

### **Response reviewer1:**

General feedback: This manuscript offers insights into a field with limited existing research, with novelty in that they do not scale a small sampling area to a whole island.

Although the topic is slightly outside my primary area of expertise, the authors clearly articulate the need for their research and situate it well within the existing literature. Their methods are strong, and they avoid overinterpreting their results. The manuscript effectively outlines the current state of knowledge, identifies the gaps their study addresses, and highlights areas for future research.

There are, however, a few points of confusion that would benefit from clarification by the authors. These areas offer opportunities for improvement.

Below, specific comments are offered:

#### **Reply:**

We thank the reviewer for the positive and constructive feedback. The suggestions will help improve the manuscript's clarity and address points of confusion. In the revised manuscript, we have clarified key methodological details, refined wording in the abstract and introduction to avoid unintended directional claims, and expanded explanations of the sampling design, transect placement, and the seasonal context of guano deposition. Furthermore, in the discussion we have provided and discussed the full ranges for predicted effects, and incorporated an additional discussion on island-specific processes such as sand nourishments and seasonal variation in nutrient inputs. We appreciated the reviewer's comments and believe the suggestions have significantly improved the paper.

#### **Abstract/Introduction:**

Ln. 75-76 Why is it likely that the fertilizing impact is underestimated when extrapolating findings from a few square meters to the whole island? Would it not be overestimating if the few square meters were in an area near bird colonies, then extrapolating that high value to the whole island? Clarification could be used here. Additionally, this point could be tied back into the discussion. What were the values of this research compared to prior research? Did it seem that other papers underestimated or overestimated the impact of guano?

#### **Reply:**

We thank the reviewer for pointing out that our original formulation was unclear and that the wording implied a directional bias (i.e., underestimation). Our intention was not to suggest consistent under- or overestimation, but rather to highlight that extrapolating from

small plots to whole islands can lead to inaccurate predictions due to strong spatial variability in guano deposition and environmental gradients. We have revised the sentence to reflect this more accurately: “This means that extrapolating plot-levels guano effects across whole-island scales can lead to inaccurate predictions, because the effect of fertilization is dependent on many environmental and biotic conditions that vary spatially and through time.”.

### **Methods:**

Figure 1 On some of the islands, the MHW does not reach the vegetation border. Consider describing how this may influence sedimentation (e.g., if there is increased sediment delivery from the water).

Reply:

We agree. We have added the following clarification to the figure caption: “On islands where MHW does not reach the vegetation border, tidal inundation does not contribute to sedimentation, instead sediment delivery to vegetated areas is predominantly steered by waves (d) or wind (a).”

Ln. 135 Can be more clear about plot level here, or leave off the (4 m<sup>2</sup>) until going into more detail in section 2.3. It feels confusing to bring up here – was it 4 m<sup>2</sup> total per island? Per plot? How many plots? This comes up in section 2.2, but is read with confusion on Ln. 135. Additionally, it is confusing to say from the plot level on Ln. 135 then on Ln. 136, saying scaled up to the island level because the point of this research was not to scale up and extrapolate to the whole island level. After reading further, this made sense, but it could use more clarification here to avoid points of confusion when initially reading through.

Reply:

We thank the reviewer for this comment. To prevent confusion, we removed the early reference to the 4 m<sup>2</sup> plot size and clarified the meaning of “plot level.” Our intention was not to imply that plot measurements were extrapolated to whole-island values. Plot data and island-scale remote-sensing data were analysed separately. We have revised Section 2.2 accordingly to ensure consistency with Section 2.3. We replaced it with:

“We used a two-tiered approach to examine how guano affects vegetation growth and sedimentation. First, we analysed guano effects on vegetation composition and plant traits using field measurements collected across the five islands. Second, we examined how spatial patterns in guano deposition correspond with island-scale variation in satellite-derived vegetation indices (NDVI, GI) and LiDAR-based elevation change ( $\Delta Z$ ) from 2021 to

2022. These two components are based on different spatial scales but capture complementary aspects of the same system and are used to investigate how small-scale field measurements compare with island-scale remote sensing analyses. An overview of the methodology is provided in Figure 2.”

Ln. 147. The range for the length of the transect, as well as the range for plots on a transect, are both reported, so it could be useful to report the range of transects within an island as well.

