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Birds influence vegetation coverage and structure on sandy biogeomorphic islands in the Dutch Wadden Sea

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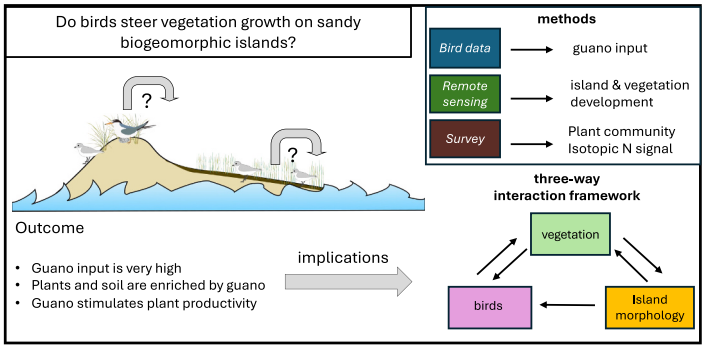
HIGHLIGHTS

- Coastal birds transport a large (50–500 kg ha^{-1} y^{-1}) quantity of guano each year to sandy islands in the Dutch Wadden Sea.
- Vegetation grows on this organic N source as indicated by elevated $\delta^{15}N$ values.
- Vegetation productivity and community composition are affected by guano.
- Coastal birds may indirectly affect sandy island morphodynamics by fuelling biogeomorphic interactions.

GRAPHICAL ABSTRACT



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ABSTRACT

Small uninhabited islands form important roosting and breeding habitats for many coastal birds. Previous studies have demonstrated that guano can promote ecosystem productivity and functionality on island ecosystems. Here, we assess the role of external nutrient input by coastal birds on the vegetation structure and coverage on sandy biogeomorphic islands, where island-forming processes depend on vegetation-sedimentation feedbacks. As a first step, we investigated whether breeding birds affect vegetation productivity on sandy back-barrier islands in the Wadden Sea. Using a combination of bird observations and plant stable isotope ($\delta^{15}N$) analyses, we demonstrate that (i) breeding birds transport large quantities of nutrients via their faecal outputs to these islands annually and that (ii) this external nitrogen source influences vegetation development on these sandy, nutrient-limited,

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islands. Based on these results we discuss how this avian nutrient pump could impact island development and habitat suitability for coastal birds and discuss future directions for research. In general, we conclude that avian subsidies have the potential to affect both the ecological and biogeomorphic functioning of coastal soft-sediment systems. However, the strength and scale of especially these biogeomorphic interactions are not fully understood. For the conservation of both threatened coastal birds and sandy back-barrier islands and the design of appropriate management strategies, we argue that three-way interactions between birds, vegetation and sandy island morphodynamics need to be further elucidated.

1. Introduction

Small, uninhabited islands are intensively used by high numbers of roosting or breeding birds worldwide (Anderson et al., 2008; Caut et al., 2012; Fukami et al., 2006; Graham et al., 2018; Wait et al., 2005). Islands that harbour dense seabird colonies accumulate enormous amounts of their faecal material, better known as guano. This bird faeces contains high concentrations of nutrients and has a long history of being used as a natural fertilizer (Cushman, 2013; Szpak et al., 2012). A recent study by Otero and co-authors (Otero et al., 2018) has estimated that seabirds collectively transfer similar magnitudes of nitrogen and phosphor from the marine environment to their breeding grounds as those produced by for instance fishing activities. These high nutrient subsidies have been found to promote ecosystem productivity both locally around the colonies, by stimulating vegetation growth, and in adjacent terrestrial or marine environments by fuelling higher trophic levels (Buelow et al., 2018; Graham et al., 2018; Kolb et al., 2010a; Lorrain et al., 2017, see Table 1 for literature overview). Previous studies have demonstrated the vital but indirect ecosystem-engineering role of birds by highlighting that avian subsidies can enhance island ecosystem productivity and foodweb functioning (e.g., Barrett et al., 2005; Fukami et al., 2006; Kolb et al., 2010b). Furthermore, through leaching, runoff and tidal flow birds can also boost the ecological functioning of the connected coastal environment such as coral reefs (Graham et al., 2018; Linhares and Bugoni, 2023), mangroves (Appoo et al., 2024; Onuf et al., 1977) and estuaries (Bildstein et al., 1992; Signa et al., 2021).

Besides boosting primary productivity and ecological interactions, we hypothesize that birds can also play an indirect landscape-engineering role in biogeomorphic landscapes, where vegetation plays a key role in trapping and binding lose sediments (Vinent and Moore, 2015; Zinnert et al., 2017). Coastal vegetated landscapes such as dunes, salt marshes, mangrove forests and seagrass meadows, are called biogeomorphic ecosystems as they are shaped by positive vegetation-sedimentation feedbacks (Corenblit et al., 2011). In those ecosystems, the vegetation improves their own living conditions with increasing vegetation coverage and biomass by attenuating wind or water, thereby capturing and stabilizing sediments (Bonte et al., 2021; Schwarz et al., 2018). Nutrient subsidies, such as guano, that foster vegetation growth, could therefore kick-start and further strengthen these biogeomorphic interactions thereby affecting landscape-forming processes.

Barrier islands protect about a tenth of our world's shoreline and are biogeomorphic landforms, where island development depends on the establishment and growth of both dune building grasses and marsh forming species (Corenblit et al., 2011; Vinent and Moore, 2015; Reijers, 2019; Zinnert et al., 2017). Situated behind these ocean-facing barrier islands, we can find smaller types of uninhabited sandy islands (~100 ha) that emerge in more fetch-limited and tide-dominated environments. Globally, >15.000 of these sandy islands have been described (Pilkey et al., 2009). Although these back-barrier or low-fetch islands are not as extensively studied as their ocean-facing counterparts (Cooper et al., 2007; Pilkey et al., 2009), they also evolve through the interaction between biological and physical processes. Aeolian-mediated dune-

Table 1
Overview of studies that looked at the role of breeding birds on island vegetation productivity highlighting their estimates of avian presence (bird density or guano deposition) and nitrogen isotopic value of present vegetation (values taken from within colony if multiple values were reported).

Island	Island type	Dominant bird	Avian density	$\delta^{15}N$ vegetation	Reference
Island northeast Australia	Mix sand and hard substrate	Torresian Imperial-Pigeon	NA	~ 7 ‰	(Buelow et al., 2018)
Réunion island	Hard substrate	King penguin	~0.8 (nests m^{-2})	~ 5 ‰	(Caut et al., 2012)
Bagaud France	Hard substrate	Yellow-legged gull	~1 (nests m^{-2})	~ 8 ‰	(Caut et al., 2012)
Surprise (New Caledonia)	Hard substrate	Red-footed booby	~0.011 (nests m^{-2})	~ 9 ‰	(Caut et al., 2012)
Teuaua French polynesia	Hard substrate	Sooty terns	~1.2 (nests m^{-2})	~ 16 ‰	(Caut et al., 2012)
Small islands north New zealand	Hard substrate	Buller's shearwater	NA	~14 ‰	(Fukami et al., 2006)
Stockholm archipelago Sweden	Hard substrate	Cormorant	~0.020 (nests m^{-2})	~14 ‰	(Kolb et al., 2010b)
Aleutian Archipelago	Hard substrate	Puffins, kittiwakes	~0.212 (nest m^{-2})	~8 ‰	(Maron et al., 2006)
St Paul island Alaska	Hard substrate	Murres, auklets, kittiwakes	~14.4 t d^{-1} (wet weight guano)	~22 ‰	(Wainright et al., 1998)
Northwest Greenland	Hard substrate	Little Auks	~0.73 (nests m^{-2})	~16.5 ‰	(González-Bergonzoni et al., 2017)
Chagos Archipelago	Hard substrate	Greater crested tern	~0.124 (nests m^{-2})	~9 ‰	(Graham et al., 2018)
Islands bahía de Los Ángeles, Mexico	Hard substrate	NA	NA	~24 ‰	(Barrett et al., 2005)
Santa Barbara (Brazil)	Hard substrate	Masked booby	~0.003 (nests m^{-2})	~19 ‰	(Linhares and Bugoni, 2023)
Siriba (Brazil)	Hard substrate	Masked booby	~0.013 (nests m^{-2})	~14 ‰	(Linhares and Bugoni, 2023)
Goëlette (Seychelles)	Sandy substrate	Brown noddy and sooty tern	~0.71 (nests m^{-2})	~13 ‰	(Appoo et al., 2024)
South island (Seychelles)	Sandy substrate	Red-footed booby	~0.003 (nests m^{-2})	~11 ‰	(Appoo et al., 2024)
Meio isalnd, Fernando de Noronha (Brazil)	Hard substrate	Masked and red-footed boobies	Colony estimate ~400 ind (masked booby) 1500 ind (red-footed)	~15 ‰	(Gaiotto et al., 2022)
Marinheiros Island, Brazil	Soft sediment substrate	Pelecaniformes species	NA	~12 ‰	(Caseiro-Silva et al., 2023)

