compounding variables will often interact with ecology in unexpected ways. The present study provides evidence that seabird nutrients are indeed moving through terrestrial and intertidal ecosystems in the UK. This finding has global implications, given the UK's international importance for breeding seabirds and waders (Stanbury *et al.*, 2017). Moreover, seabird populations have been decimated on 90% of temperate and tropical island groups (Jones *et al.*, 2008), and the UK's islands support 80% of the UK's seabird breeding pairs (Stanbury *et al.*, 2017). Furthermore, the threats to seabirds are mounting, and include not only local and regional threats such as commercial fishing and invasive mammals, but global threats too, such as climate change (Croxall *et al.*, 2012). Therefore, the findings of the present study promote seabird island conservation management in the UK for both global and UK importance, such as the undertaking invasive alien vertebrate eradication programmes on the 25 UK islands that would most benefit from them (Stanbury *et al.*, 2017).

Whilst stable isotope analysis has been heralded as the best method of tracking nutrient flow through ecosystems and up trophic levels (Young *et al.*, 2011; Kazama, 2019), it is important, too, to determine if this flow of nutrients are impacting biological processes. Increased seabird nutrient resources increase productivity, functioning, diversity, biomass, community dynamics, food availability, food quality, and providing ecosystem resilience (Polis *et al.*, 1997; Lundberg & Moberg, 2003; Loreau & Holt, 2004; Benkwitt *et al.*, 2019), and should be expected to be similarly impacting the Farne Islands. Such impacts are, arguably, more difficult to measure and potentially more subject to additional variables, which might form part of the reason for why comprehensive effects of seabird nutrients on whole communities are rare, with most studies focusing on individual species or trophic levels (Kazama, 2019). Some examples do exist, though, including seabird guano altering rocky intertidal community structures by causing the formation of extensive foliose algae mats, which mussel spat, polychaetes, and crustaceans settle in, providing food for predatory shorebirds

(Bosman & Hockey, 1986). This finding shares some similarities with those found in the present study, with the substantially increased predators existing on seabird islands. Further, seabird nutrients can alter algae herbivore feeding habits (Gagnon *et al.*, 2013), whilst benthic community structures show little difference due to seabird nutrient input in tropical systems (Benkwitt *et al.*, 2019). The findings of the present study are approximately consistent with these studies, with community biodiversity differences not large on seabird islands, but some differences existing.

As well as increased limpet growth rates (Bosman & Hockey, 1988), other biological outputs caused by seabird nutrient input include increased manta ray and zooplankton abundance (McCauley *et al.*, 2012), increased macroalgae growth rate (Bosman *et al.*, 1986), increased biomass and growth rate of damselfish (Graham *et al.*, 2018; Benkwitt *et al.*, 2021a), increased growth rates of coral (Savage, 2019), and increased growth rate and mean body size of parrotfish (Benkwitt *et al.*, 2021b). Mixed results have also been reported in invertebrate abundances (Kolb *et al.*, 2010), whilst seabirds can negatively impact lichen, macroalgae, and barnacle abundances (Wootton, 1991). It was surprising that no statistical difference existed in limpet growth rate, given the effect size indicated 20% larger limpets on seabird islands. Between site differences were likely the reason for the lack of significance, but the results found in the present study are very suggestive that a difference does exist in limpet growth rate due to nutrient input that this study was unable to detect.

The recolonisation rates of intertidal species remains an understudied area of research. Algae recolonisation rates are often the focus of such studies, and limpets and barnacles are more frequently observed as part of the overall succession following disturbance events (e.g., Menge *et al.*, 1993; Benedetti-Cecchi & Cinelli, 1996; Benedetti-Cecchi, 2000). In the present study, barnacles and limpets recolonised much more rapidly than algae, which could have implications for recovery following disturbance events. Indeed, with climate change forecast to increase the frequency and severity of extreme weather in the near future, including storm events (Beniston *et al.*, 2007; Noyes *et al.*, 2009), the rapid recolonisation by limpets and barnacles over algae may suggest shifts in community structures from algal-dominated shores to sessile filter-feeder shores on UK shores and possibly beyond.