Reply:

We agree and we now also report the range of transects per island.

Ln. 149 Transects were placed to capture variation in guano deposition, both within and outside bird colonies, but how did transects vary by island morphology and hydrodynamics of the island? Statement in the introduction on Ln. 76-79 about how the effects of guano are heterogeneous, varying in both magnitude and direction, depending on local conditions such as topography and hydrodynamics. If transects were set based on guano deposition/colony location, are the plots also representative of local conditions?

Reply:

We thank the reviewer for this helpful comment. Indeed, our sampling design aimed to capture not only variation in guano deposition but also the full range of environmental conditions across each island. To clarify this, we have revised this sentence “Transect placement was designed to capture variation in guano deposition both within and outside bird colonies, while also encompassing environmental variability by sampling across pioneer and climax vegetation, and sandy and muddy substrates.” This better reflects that plots were representative of the local physical conditions that modulate guano effects.

Ln. 152 Could add a statement about how sampling during the breeding season influences results (e.g., more or less guano deposition during breeding season). Could also add here that this is the plant growing season, making this the optimal time for sampling.

Reply:

We agree with this addition. We have added extra context: “Sampling was conducted in August and September 2022, shortly after the breeding season when guano deposition is at its annual peak and at the end of the plant growing season when vegetation has actively assimilated available nutrients, making guano–vegetation relationships likely most pronounced and detectable.”

Ln. 156 The sentence on rooting depth is separated from the sentence that says, “At each sampling plot,” so consider adding this back in here. It is unclear whether two 1 m depth soil profiles were taken per plot, per transect, or per island.

Reply:

We added: “at each sampling plot” to this sentence.

Ln. 325 and 327 Could it be important to explicitly say slightly positive and slightly negative? These values both feel quite near 0. I feel some readers will skip over the values and simply read positive and negative.

Reply:

We have added this nuance to the text by adding “*slightly*”.

### Results:

Figure 7 caption, wrt may be common in some context, but this is a bit ambiguous. It’s never introduced, and some readers may not know what it stands for. Additionally, the colonies line and >1.2 m elevation line are too similar in appearance, which gets particularly confusing for Rottumerplaat. A possible suggestion is adding hatching or stippling to the colonies to help differentiate. Transect lines could be added in a different color to the figure as well, but that may make it even busier.

Reply:

Wrt has been written in full: “*with respect to*”. For the full revision, we have portrayed the colonies with a stippling symbology.

Ln. 426 Curious what the range is, not just “up to,” as this could make the impact seem larger than it is. (This is the same for line 373).

Reply:

We agree that a statement about the range, and in addition a disclaimer on spatial variability would sharpen the statement. We will provide the full range of predicted effects and clarify where higher values occur: “Across the landscape, guano–vegetation interactions contributed modest amounts to modelled sediment bed-level change (~1–3% on average), but stronger effects occurred close to seabird colonies, reaching ~6% in the GI-based model and ~13% in the NDVI-based model (99<sup>th</sup>-percentile of the predicted proportion  $\Delta Z$  by guano). These localised peaks are obscured when averaging across entire islands (Figure 7).”

**Discussion:**

Any further discussion on how sand nourishment (nutrient-poor sand) at Griend could impact results? Mentioned in methods but not brought up again.

This research was done in the spring/summer, but there is never a mention of how these trends and influences may vary during different times of the year. Is there a long-term benefit to guano deposition with sediment accretion? Is there any benefit to guano deposition outside of the plant growing season? How may guano deposition vary outside of the breeding season?

**Reply:**

We thank the reviewer for this helpful suggestion. We have added context in Section 4.1 clarifying that the sand nourishment at Griend may influence vegetation dynamics through functional and compositional pathways by altering sediment characteristics and nutrient availability. Yet, because our study was conducted approximately six years after nourishment, and sediment nutrient levels in comparable systems typically converge toward background conditions within several years, any direct nourishment-related nutrient signal was likely weak at the time of sampling. We also have clarified that guano effects are expected to be strongest during the growing season, while off-season deposition likely contributes mainly to longer-term nutrient pools.