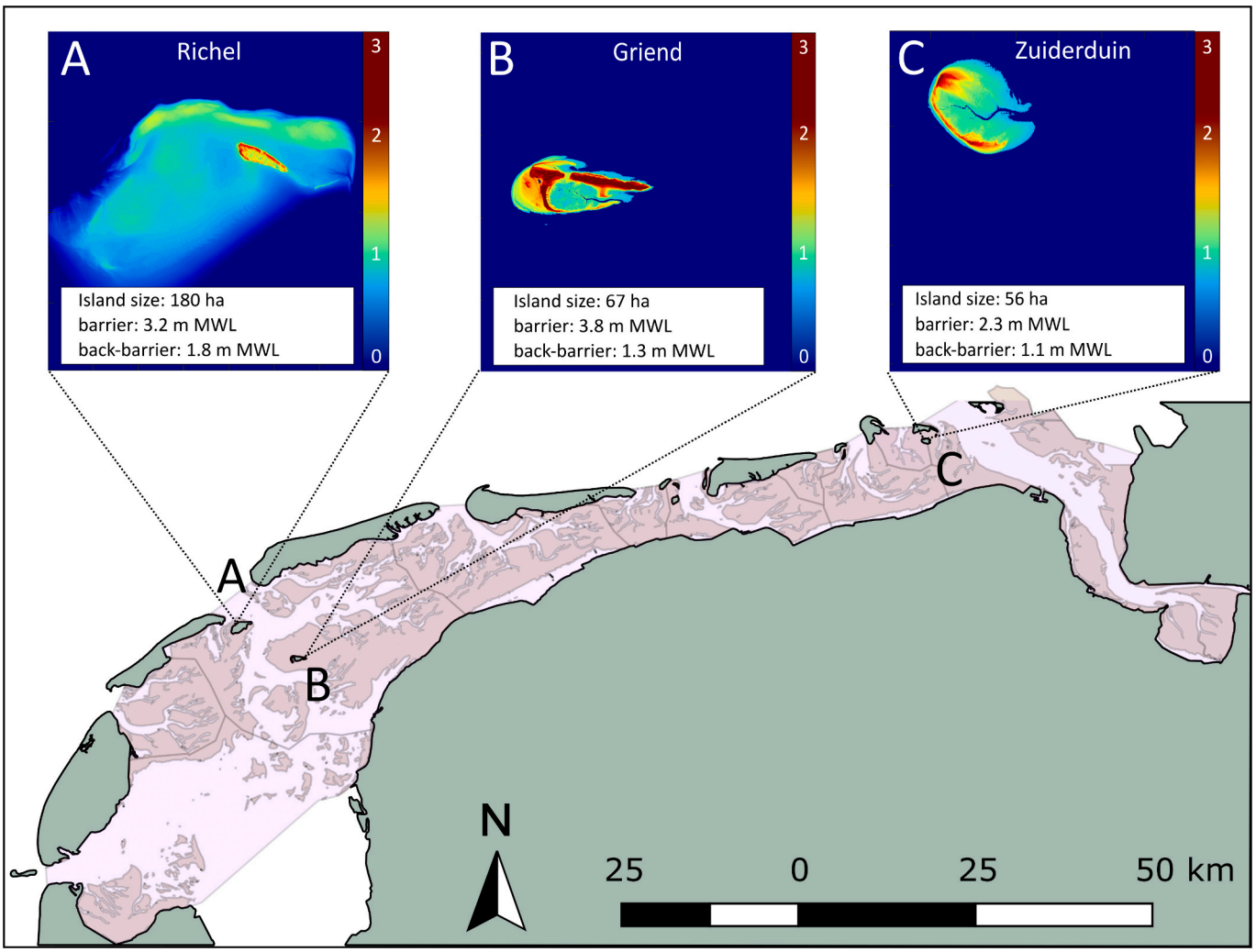

Fig. 1. Position and general characteristics (island size, threshold at >1.0 m above mean water level (MWL)) and surface elevation (in m above MWL) of the three back-barrier islands in the Dutch tidal Wadden Sea with A) Richel, B) Griend and C) Zuiderduin, respectively.

building processes are often absent and instead, they accommodate a beach or chenier barrier ridge on the exposed island side, which is formed by coarse-grained sediment, shells, and wrack debris transported during high-energy storm events (Otvos, 2000; Pilkey et al., 2009). Vegetation on these islands plays a key role in stabilizing these islands – by increasing resistance to wave swash, accumulating organic matter, increasing soil cohesion, and reducing bottom shear stress – which all contribute to island development and reduce island mobility (Christiansen et al., 2000; Marin Diaz, 2022; Pilkey et al., 2009). However, strong physical forcing by tides and waves combined with low nutrient availability in coarse-grained sediments (Reijers et al., 2020), can negatively impact vegetation growth which could potentially keep the islands in a low, unvegetated state (Vinent and Moore, 2015). Overcoming these initial vegetation establishment thresholds and allowing vegetation to rapidly recover following storm surges could therefore have a strong impact on island ecosystem functioning.

The tidal mudflat or wetland ecosystems surrounding these sandy islands, such as the Yellow Sea, Ria Farmosa, the US Atlantic coast or the Wadden Sea, form important breeding, staging, and roosting habitat for many (migratory) coastal birds or shorebirds (Melville et al., 2016; Piersma and Lindström, 2004; Smith et al., 2023; Sousa et al., 2020). However, human activities, including habitat exploitation, infrastructure development and land reclamation have caused dramatic changes to the natural environment and put migratory coastal birds globally at risk (Piersma et al., 2016; Piersma and Lindström, 2004). The Wadden Sea for example, is home to almost one million coastal breeding birds belonging to 31 species (Koffijberg et al., 2015). However, most of these breeding birds (~60 %) have shown significant declines in breeding success and numbers since the early 1990s, which is for a large part attributed to a decline in suitable breeding habitat (Koffijberg et al., 2015; Koffijberg et al., 2016). As mammalian predators (e.g., red foxes, mustelids) are mentioned as one of the most important causes of these declines, small uninhabited islands that do not accommodate ground predators and are not visited by people could form relatively safe breeding sites for these threatened bird species. We therefore hypothesize that these small uninhabited sandy islands accommodate a relatively high density of breeding birds that influence vegetation dynamics, thereby indirectly affecting vegetation-sedimentation feedbacks.

Here, we studied the effects of nutrient input by breeding birds on vegetation dynamics for three uninhabited back-barrier islands in the Dutch Wadden Sea (Richel, Griend and Zuiderduin) by (i) aggregating data on yearly breeding bird counts to estimate island-specific faecal input, (ii) analysing island vegetation development in relation to faecal input and by (iii) collecting vegetation and soil data in situ to assess whether plants use this bird-derived nutrient source. We further illustrate the importance of vegetation-sedimentation feedbacks for sandy island morphodynamics by zooming in on the recent development of a nourishment area on the island Griend. Finally, we pose a conceptual model of how birds could steer the development of the islands on which they roost and breed by boosting vegetation growth and thereby

biogeomorphic interactions.

2. Methods

2.1. Description of study sites

We collected field and remote sensing data from three sandy back-barrier islands in the Dutch Wadden Sea: Griend (53°15′N, 5°15′E), Zuiderduin (53°31′N, 6°35′E) and Richel (53°17′N, 5° 8′E) (Fig. 1; Fig. A.1). The Wadden Sea is the world's largest coastal tidal system with extensive tidal flats, harbouring approximately 63 small back-barrier islands, protected by chains of barrier islands (Hellwig and Stock, 2014; Oost et al., 2017). It stretches for ~500 km along the coasts of the Netherlands, Germany, and Denmark. With a total surface area of ~1460 km^2, the tidal flats of the Dutch Wadden Sea harbour a high abundance of benthic primary producers that form the prime energy source for the rich diversity of marine species at higher trophic levels, including worms, molluscs, crustaceans and fish (Christianen et al., 2017). For the 10 to 12 million birds that annually visit the Wadden Sea to moult, breed, winter, or fuel up during their long migratory flights, the high availability and proximity of foraging habitat make the Wadden Sea invaluable (Boere and Piersma, 2012; Horn et al., 2019). Additionally, the high availability and diversity of supratidal landforms in the Wadden Sea, such as salt marshes, sand shoals, beaches, and coastal dunes, serve as breeding and roosting habitats for coastal birds (Koffijberg et al., 2015, 2021).