Future directions

Perhaps one of the most notable findings of the present study was the insight to the complexity of the Farne Island system. The Farne Islands were chosen as the study site due to high seabird abundances, which number in the hundreds of thousands (National Trust, 2022a). These seasonal breeders play a large role in the complexity of the ecosystem on the islands, by inputting such vast quantities of nutrients within a moderately short timeframe. Their subsequent absence creates extreme temporal differences of nutrient input, a phenomenon which remains understudied (Kazama, 2019). However, seabirds are not the only group of animals that use the Farne Islands as a breeding ground, with thousands of seals using the islands as rookeries. Determining and differentiating the impacts of seabirds and seals to the islands was beyond the scope of the current study and would provide an intriguing area for future research. As would establishing the interaction between seals and seabirds. It is possible that seabird nutrient input is propagating into the surrounding marine ecosystems, which is ultimately increasing food resources available to seals. Nitrogen stable isotope analysis of seal prey types, such as crustaceans and fish, would help track seabird nutrients, whilst carbon stable isotope analysis would help determine whether seal prey are sourced from benthic or pelagic locations. Moreover, research into the impact of seal nutrient input is extremely limited, and it is possible that, similarly to seabirds, seals are providing ecosystems with an allochthonous nutrients that link marine and terrestrial environments, contributing to inter-habitat connectivity. Some studies have been performed, largely in Antarctica (e.g., Bokhorst *et al.*, 2007; Toro *et al.*, 2007; Bokhorst *et al.*, 2019; Wing *et al.*, 2021) and the Farne Islands presents an opportunity to research the impacts of seal nutrient input to temperate systems.

The Farne Islands provide an ideal natural experimental set up to test for the effect of seabird nutrient input to recipient ecosystems, because, as well as the high seabird density islands that were used in the present study, there are also low seabird density islands. Unfortunately, it was not possible to access the low seabird density islands, as the present study was reliant on the National Trust boats to gain access to Inner Farne, Staple, and Brownsman, and the low seabird density islands are less frequently visited. Moreover, the National Trust survey 15 islands across the archipelago (National Trust, 2022a), and there is a wide

range of seabird densities across the islands that would allow different gradients of seabird densities to be studied. Another area of research for which the Farne Islands is well suited is the recovery of seabird populations following invasive mammal eradication programmes, due to the rat eradications that Staple island has undergone 2006 and 2009 (DIISE, 2022). While seabird recovery following eradications is a well-studied topic globally (e.g., Kurle *et al.*, 2005; Mulder *et al.*, 2009; Jones, 2010; Glen *et al.*, 2013; Brooke *et al.*, 2018; Benkwitt *et al.*, 2021a), there remains an absence of studies performed in the UK, although some studies do exist (e.g., Bell *et al.*, 2019). Indeed, interestingly, despite the success of the previous rat eradications on Staple, Brownsman and Staple remain in the top 25 islands in the UK prioritised for brown rat biosecurity measures (Stanbury *et al.*, 2017).

Expanding the search into the impact of seabird nutrients to UK ecosystems into other areas of high seabird densities, such as Skomer, Skokholm, and Ramsay Island, in Pembrokeshire, would provide a more holistic understanding of seabird nutrient impact in the UK. Further research on the impact of seabird nutrients on the Farne Islands ecology should prioritise limpet growth rate, due to the findings of the present study strongly suggesting a difference would be found with a greater number of study sites. Recolonisation pattern experiments would be better performed over greater timescales, of at least two years, to allow algae recolonisation to occur (Benedetti-Cecchi & Cinelli, 1996). Further, the temporal impacts of disturbance events could be investigated by clearing plots at different times of the year, whilst clearing plots at different shore heights might give a greater understanding of community-wide spatial responses to disturbance events.

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