“In this context, sand nourishment may further influence vegetation through both functional and compositional pathways by altering sediment characteristics and nutrient availability. Although the nutrient content of the nourished sand at Griend is not known, any direct nourishment-related nutrient signal was likely weak during our study, which was conducted approximately six years after nourishment. Evidence from comparable coastal systems suggests that sediment nutrient levels tend to converge toward background conditions within several years following nourishment (Pit et al., 2020). Additionally, we do not expect strong year-round effects of guano, as winter roosting birds defecate mainly along the island edges where little vegetation grows, and most guano nitrogen is rapidly lost through leaching, volatilisation, and runoff (Loder III et al., 1996; Otero et al., 2018; Peña-Lastra et al., 2022; Riddick et al., 2012); only a small fraction may persist in slowly decomposing plant material and influence early spring growth (Kooijman & Besse, 2002).”

**Technical Corrections:**

Ln. 48 The species name for Marram grass could be added.

**Reply:**

This is added: *Ammophila arenaria*; synonym *Calamagrostis arenaria*

Ln. 101 and Ln. 108 Inconsistency in describing the study islands as inhabited or uninhabited. I believe that Ln. 101 should say uninhabited.

Reply:

That is correct, we changed it into uninhabited.

## Response reviewer2:

In the manuscript 'Nutrient flows and biogeomorphic feedbacks: linking seabird guano to plant traits and morphological change on sandy islands', F. van Rees and colleagues investigated the interactive effects of plant traits and seabird guano on shoreline geomorphology on small, dynamic, sandy islands in the Wadden Sea. The findings are highly interesting and novel, and complement ongoing research on the circular seabird economy system with new evidence from temperate region and on the cascading effects of seabird guano to island geomorpho-dynamisms. The manuscript is well written and summarises the context and key findings of the study well, but I miss some clarity around the specificities of island ecosystems, where this study was carried out. For example, the role of allochthonous nutrient inputs for terrestrial productivity is most pronounced on islands (see seminal work by Wendy Anderson, Gary Polis, in the 1990s-early 2000s) relative to mainland systems. Similarly, the geodynamisms of sandy islands are quite different to mainland sandy shorelines, as sediments can be reworked around islands 360°. Also, seabird colonies are nowadays often restricted to small islands because mainland shorelines are often too developed and/or disturbed, so the downstream implications are mostly relevant to island ecosystems and island conservation. Given that your study has major implications for seabird conservation and island ecosystem restoration (see also my comment further below to elaborate on these implications in the discussion), I would recommend emphasising the context specificity of island systems in the abstract and throughout the main manuscript (in particular introduction, discussion). Below are specific comments that I suggest addressing before publication. Especially the methods section lacks some key information details to understand your work. All in all, I applaud the author team to a great and relevant study, and I look forward to seeing it published and citing it in my own work:

Reply:

We thank the reviewer for their enthusiasm regarding the implications and novelty of our work, while simultaneously highlighting the importance of more clearly explaining the ecological and geomorphological characteristics of our island systems. In the revised manuscript, we have strengthened this contextual framing across the abstract, introduction, and discussion.

First, in the abstract, we have explicitly described small, uninhabited sandy islands as geomorphically dynamic systems whose productivity relies heavily on allochthonous nutrient inputs. This has clarified why these islands are particularly sensitive to seabird-derived subsidies and thus central to our study.

Second, in the introduction, we have incorporated the concept of the circular seabird economy (Jones et al., 2023, 2025) to emphasise the unique cross-ecosystem nutrient linkages characteristic of island environments. We have further elaborated on how guano-mediated vegetation–sediment feedbacks are especially pronounced on small islands due to their nutrient limitation and geomorphic dynamic nature, thereby distinguishing them more clearly from mainland coastal systems.

Finally, in the discussion, we have explicitly expanded on the conservation and restoration relevance of our findings in the context of small, geomorphically dynamic islands. We have clarified that seabird restoration measures (e.g. acoustic luring, decoys, nest translocation) not only influence bird populations but can also drive changes in plant community composition through guano enrichment, with cascading effects on island resilience. We have further outlined how restoration strategies can anticipate these vegetation–sediment feedbacks, highlighting the importance of supporting nitrophilous, sediment-accreting plant species so that seabird-derived nutrient inputs reinforce, rather than undermine, geomorphic stability.