All three back-barrier islands are uninhabited and protected nature reserves, closed to the public all year round. Unfortunately, for this study we could not identify suitable bird-free islands to compare vegetation development in presence or absence of bird colonies as other studies have done (Benkwitt et al., 2021; Fukami et al., 2006; Graham et al., 2018), as all uninhabited sandy island in the Wadden Sea accommodate shore bird colonies. In contrast, the nesting density in the North Sea facing barrier islands is much lower, but these islands are also inhabited, partly converted to agricultural area and artificially stabilized and nourished frequently (Brand et al., 2022; Oost et al., 2017). Richel and Zuiderduin are relatively young islands that developed naturally during the 20th century. Griend, however, has existed since the Middle Ages, but the island has changed drastically during those centuries. After extensive island erosion due to the construction of the closure dam in the western Dutch Wadden Sea in the 20th century, the island has been artificially stabilized from 1980 onwards by building a protective barrier. In 2016, new management measures, including a large (200.000 m^3) sand nourishment on the western side of the island, were implemented to ensure that the island and its important function as a breeding and roosting habitat will be protected for the next decades (Govers and Reijers, 2021). The sand used for the nourishment was locally (~5 km) extracted during channel dredging activities and was relatively nutrient poor (<0.5 % OM). After the 2016 nourishment no new management measures including mowing or vegetation plantings have been implemented on the island.

2.2. Bird data collection & analyses

To estimate nutrient input through guano of breeding birds, we used data from the national bird monitoring scheme, coordinated by Sovon Dutch Centre of Field Ornithology. Every year during the breeding season, bird wardens are stationed at each island to collect detailed information on the numbers and breeding successes of all breeding birds. Total breeding bird biomass per year was estimated by multiplying the number of nests per species by two (i.e., two adults per nest) and the average species-specific body mass (Del Hoyo et al., 2017). Total annual bird excretion per hectare per island (*FI*) was calculated by multiplying the number of nests per species (*N*) by the mean number of birds occupying those nests (*AvB*), the breeding period per species (*Time in days*), the daily excretion rate based on species' biomass (*Excr*) and island surface area (*IsArea*) (Eq. (1)) (Graham et al., 2018; Young et al., 2010), with *i* signifying each bird species and *j* each island.

$$FI_{ij} = \frac{N_{ij} * AvB_{ij} * Time_{ij} * Excr_i}{IsArea_j} \quad (1)$$

To estimate the mean number of birds per nest (*AvB*), we assumed that during the breeding period on average 1.5 adult birds were present per nest in line with the guidelines provided in the bird census manual from Sovon (Vergeer et al., 2023). For the number of chicks, we multiplied the number of nests by the breeding success (fledglings per pair) and the average chick-rearing period per species.

The species-specific excretion rate (*Excr*) was estimated by calculating the daily energy requirement (*DER*) using the allometric relationship based on species' body mass (*BM*) (Eq. (3)) (Nagy et al., 1999), the gross energy content of food (*E*), its metabolizable energy coefficient (*AM*) (and the ratio between food intake and excretion (α) (Eq. (2)) (Hahn et al., 2007):

$$Excr_i = \frac{DER}{E * AM} * \alpha \quad (2)$$

$$DER = BM^{0.68088} * 10^{1.10195} \quad (3)$$

We used values reported by Karasov (1990) for carnivorous diets for *E* (23.9) and *AM* (0.76), respectively. For α we assumed a value of 0.395, which was previously found for herring gulls (*Larus argentatus*) and black-headed gulls (*Chroicocephalus ridibundus*), which have mixed diets to compensate for differences in diet between benthivorous and piscivorous species (Hahn et al., 2007).

2.3. Island area and vegetation cover analyses

We obtained LIDAR-derived elevation maps (5 m grid size resolution) of the islands and surrounding mudflats from Rijkswaterstaat (Dutch Ministry of Infrastructure and Water Management). The island surface area was estimated by counting all grid cells from 1.2 m above mean water level (MWL). This threshold was based on water level data obtained from three nearby water stations (Vlieland [53°17′N; 5°5′E], Terschelling [53°21′N; 5°13′E], Schiermonnikoog [53°28′N; 6°10′E]). Island volume was calculated by summing the total elevation of all grid cells from 1.2 m above MWL, which was the highest mean high, high water level of all three stations and can therefore be perceived as a conservative threshold for identifying the transition from an intertidal to a supratidal landform (Fig. A.2).

Island vegetation cover was analysed using satellite images with a spatial resolution of ~5 m (RapidEye: 2009–2019 with a temporal resolution of ~6 days) and ~ 3 m (Planetscope: 2017–2019, with daily images) (Cooley et al., 2017). We selected images from the breeding season (May till September) with a maximum cloud cover of 20 % and estimated vegetation cover using the Normalized Difference Vegetation Index (NDVI) expressed as NDVI = (NIR-R)/(NIR + R). Based on previous research, we considered all grid cells with an NDVI value below 0.2 as bare soil (Tang et al., 2015) and calculated the percentage of the island that is vegetated by dividing the total vegetated area (ha) by the total island surface. The relation between vegetation growth and landscape development was further analysed on the island Griend, where the construction of a nourishment area and the availability of high-resolution data (high spectral coastal areal imagery of 25 cm resolution and surface elevation models of ~1 cm resolution) provides the opportunity to study these processes during early island development (Govers and Reijers, 2021). For this we created binary masks of the vegetation (using the NDVI threshold of 0.2) and assigned each pixel to one of the following classes: disappearing (present in 2018, absent in 2019), no vegetation (absent in both years), new vegetation (only present in 2019) and stable vegetation (present both years). Furthermore, we calculated the difference in surface elevation by subtracting the 2018 surface elevation model from the 2019 surface elevation model. We then

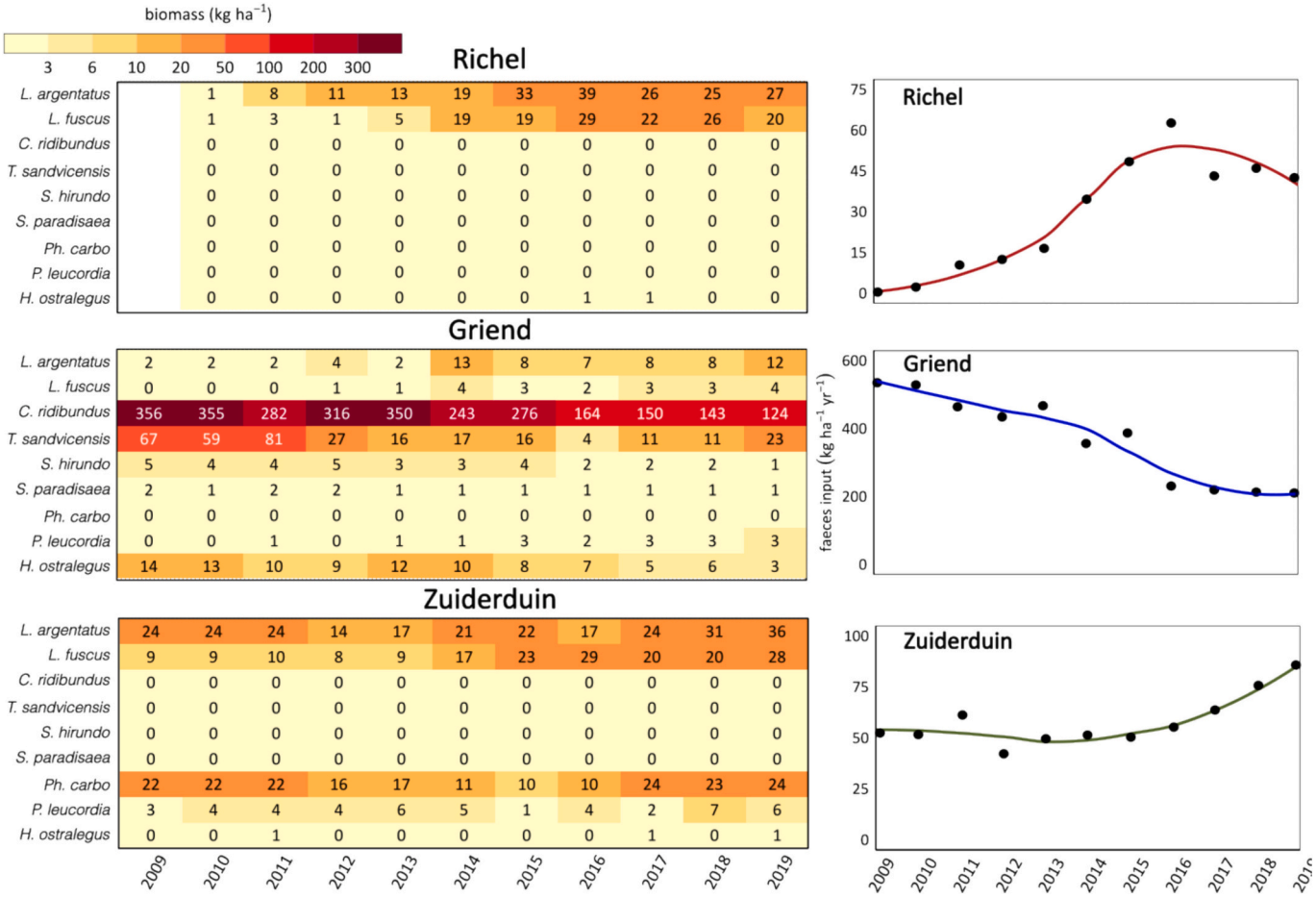

Fig. 2. Biomass estimates (kg ha^{-1}) from 2009 till 2019 for the nine dominant breeding birds for Richel, Griend and Zuiderduin, respectively. Faeces input by breeding birds during the breeding season (in kg ha^{-1} yr^{-1}) was estimated based on nest numbers and breeding success (lines indicate smoothing functions for the different islands with red: Richel, blue: Griend and green: Zuiderduin, respectively). Bird species names are from top to bottom: *Larus argentatus argenteus, Larus fuscus graellsii, Chroicocephalus ridibundus, Thalasseus sandvicensis, Sterna hirundo, Sterna paradisaea, Phalacrocorax carbo, Platalea leucordia, Haematopus ostralegus.* See table A.1 for additional information on bird characteristics.

sampled 10,000 random points on the area to investigate whether the different vegetation classes differed in their elevation and elevation difference, respectively.

2.4. Isotope data collection & analyses

Vegetation biomass and isotope samples were collected on all three islands after the end of the breeding season in August 2019. We first estimated plant species identity and coverage in plots of 25 m^2 on the island's barrier ridge (i.e., chenier, beach or dune ridge) and on the island's interior back-barrier system which consisted of a tidal marsh or green beach ($N = 5$ per system). Plot location was chosen haphazardly and without prior knowledge of the presence of breeding bird colonies or nests. However, on Zuiderduin, nests of cormorants (*Phalacrocorax carbo*) were visibly scattered along the whole barrier system, and we are therefore confident we sampled near their former colonies. We collected ~5 leaf samples of three individuals per plant species, of which multiple individuals were present in the plots to determine isotopic nitrogen values and nitrogen content. After drying at 60 °C to constant weight, these samples were ground using a ball mill (MM400, Retch, Haan, Germany). We then weighed ~1 mg homogenized samples in tin cups to determine nitrogen stable isotope composition with an elemental analyser (Carlo Erba NA1500, Thermo Fisher Scientific, Waltham, MA, USA), coupled online via an interface (Finnigan Conflo III) to a mass-spectrometer (Thermo Finnigan DeltaPlus USA). Nitrogen isotope ratios were expressed in ratio from heavy-to-light isotope ($^{15}N/^{14}N$) on a delta scale (δ^{15} N), which indicates the deviation in parts per thousand (‰) relative to atmospheric nitrogen. Additionally, we collected soil samples at a 5 cm depth at each plot to determine soil nitrogen content and soil nitrogen isotopic ratio on freeze-dried homogenized soil samples using the same methods as described for plant material, but weighing 60 mg due to the low nitrogen content. Median grain size was determined on freeze-dried homogenized soil material with polarized intensity differential scattering (Beckman Coulter LS 133320; NIOZ Texel). Finally, soil organic matter content was estimated as loss on ignition by burning dry homogenized sediment samples at 550 °C for 4 h. To relate the isotopic signals from the plant species to various nitrogen input sources found on the islands, we collected guano samples on the islands ($N = 18$, bird identity unknown), particulate organic matter from Wadden Sea samples ($N = 3$), algae sources on the island (N = 5) and diatoms ($N = 2$) (Fig. A.3).

2.5. Data analyses

All NDVI calculations were done in Matlab (version 2020b, The Mathworks, Inc) and QGIS (version 3.38), and all data analyses were performed in R (version 3.4.0). The potential relation between bird faeces input and vegetation development (from 2009 till 2019) was analysed for all islands together using a non-linear regression and for each islands separately using Pearson correlation as the data did not violate assumptions of normality. The relationship between nitrogen content and nitrogen isotopic signatures for plant and soil samples was

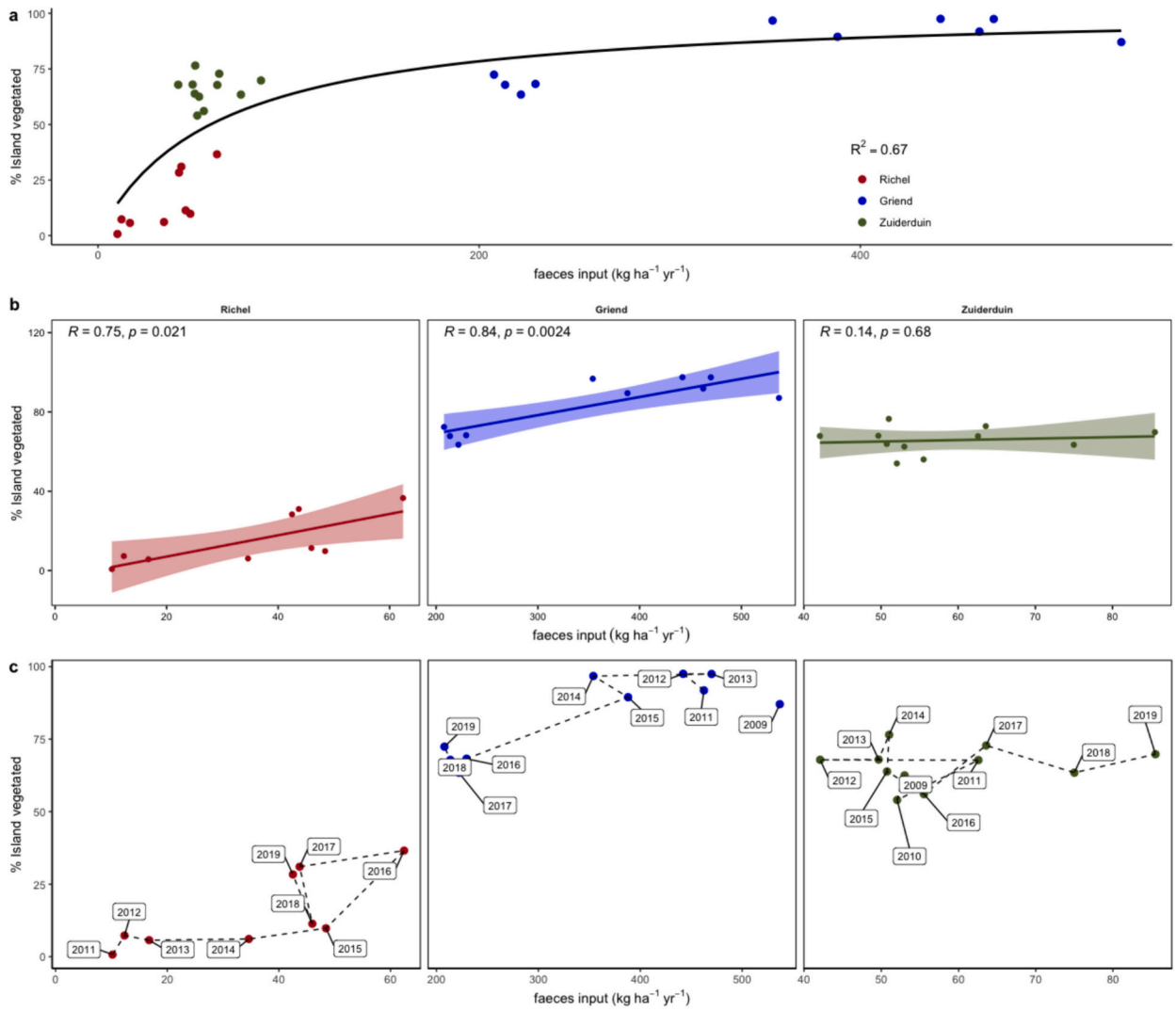

Fig. 3. a) relation between faeces input and vegetation coverage for all three islands combined. The black line represents a monod curve with formula: y ~ Vmax * x / (k + x), with Vmax the y-asymptote (Vmax = 103 ± 9) and k the value where y = 0.5*Vmax (k = 62 ± 17) with a R^2 of 0.67. Panels b and c depict the relation between faeces input and mean vegetation coverage for Richel (red, left graphs), Griend (blue, middle graphs) and Zuiderduin (green, right graphs), respectively. Panel b indicates the correlation between variables for each of the three islands and panel c shows the vegetation and faeces input labeled through time.

analysed using a linear and quadratic relation. To explore how environmental conditions (i.e., soil organic matter and grain size) and faeces input (i.e., δ^{15} N and soil N content) influence vegetation composition, we used nonmetric multidimensional scaling (NMDS) by the vegan package. Finally, we analysed the relation between vegetation classes (dissapearing, no vegetation, new vegetation and stable vegetation) and surface elevation differences and absolute surface elevation for the nourishment area of the island Griend for the years 2018 and 2019 using a Dunnett T3 post-hoc test due to unequal variance and sample size.