Specific comments:

l. 46–47: what kind of ‘physical processes’ are you referring to here?

Reply:

This has been changed to “aeolian and hydrodynamic sediment transporting processes”.

l. 55–58: around here I would have wished to read more about the uniqueness of island systems, in which autochthonous production is small relative to allochthonous input. I think this is an important context specificity of your study that needs explicit attention and introduction.

Reply:

We have added:

“Especially on small islands where autochthonous production is small relative to allochthonous nutrient input from the sea (Anderson & Polis, 1999a; Polis et al., 1997).”

l. 67: ‘guano fosters vegetation growth’ – this is a bit too oversimplified. Increasingly higher guano loads can cause plant community composition shifts, reduce species richness, and cause plant die-back (especially when paired with low rainfall; see Gulf of California island studies). As you are also speaking about plant trait-dependencies for soil stabilisation, it might be worth introducing that guano is not a universal ‘booster’ for any plant growth but

can also shift plant communities to certain species, growth forms, or traits (which may or may not be beneficial to soil stabilisation in your study system).

Reply:

We agree and have added the following nuance:

“Guano can stimulate vegetation growth, but its effects are not universally positive; high nutrient loads can shift plant community composition, reduce species richness, or cause die-back under dry conditions, leading to trait changes that may or may not enhance soil stabilization (Anderson & Polis, 1999; Barrett et al., 2005; J. Ellis, 2005; Maron et al., 2006; Young et al., 2011).”

Later in the section, we have reflected further on the “boost” versus “decline” scenario.

l. 72: Island systems come out of the blue here (before: only ‘coastal landscapes’), so I recommend some more specific introduction earlier, see comments above.

Reply:

The specificity of island systems has been highlighted earlier when discussing the uniqueness of island ecosystems in terms of autochthonous production versus allochthonous nutrient inputs (see reply to l. 55–58).

l. 80–81: I wonder whether the relevance of your work can be packaged slightly differently? Testing whether seabirds exert a measurable, and ecologically meaningful influence on island shoreline stability would demonstrate that seabird conservation and active ecological restoration is not only a tool for species-centric conservation efforts but constitutes an ecosystem-based adaptation for small, uninhabited sandy islands.

Reply:

We thank the reviewer for this suggestion. We have changed the last sentence of the paragraph to:

“As coastal ecosystems and their threatened avian inhabitants face mounting pressures from sea-level rise (van de Pol et al., 2024) and, on developed mainland coasts, coastal squeeze (Lansu et al., 2024), understanding how guano alters habitat structure at fine spatial scales is critical for conserving already declining bird populations (Paleczny et al., 2015). This is key for identifying system-specific pathways, particularly on small sandy islands, through which seabirds can enhance vegetation–sediment feedbacks that contribute to shoreline stability.”

l. 83: define ‘biogeomorphic islands’.

Reply:

We have added the following clarification:

“where biological communities and geomorphic processes are tightly coupled through reciprocal feedbacks that allow organisms and landforms to co-shape each other (Stallins, 2006).”

l. 84: ‘ideal laboratories’ but because of their unique dynamic nature, they constitute a specific system that does not necessarily inform about feedback loops between seabirds and shoreline dynamism on mainland coasts.

Reply:

We have toned down the wording by revising the sentence to:

“To understand the role of bird–plant interactions in soft-sediment coastal ecosystems, small uninhabited barrier islands offer a particularly informative setting, because of their dynamic biogeomorphological nature and dependence on external nutrients for stimulating internal vegetation productivity.”

l. 87: Why is the Dutch Wadden Sea a model system? Model for what?

Reply:

We have revised the sentence to avoid implying a formal model system:

“We applied a multi-variable framework on two spatial levels on islands in the Dutch Wadden Sea.”

l. 101: I presume you mean uninhabited, not inhabited, islands?

Reply:

That is correct; this has been changed to “uninhabited”.

l. 110: In the title, you refer to these birds as ‘seabirds’ but here (and also at a few other places throughout the manuscript) you use the term ‘coastal birds’. I suggest sticking to one term only, and I recommend using ‘seabird’ as the more widely recognised group of birds that drive cross-system energy flow. Along these lines, you may find the framework of the ‘Circular Seabird Economy’ also interesting to contextualise your study.