3. Results

3.1. Breeding bird subsidies

All three islands were used as breeding locations by multiple coastal bird species (Fig. A.4). Richel supported the lowest number of breeding birds over the years 2009 till 2019 (6 ± 1 species, all values are reported as mean ± sd). Griend and Zuiderduin had comparable numbers with 22 ± 2 and 24 ± 6 species for Griend and Zuiderduin, respectively.

We depicted bird biomass estimates (in kg ha^{-1}) of the nine most dominant breeding birds for all three islands (Fig. 2). On all three islands, colony breeding species, such as gulls, terns, and cormorants contributed most to the total bird biomass. From these biomass estimates, we estimated faeces input (see methods) in kilograms wet weight per hectare per year. Faeces input increased from 2010 till 2017 on Richel (max: 62 kg ha^{-1} yr^{-1}) after which it stabilized at ~45 kg ha^{-1} yr^{-1} (Fig. 2). On Zuiderduin, nutrient input by birds was comparable with ~50 kg ha^{-1} yr^{-1} till 2015, but has increased in recent years (to 86 kg ha^{-1} yr^{-1} in 2019) (Fig. 2). This increase coincided with the increase in breeding pair numbers (Fig. A.5). Lastly, the island of Griend received the highest yearly faecal input of the three islands (~5 times higher), but in line with a recent decline in breeding bird numbers (Fig. A.5) this has decreased more than twofold over the last decade from ~590 kg ha^{-1} yr^{-1} in 2009 to ~210 kg ha^{-1} yr^{-1} in 2019 (Fig. 2).

3.2. Relation between guano input and vegetation development

Although we observed a positive relation between faecal input and mean island vegetation cover for the period 2009–2019 for all three islands combined (Fig. 3a), we also found the three islands to clearly group together. Therefore, we additionally examined the relation between faecal input and vegetation coverage for all island separately. We found a positive correlation for both Richel (R = 0.75) and Griend (R = 0.84) independently, while for Zuiderduin we observed no correlation

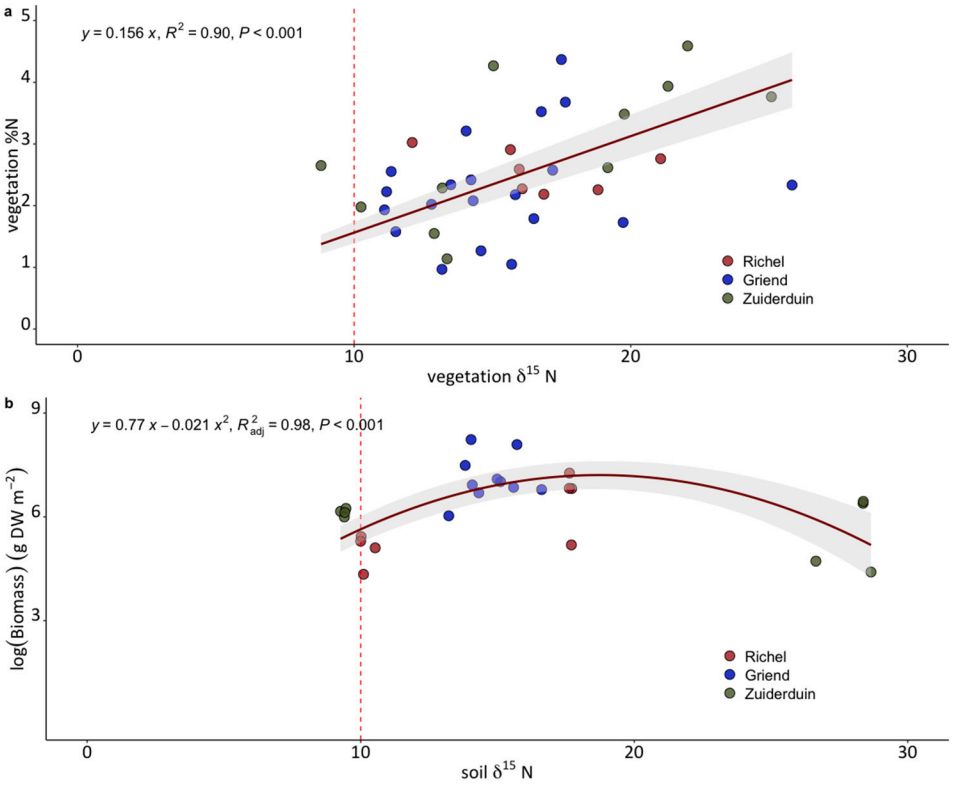

Fig. 4. Relationship between nitrogen isotope ratio ∂^{15}N and N content for all sampled plant species (a) and relation between soil ∂^{15}N values and vegetation biomass (g DW m^2) (b). Colors indicate the different islands with red indicating Richel, blue Griend and green Zuiderduin. The vertical dashed red line at $\partial^{15}N = 10$, indicates the guano threshold which corresponds with Fig. A.3. Red lines depict linear relationships with 95 % confidence intervals. Model equations, R^2 and *p*-values are shown.

(Fig. 3b). Similar correlations were found using the faeces input from the previous year to explain the vegetation coverage the following year (Fig. A.6). While Richel showed an increase in faeces input and vegetation cover from 2009 to 2016, in more recent years there has been a mild decline (Fig. 3c). For Griend, faeces input showed a declining trend from 2009 to 2015, but especially after the 2016 nourishment both vegetation coverage and faeces input decreased (Fig. 3c). Zuiderduin showed yearly fluctuations in vegetation coverage, while faeces input generally shows an increase over time (Fig. 3c). In recent years, both Richel and Griend demonstrated changes in island morphology while Zuiderduin remained relatively stable both in island size and vegetation cover. Griend increased 1.5 fold in size after the 2016 sand nourishment, and Richel transitioned from a bare shoal (0 % island vegetation, volume:size ratio of ~0.1) to a sandy island with a permanently vegetated and higher elevated part (25 % vegetation, volume:size ratio of 1.2) (Fig. A.1, Fig. A.7, and Fig. A.8).

Nitrogen isotopic values revealed that vegetation from all islands was strongly enriched (average > 10 ∂^{15}N) (Fig. 4). Isotopic signatures from multiple nitrogen sources on the island (i.e., diatoms, organic matter seawater, algae, and bird faeces showed that only the faecal samples all had nitrogen isotopic signatures above 10 ∂^{15}N indicating that plants have incorporated organic nitrogen from guano (Fig. A.3). We found that plant leaf nitrogen content (%N), a proxy for plant productivity, increased with an increasing ratio of ∂^{15}N ($R^2 = 0.90$, $p < 0.001$, Fig. 4). Additionally, we observed a quadratic relationship between soil enrichment (i.e., soil ∂^{15}N) and vegetation biomass, indicating that while soil enrichment may first stimulate vegetation biomass, this positive effect declines at higher values (>25 ∂^{15}N) as found near the cormorant colony on Zuiderduin. Nitrogen isotopic signatures and content differed between the islands and island locations with plants sampled on Zuiderduin generally exhibiting the highest values on the island ridges, while the island interior values were lowest (Fig. A.9). By comparing the same species across islands and habitats, we found that individuals growing on Zuiderduin on the island ridge on average had a higher %N (+0.66 %N) and higher ∂^{15}N value (+1.95 ∂^{15}N) than individuals of the same species growing on Griend. For salt marsh species growing on the island interior we found an opposite pattern with ∂^{15}N isotopic ratio being higher on Griend than on Zuiderduin (+3.65 ∂^{15}N) (Fig. A.9).

Plant community composition differed between islands and island location (island interior vs. island ridge) and was influenced by grain size ($r^2 = 0.74$, $p = 0.001$), soil nitrogen signature ($r^2 = 0.66$, $p = 0.001$), soil organic matter ($r^2 = 0.45$, $p = 0.002$) and soil nitrogen content ($r^2 = 0.36$, $p = 0.005$) (Fig. 5). The vegetation composition on the island interior of Zuiderduin and Griend was quite similar, consisting of salt marsh species, while the vegetation composition on the sandy interior of Richel was closer to the vegetation on the island ridge of Griend (Fig. 5).

3.3. *Relation between vegetation development and surface elevation on an island nourishment area*

There were differences in both absolute elevation in 2019 and elevation differences (2019–2018) between the four vegetation classes. While the elevation differences between 2019 and 2018 for the whole nourishment was slightly negative (−0.06 ± 0.11 m) there were differences between vegetation classes with the areas that had stable vegetation slightly accreting (0.12 ± 0.12 m, $N = 331$), while the bare areas were mostly eroding (−0.08 ± 0.10 m, $N = 6782$) (Fig. 6d). New vegetation mostly established on slightly higher elevated areas (1.94 ± 0.23 m MWL, $N = 2829$) compared to the areas that remained bare (1.75 ± 0.28 m MWL, N = 6782) (Fig. 6e).

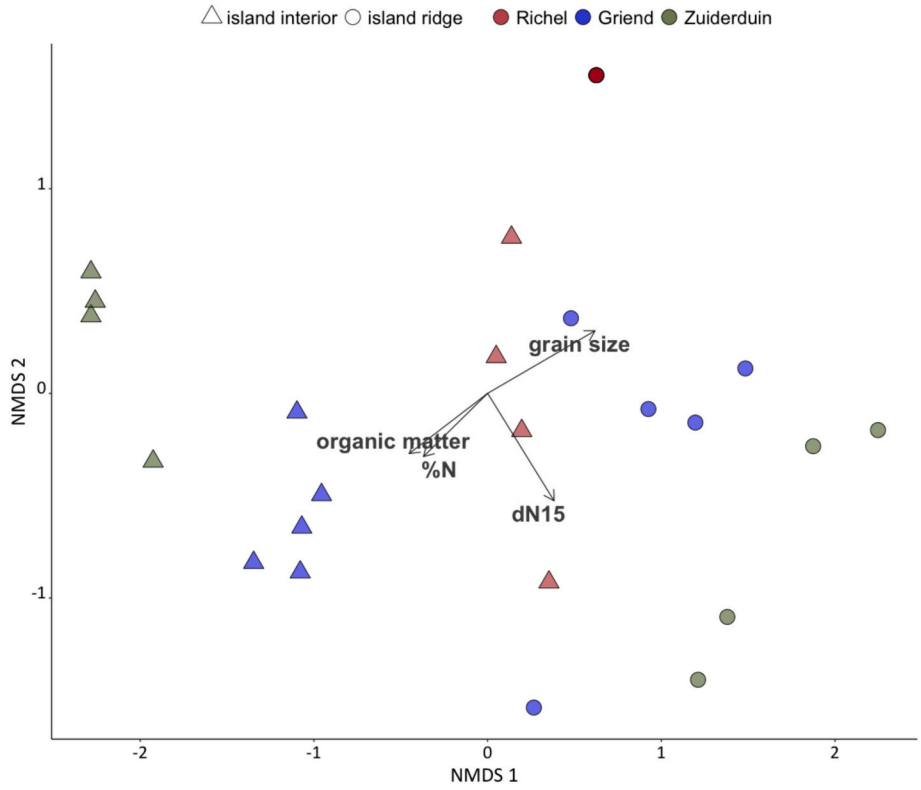

Fig. 5. Two-dimensional NMDS ordination of plant community composition (stress =0.09) with (a) symbol colors representing the different islands with Richel depicted red, Griend blue and Zuiderduin green. Symbol shapes indicate plot location with circles representing plots positioned on the dune or beach ridge barrier of the island and triangles representing plots positioned inland on the back-barrier marsh or sandy system. Vectors include sediment grain size, soil organic matter, soil %N and soil ∂^{15}N.

4. Discussion

As a first step in disentangling the role of birds as sandy island engineers, we here show that breeding birds can strongly affect vegetation productivity on sandy back-barrier islands that are typically uninhabited but have an important ecological function. In our study system, coastal birds contribute a large (50–500 kg ha^{-1} y^{-1}) nutrient subsidy to the sandy islands on which they breed. These guano subsidies enrich the soil locally and are taken up by the vegetation as evidenced by elevated foliar ∂^{15}N values (average ~ 16 ‰ ∂^{15}N), that were comparable to previous studies on guano-enriched islands (Table 1). Soils on sandy barrier islands are generally nutrient-poor and N-limited and subsidies from coastal birds can thus play an important ecosystem-structuring role (Brown et al., 2022; Reijers et al., 2020).

4.1. A three-way interaction between birds, vegetation and sandy islands?

In our study we investigated the role of avian-mediated subsidies on soft-sediment island ecosystems that are formed by biogeomorphic interactions between vegetation and sedimentation processes (Cooper et al., 2007; Feagin et al., 2015; Marin Diaz, 2022). On the higher elevated areas of sandy shoals vegetation can establish that traps and stabilizes sandy sediments thereby promoting island development (Durán Vinent and Moore, 2015; Reijers et al., 2019). In turn, sediment trapping and landscape development can promote vegetation expansion and establishment, thereby further promoting landscape development. The development of the sand nourishment area on the western side of the island Griend provides an example of these biogeomorphic feedbacks with new vegetation establishing on higher elevated areas and the stable vegetation promoting landscape accretion (Fig. 6). However, these biogeomorphic feedbacks typically occur beyond a critical vegetation density or patch size (Reijers et al., 2019; Temmink et al., 2020). Nutrients provided by birds (found between 50 and 500 kg ha^{-1} y^{-1} for our study systems) stimulate plant productivity, and this growth stimulation can aid in surpassing these density or patch-size related thresholds. Avian subsidies could, therefore, fuel these vegetation-sedimentation feedbacks and reduce vegetation recovery time after storm surges, thereby increasing island stability (Bakker et al., 2023; Balke et al., 2014; Vinent and Moore, 2015). However, under very high nutrient loadings – as observed close to the cormorant colony on Zuiderduin – vegetation development could be suppressed due to ammonium poisoning (Kolb et al., 2010b). Additionally, nutrient enrichment can impact vegetation composition and corresponding functional trait expression by favouring the growth of nitrophilous species, reducing vegetation rooting depth, or reducing the production of finer roots, which all lower the soil stabilizing strength of the vegetation (Ola et al., 2015). Vegetation development in turn might stimulate breeding bird habitat suitability, especially in the early island developmental stages where low, bare sand shoals transform to higher, vegetated islands as observed for Richel in the last two decades (Fig. A.1, Fig. 3). In contrast, it might also reduce bird numbers if vegetation encroachment reduces habitat suitability for critical species that rely on open, patchy vegetation structures, such as terns or black-headed gulls (Burger, 1976; Raynor et al., 2012).

Based on our findings, we hypothesize that three-way interactions between birds, vegetation, and morphodynamical processes may be present on sandy back-barrier islands (see Fig. 7 for a schematic representation of our hypotheses). Changes in either of these state variables (i.e., birds, vegetation, or island morphology) can provoke changes in others due to complex interdependencies. However, the potential of multiple feedback interactions between these state variables, and the fact that the strength and importance of these feedback interactions might vary depending on environmental conditions, strongly complicates direct analyses between state variables (Maxwell et al., 2017).