Reply:

All occurrences of “coastal bird” have been changed to “seabird”. We have also incorporated the circular seabird economy framework in the introduction:

“These cross-ecosystem nutrient exchanges form part of what has recently been termed the circular seabird economy, describing the bidirectional flow of nutrients between oceans, islands, and nearshore habitats (Jones et al., 2025).”

l. 110: what is a 'classic' barrier island?

Reply:

We have removed the term "classic" and now simply refer to both islands as barrier islands.

l. 126: I would have liked to read total breeding pair numbers (summed across all species) per island here to get a rough understanding about the colony sizes and seabird influence. Are we talking 100s, 1000s, or millions of birds per island?

Reply:

We have added the total number of breeding pairs per island at the start of the paragraph and have referred to the Supplementary Materials for species-level details.

Figure 1: I find the green line visualising the vegetation border a bit hard to see with the colour-scale background. Consider changing to a more strongly contrasting colour.

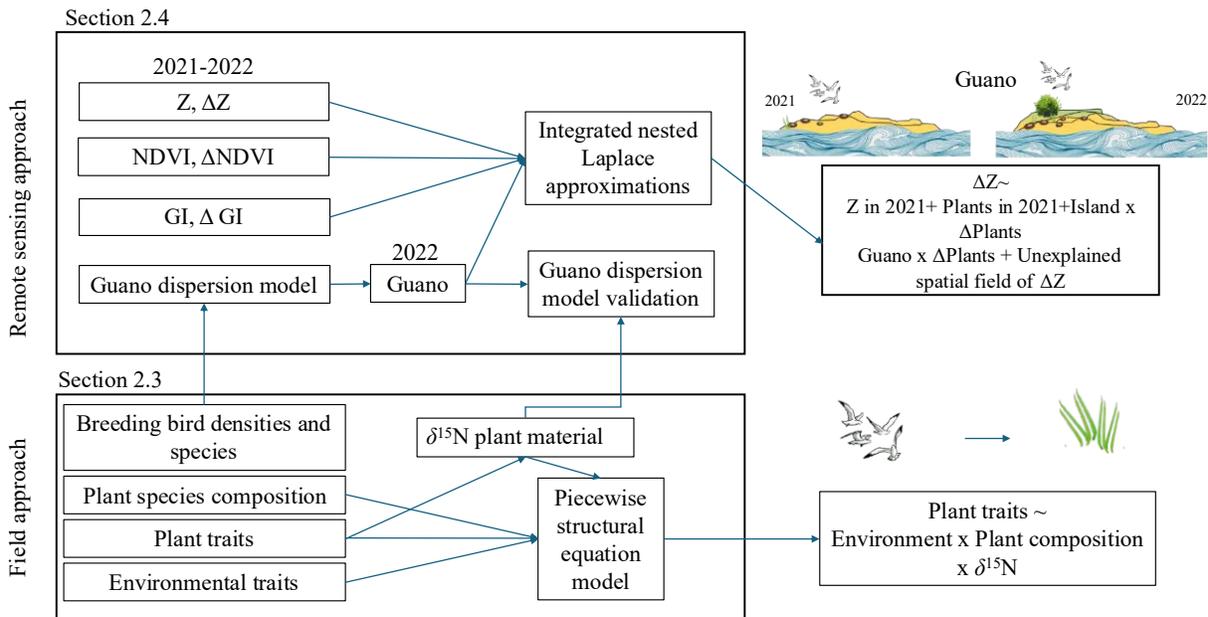
Reply:

We have added a thin black dashed line on top of the green vegetation boundary to improve visibility.

Figure 2: This is a very useful schematic figure, thank you! My only suggestion is to directly link each block in the figure to the corresponding section in the methods (e.g. I presume 'field approach' is section 2.3; 'NDVI' corresponds to section 2.4.1., etc). I think this would make your very extensive methods and data types even more accessible.

Reply:

This has been addressed by adding section numbers to each block in the figure:



l. 148: How did you handle the differing transect lengths in downstream modelling?

Reply:

Transect length did not directly enter the downstream modelling because all analyses were performed at the plot level. Points along the same transect are not necessarily closer to each other than points across transects, and plot-level observations were therefore treated as independent. However, spatial autocorrelation may still occur when nearby plots, regardless of transect ID, are more similar than distant ones. We accounted for this by implementing linear spatial lag models (lagsarlm function, spatialreg package v.1.3-2), which explicitly models spatial dependence among plots. To avoid confusion, we finalized section 2.3 with: “All analyses were conducted at the plot level, so transect identity or transect length were not included as model terms.”

l. 148: How did you spread your plots along each transect?

Reply:

Plots were spaced evenly along each transect, and each plot was positioned at a location whose vegetation composition and topography was representative of its immediate surroundings:

“Plots on transects were spaced evenly, and for each plot we choose a representative location based on surrounding vegetation and topography.”

l. 151: explain in more detail what this 'haphazard' sampling looked like?

Reply:

We have removed haphazard as it is indeed confusion but instead explain that the variation in sampling design on these narrow islands ensured a broad variety in sampling locations was included:

“On Richel and Rottumeroog, plot locations (N = 30 and N = 29, respectively) were distributed across the islands, as island width was insufficient to accommodate transect sampling, while still ensuring that a broad range of habitats and guano densities was sampled.”

l. 153: 4m<sup>2</sup> plots – I assume these were 2x2 meter, but can you state this explicitly?

Reply:

Correct, this has been clarified.

l. 153: how did you conduct the percent cover estimation? Was this based on %-increment bins?

Reply:

Percent cover was visually estimated using 5% increments for most species. For species contributing less than 5% cover, we used 1% increments to record their presence while assigning proportionally low abundance. We have made a reference to Lansu et al (2025) for methods.

Lansu, E. M., Fischman, H. S., Angelini, C., Hijner, N., Geelen, L., Groenendijk, D., ... & van der Heide, T. (2025). How human infrastructure threatens biodiversity by squeezing sandy coasts. *Current Biology*, 35(21), 5210-5219.

l. 155: where within your plots did you place the soil profile measurements?

Reply:

Soil cores were collected at representative locations within each plot. We placed one core beneath the most abundant plant species, and when two species were equally abundant, we placed one core beneath each species. This approach ensured that rooting depth measurements captured the dominant vegetation in each plot. We have added this clarification to the section:

“Rooting depth was determined at each sampling plot as the average of two 1 m depth soil profiles, placed beneath the dominant vegetation (or each of two co-dominant species), from which we measured the distance between the surface and the deepest living root.”

l. 160: Was this your fixed threshold ( $\delta^{15}\text{N} > 10$ ) to determine seabird influence on plant communities in downstream modelling?

Reply:

The threshold of  $\delta^{15}\text{N} > 10\text{‰}$  was mentioned only to illustrate typical values associated with guano-derived nitrogen based on previous studies. This threshold was not used in any part of our statistical modelling, nor did we classify plots or species based on this value. All  $\delta^{15}\text{N}$  measurements were included as continuous variables in the analyses. We have clarified this in the Methods to avoid this possible misunderstanding:

“Elevated  $\delta^{15}\text{N}$  values ( $\delta^{15}\text{N} > 10$ ) indicate that plants have incorporated organic nitrogen derived from guano (Maron et al., 2006; Reijers et al., 2024). This threshold was used only for interpretation and was not applied in any statistical modelling as  $\delta^{15}\text{N}$  was analysed as a continuous variable.”

l. 161: For what kinds of measurements did you do this procedure?

Reply:

The environmental PCA included mean elevation, distance from the coast, and soil organic matter content, whereas the plant-trait PCA was based on vegetation height, rooting depth, vegetation biomass, foliar carbon and nitrogen concentrations, and the C:N ratio. We have clarified this in the text:

“The environmental PCA included mean elevation, distance from the coast, and soil organic matter content, whereas the plant-trait PCA was based on vegetation height, rooting depth, vegetation biomass, foliar carbon and nitrogen concentrations, and foliar C:N ratio.”

l. 184: Did you center and scale your variables prior to PCA computation? Given that your variables are all on different scales with probably greatly varying ranges and means, I think you should center-scale them for proper PCA representation.