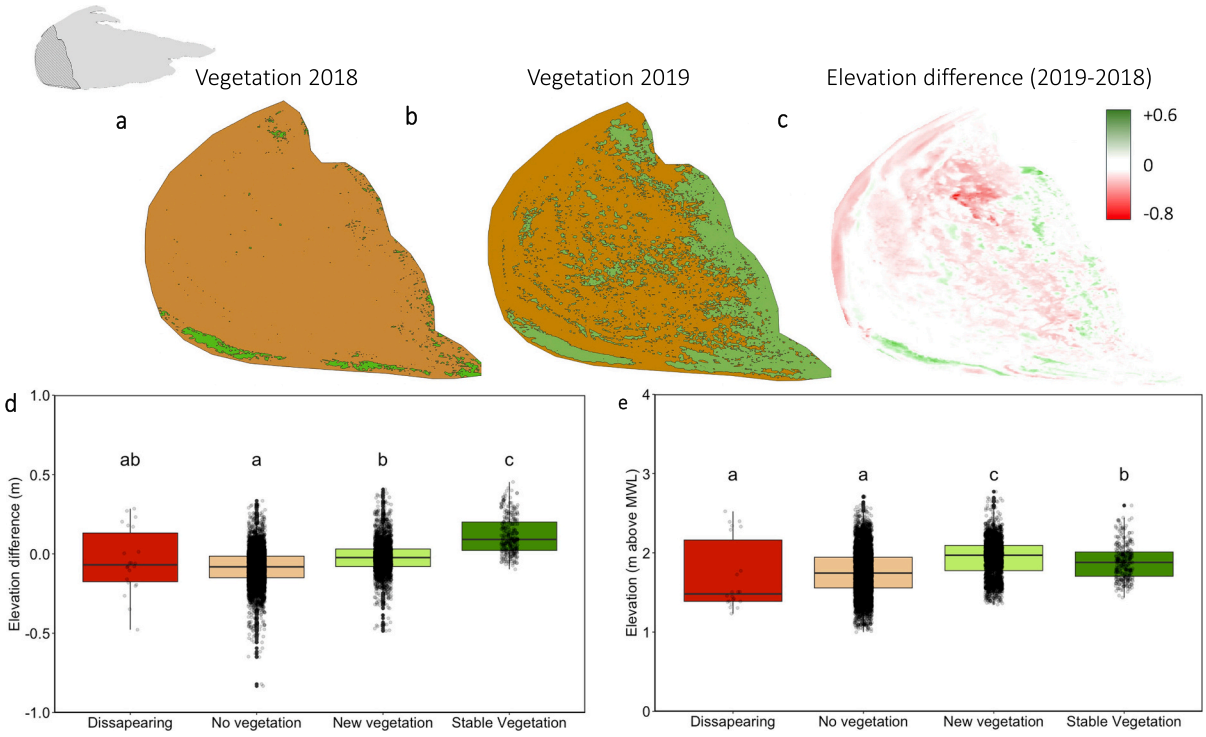

Fig. 6. Relationship between vegetation development and landscape morphology on the nourishment area on the western side of Griend (depicted on the small island insert top left of Figure) a) Vegetation presence in 2018, b) Vegetation presence in 2019, and c) Elevation difference between 2019 and 2018 in meters. d) Surface elevation differences and e) surface elevation for 2019 are depicted for different vegetation categories including Disappearing (vegetation present in 2018, absent in 2019, 0.2 % sampling points), No vegetation (vegetation absent both years, 68 % points), New vegetation (vegetation only present in 2019, 28 % points), and Stable vegetation (vegetation present in both years, 3.3 % points). Letters depict statistical differences using a Dunnett T3 post-hoc test.

Vegetation growth, for instance, might be either stimulated or suppressed by faecal input depending on the vegetation type and guano type and quantity, but changes in vegetation cover are also steered by successional processes related to island development. In turn island development and vegetation coverage also affects bird numbers (Fig. 3). In addition, climatic conditions such as precipitation, temperature and storm climate can all lead to temporal fluctuations in vegetation growth and nesting success too (Van De Pol et al., 2010). While we expect that island development and vegetation succession can be stimulated by the nutrient subsidy provided by birds, we cannot draw this conclusion based on our study and we therefore looked at correlations between state variables. Instead, we can only conclude that the vegetation on these sandy bird islands has taken up guano-derived N and theorize how guano can affect vegetation growth and vegetation-sedimentation feedbacks. Hence, our current study set-up, which includes a low number of island replicates without comparable bird-free islands, limits our capacity to disentangle the complex three-way feedback-dependent interactions between birds, vegetation and island morphology.

To elucidate these three-way feedback interactions, we therefore emphasize the need to study both vegetation dynamics (e.g., species composition, functional trait expression, biomass productivity) in relation to island morphodynamical processes (e.g., sedimentation and erosional processes) and bird population dynamics (e.g., species identity, abundances, residence time of roosting birds and breeding success) on a higher spatio-temporal resolution than was currently possible. Unfortunately, for this study, we lacked spatial information on breeding birds, which restricted our analyses to correlations on an island scale. However, based on the literature and our observations, we expect strong local effects in relation to bird nest proximity, with vegetation suppression within the colony and stimulation around its edges that diminishes with increasing distance (Caut et al., 2012; Wainright et al., 1998). How this enhanced or suppressed vegetation productivity and potential changes in vegetation composition, in turn, affects the biogeomorphic strength of the vegetation locally could be investigated by measuring differences in surface elevation. Similar to previous wrack manipulation and flume experiments, we expect that this biological nutrient source could stimulate post-storm recovery and erosion resistance (De Battisti and Griffin, 2020; Joyce et al., 2022).

4.2. *Breeding versus roosting birds*

In our study, we observed similar nitrogen isotopic values compared to previous studies on the role of guano on ecosystem functioning (Table 1). However, we observed no relation between bird numbers and vegetation $\partial^{15}N$ signatures between our study islands: as Griend accommodates most birds per hectare, but isotopic values for the same plant species on the barrier of Griend were lower compared to Zuiderduin (Fig. A.9). However, as mentioned, in our study we took random samples on the islands, whereas birds breed highly localized. Therefore, we argue that for understanding the (non-linear) relations between guano input and vegetation development, it is essential to sample along transects with increasing distance from bird nesting areas (Gaiotto et al., 2022). Furthermore, bird identity and diet strongly affect the nitrogen content and isotopic signature of guano samples, with guano from piscivorous species having higher nitrogen isotopic signals than guano from birds feeding on lower trophic level prey, such as worms or bivalves (Christianen et al., 2017). Additionally, soil physical and chemical composition affect soil nutrient retention levels, while vegetation nutrient use efficiency determines nitrogen take up rates. Hence, a simplistic relation between bird numbers/nesting density and vegetation $\partial^{15}N$ signatures that disregards all these complexities is not expected (Linhares and Bugoni, 2023). Our literature overview also illustrates that on other islands, there is no correlation between nesting densities and vegetation nitrogen signatures (Table 1). Additionally, in this study we focussed solely on excretion input by breeding birds, whereas other bird-derived nutrient sources such as faecal input by