Reply:

All environmental and plant-trait variables were centered and scaled prior to PCA computation using `center = TRUE, scale. = TRUE` in the `prcomp()` function. We now state this explicitly in the Methods to avoid any ambiguity:

“Principal components were computed using singular value decomposition (SVD) via the `prcomp()` function in R, which ensures numerical stability and accurate handling of correlated variables, and all variables were centered and scaled prior to PCA to ensure equal weighting across predictors.”

l. 206: Delete double full-stop.

Reply:

Full-stop has been removed.

l. 211: Please provide some more detail on the field methodology for determining location and density of seabird nesting on the islands. Were these protocols harmonised across your five islands?

Reply:

During the 2022 breeding season, bird wardens recorded the location and density of nesting birds following the standardized protocols of the Trilateral Monitoring and Assessment Program (TMAP) (Koffijberg et al., 2017). Counts of breeding pairs were therefore derived from this harmonized monitoring scheme, in which colonial species are surveyed through complete nest or pair counts and widespread breeders are counted within standardized census areas. We have mentioned this in the text now.

l. 216: Since nesting in your temperate system is highly seasonal, does it make sense to calculate guano deposition per year?

Reply:

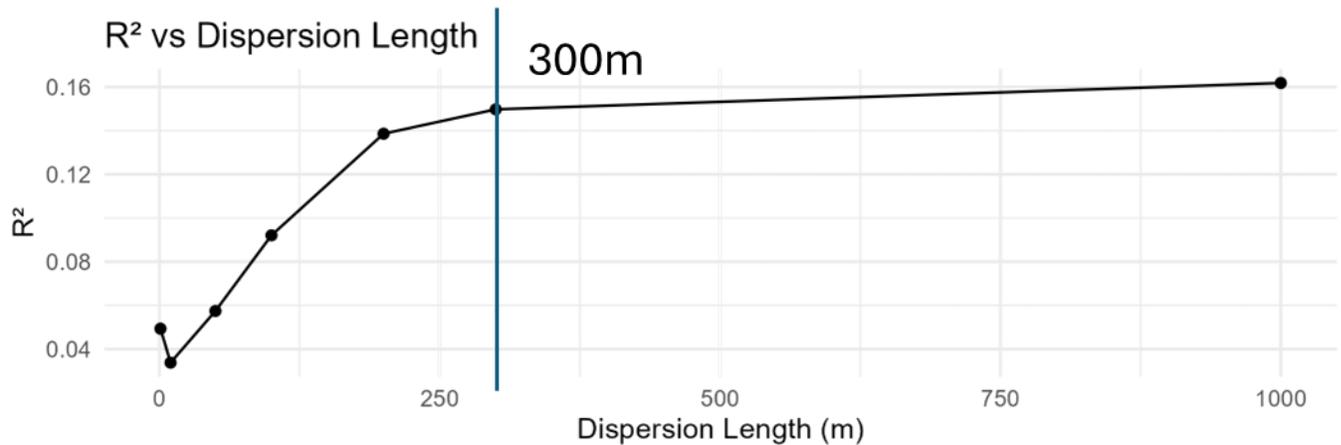
We agree that guano production is strongly seasonal. In our analysis, “per year” does not imply continuous year-round deposition but refers to the total guano load produced during the breeding season, which is the ecologically relevant pulse affecting vegetation and sediment dynamics. To avoid misunderstanding, we now explicitly state that annual deposition estimates represent the integrated output over the breeding period only.

l. 227: You set the limit of your guano dispersion model to 300 m (l. 218), then tested dispersion length up to 300 m (l. 224), and then report that your dispersion model detects best fit at exactly this limit (l. 227). Isn't there some circularity in this approach?

Reply:

Thank you for this helpful comment. Following your suggestion, we extended the dispersion-length sensitivity analysis from 300 m to 1000 m. This showed that model fit ( $R^2$ ) increases only marginally beyond ~300 m and approaches an asymptote, indicating that

most guano-related nitrogen enrichment is captured within this range. This plateau supports the literature-based expectation that guano effects typically attenuate within a few hundred meters of a colony. For consistency with empirical studies and because additional range provided no meaningful improvement in explanatory power, we retain 300 m as the operational dispersion length in the main text. We reported the extended 1000 m sensitivity analysis in the supplementary materials of a revised manuscript, see plot below:



l. 240: I am not too familiar with the phenology of Wadden/ temperate seabirds but is there also relevant overwintering (of potentially different seabird species) that may further increase guano input in autumn and winter months?