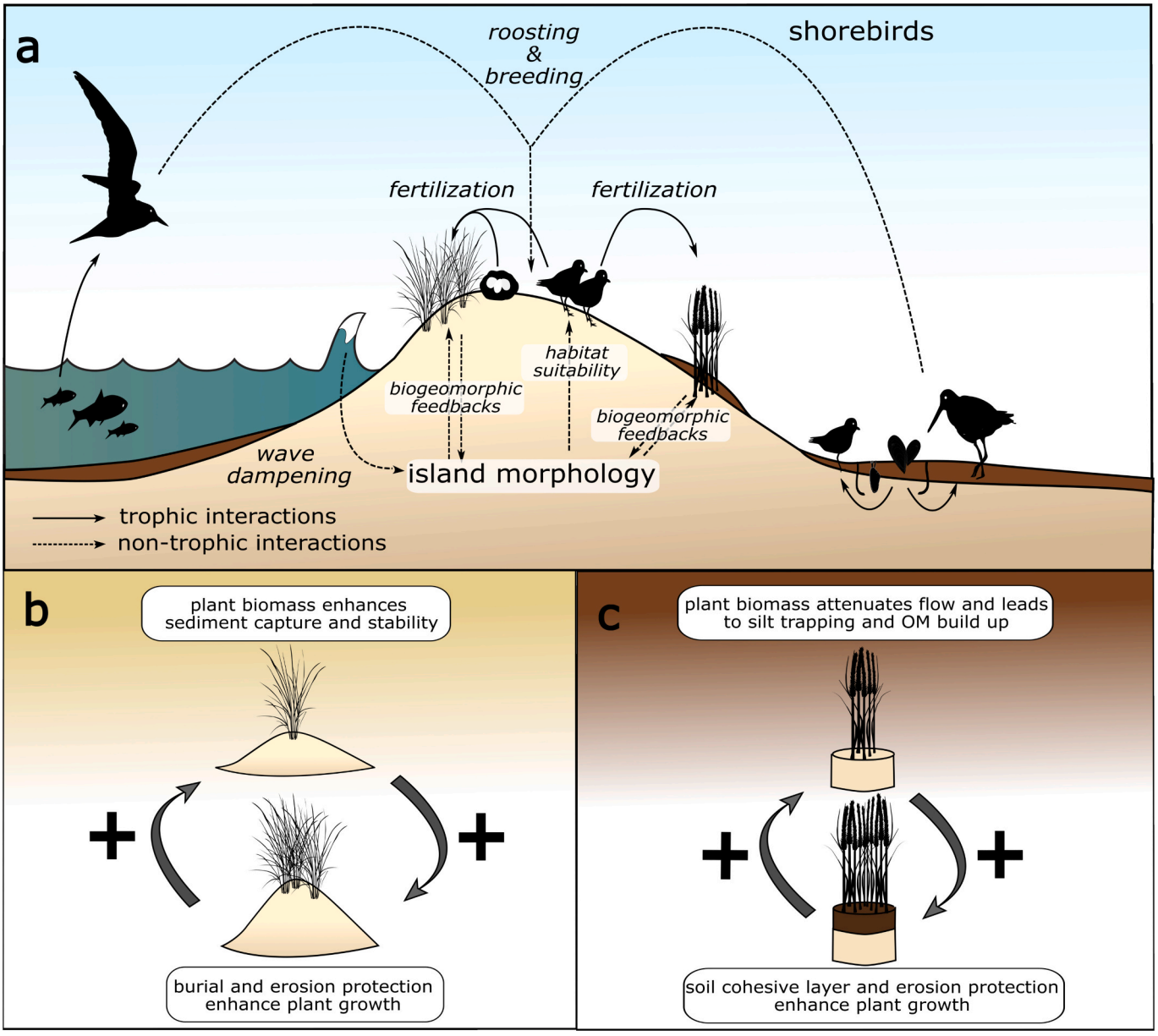

Fig. 7. a) Schematic representation of hypotheses related to three-way trophic and non-trophic interactions between birds, vegetation, and sandy islands. We hypothesize that coastal birds that forage in nearby oceans or tidal flats fertilize the soil of sandy islands they use for breeding or roosting. This fertilization promotes vegetation growth and thereby the strength of biogeomorphic interactions between vegetation growth and sedimentation processes that steer island morphology. Island morphology affects: storm-resistance by attenuating waves, vegetation cover and community composition and habitat suitability for coastal birds by, for example, providing protection against overwash processes. However, increased vegetation cover can also negatively influence habitat suitability by decreasing visibility, thereby creating a landscape of fear. The biogeomorphic interactions that affect the stability and development of the protective barrier island ridge and the island interior or back-barrier marshes are in more detail explained in panels (b) and (c), respectively. On the island ridge where wind or waves stimulate sediment transport, the vegetation can trap sediment which in turn stimulates plant growth (Bonte et al., 2021; Feagin et al., 2015), whereas on the island interior the trapping of fine particles and accumulation of organic matter can stimulate the production of a cohesive layer that increases soil resistance to sheet and cliff erosion (Marin Diaz, 2022; Marin-Diaz et al., 2022).

roosting birds or carrion also contribute to the total avian-mediated nutrient input. Roosting birds visit the islands year-round, with peaks during the spring and autumn migrations. In contrast to most breeding birds, roosting birds often prefer the open or sparsely vegetated beach-front of the islands (Peters and Otis, 2007; Piersma et al., 1993; Rogers et al., 2006). Bird count numbers on the three islands indicate clear differences with Richel, with >75 % of the island consisting of unvegetated sand flats (Fig. 3, Fig. A.8), accommodating ±90.000 coastal birds during high tides in autumn, whereas on Griend (± 53.000) and especially Zuiderduin (± 14.000) these numbers are lower but also highly concentrated on the island edges. We expect that, especially for islands transitioning from bare, sandy shoals to vegetated islands, the faecal input by roosting birds, which prefer open habitats, can play a critical role in driving this biogeomorphic succession (Fig. 7). In contrast, we expect that breeding birds can accelerate vegetation recovery time after overwash events on already vegetated islands as we observed higher plant nitrogen levels, a proxy for productivity, in relation to soil N enrichment. However, when anthropogenic modifications such as nourishments or the construction of dikes on sandy islands inhibit these natural overwash processes that reset vegetation succession, nutrient enrichment by birds might lead to climax vegetation types that are less preferred by many coastal breeding bird species. This

indicates that for future studies that focus on the role of coastal birds as ecosystem engineers on sandy islands, it is important to make estimates of all potential nitrogen contributing sources (e.g., atmospheric, overwash, internal and external biological material) during various stages of landscape development.

4.3. Birds as indirect ecosystem engineers of soft-sediment tidal systems

Next to the local terrestrial effects of bird-derived nutrients in soft-sediment tidal systems, we hypothesize that birds could potentially affect ecosystem productivity and community assembly on adjacent tidal flats. Previous studies on coral systems found a strong effect of nutrient leaching, boosting ecosystem productivity and functioning in near-shore (± 250 m) marine environments (Benkwitt et al., 2021; Graham et al., 2018; Lorrain et al., 2017). From aerial photographs (Fig. A.10) and previous bird foraging studies, it appears that mudflats surrounding back-barrier islands are often rich in primary productivity and can support large populations of macrozoobenthic species (Bijleveld et al., 2016; Piersma et al., 1993). We expect that nutrient run-off from these islands during tidal floodings could influence surrounding benthic productivity and, therefore the foraging habitat suitability of waders. We thus suggest that for future research isotopic nitrogen values of microphytobenthic species and their consumers (e.g., lugworms (*Arenicola marina*), Baltic tellins (*Limecola balthica*)) with increasing distances from back-barrier islands should be investigated to determine the nutrients flows between supratidal landforms used for breeding and roosting and the tidal flats that are extensively used for foraging (Bijleveld et al., 2016; Christianen et al., 2017; Piersma et al., 1993). Hence, to gain a complete picture of the trophic and non-trophic (biogeomorphic) relations between birds, ecosystem functioning, and landscape development in coastal soft sediment systems, all these interactions between different bird species, their preferred habitats for foraging, breeding, and roosting in relation to ecological and biogeomorphic interactions in both local (terrestrial) and adjacent (marine) habitats need to be considered. For this we suggest to first quantify nutrient flows and uptake in different habitats in relation to guano deposition using stable nitrogen isotopes measurements. Second, we suggest relating this local uptake of guano-derived nitrogen to ecological functioning by, for instance, assessing the biogeomorphic strength of the vegetation in enriched plots to similar vegetation types in guano-free environments.

4.4. Conclusions and implications

Our findings highlight that bird-derived nutrients boost vegetation productivity on small sandy islands and thereby contribute to the growing body of literature that emphasizes the key role of birds in nutrient flows between marine and terrestrial ecosystems (González-Bergonzoni et al., 2017; Graham et al., 2018; Groff et al., 2020; Otero et al., 2018). As many coastal soft-sediment systems (e.g., islands, salt marshes, seagrass meadows and benthic reefs) are biogeomorphic systems, we expect bird-derived nutrients to stimulate the growth of habitat-forming species which in turn can affect breeding, roosting and foraging habitat suitability for coastal birds. However, our study focussed on a relatively small number of islands and aggregated data on the island level. As a result, we found strong local and location-dependent effects. We therefore suggest that further research into these local effects on a larger temporal scale across multiple sandy islands differing in bird abundance is necessary to gain a more complete understanding of how guano influences vegetation dynamics, and coastal landscape development, and ecological functioning. This information can be applied to inform nature managers to design appropriate strategies to conserve threatened bird species by, for instance, locally manipulating vegetation development through mowing or sod cutting to stimulate threatened bird species that prefer open habitats. On an island level, engineering solutions that target island morphodynamics, such as sand nourishments or the creation of overwash areas, can also promote open-habitat breeders, whereas engineering solutions that focus on stabilization by creating barriers can stimulate bird species that prefer higher and more vegetated habitats.

CRediT authorship contribution statement

Valérie C. Reijers: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Floris van Rees:** Writing – review & editing, Conceptualization. **Tjisse van der Heide:** Writing – review & editing, Funding acquisition, Conceptualization. **Albert P. Oost:** Writing – review & editing, Conceptualization. **Gerben Ruessink:** Writing – review & editing, Supervision. **Kees Koffijberg:** Writing – review & editing, Resources. **Kees C.J. Camphuysen:** Writing – review & editing. **Emma Penning:** Writing – review & editing, Investigation. **Nadia Hijner:** Writing – review & editing, Investigation. **Laura L. Govers:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Upon acceptance, the data supporting our results will be freely available and the data DOI will be included.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.175254. Data is available on Zenodo (doi:10.5281/zenodo.13153525).

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