Reply:

In our system, guano relevant to vegetation and sediment dynamics is produced almost entirely during the spring–summer breeding season. Although some seabirds overwinter in the Wadden Sea, they mainly roost on island edges rather than on the vegetated island areas we studied. Winter inputs therefore form only a minor contribution, and our estimates intentionally reflect the breeding-season nutrient pulse. We have made this explicit:

“Because overwintering seabird roost mainly on bare island edges, winter guano inputs to vegetated areas are minimal; thus, our guano estimates reflect the breeding-season nutrient pulse.”

l. 267: how did you handle the spatial replication across five islands? Were these captured with group-level intercepts? From your model equations, it looks as if ‘island’ was treated as main effect – why not as group-level effect (“random intercept/slope” in frequentist language)

Reply:

In our models, spatial dependence was handled through a continuous spatial random field (SPDE), which captures spatial autocorrelation both within and across islands. Because this field already accounts for spatial clustering and island-level spatial structure, adding island as a group-level (random) effect would be redundant and potentially confounded with the spatial field. We therefore treated island as a fixed/main effect (factor), allowing us to model island-specific differences in the vegetation–guano relationships through interaction terms (Island  $\times$   $\Delta$ GI or Island  $\times$   $\Delta$ NDVI). This approach captured ecological differences among islands while avoiding overparameterization given the relatively small number of islands ( $n = 5$ ).

l. 274: Normality and homoscedasticity are not obligate requirements for Bayesian models (e.g. you could capture heteroscedastic data with a distributional modelling framework). However, I would have liked to read some more information on the Bayesian model evaluation, incl. prior sensitivity analysis, convergence, effective sample size, and posterior retrodictive checks? (e.g. see the WAMBS checklist: <https://doi.org/10.1037/met0000065>)

Reply:

Thank you for raising this important point. We fully agree that Bayesian model evaluation should extend beyond normality and homoscedasticity checks. Some elements of the WAMBS checklist, particularly those concerning MCMC chains (e.g. autocorrelation, trace plots, effective sample size), do not apply directly to INLA because INLA relies on deterministic Laplace approximations rather than Markov chain sampling. However, other WAMBS components are directly relevant and feasible within the INLA framework. In response to your comment, we reported (i) prior sensitivity analyses for key main effects and SPDE hyperparameters, (ii) mesh and resolution sensitivity tests to evaluate numerical stability of the spatial field, and (iii) posterior predictive checks comparing observed  $\Delta Z$  values with posterior predictive replicates. We have assessed the influence of Penalized Complexity priors by comparing models with alternative prior specifications. We added a brief description of these checks to the Methods and include full diagnostic outputs in the model validation part (S12-S14) in the Supplementary Materials.

Figure 4: in panel (b), scientific names should be italicised.

Reply:

We changed all scientific names to italics.

l. 304: You report that the model explains 9% more variance when adding guano as an additional parameter. However, mathematically, adding parameters to a model almost always increases  $R^2$  because the model gets more degrees of freedom to explain variation, so reporting the 9% alone is not necessarily evidence for an ecological effect. I would like

to see more evidence that this 9% increase is indeed an ecological effect attributable to guano, rather than a mathematical byproduct of increasing the number of predictors.

Reply:

We agree that increases in  $R^2$  alone cannot be taken as evidence for an ecological effect. To address this, we have revised the manuscript to clarify that our interpretation does not rely solely on the increase in explained variance. Instead, we have highlighted that  $\delta^{15}\text{N}$  (as a proxy for guano assimilation) contributes significantly and directionally to the causal structure of the SEM, with path coefficients that align with known ecological mechanisms:

“When we include  $\delta^{15}\text{N}$ , the model explains 9% more variance in plant species composition (NMDS2), and 5% more variance in plant traits ( $\text{PC2}_{\text{plant trait}}$ ). Although increases in  $R^2$  alone can arise from adding predictors, the ecological relevance of guano assimilation is supported by the significant and directionally consistent paths in the SEM: guano assimilation shifts composition toward climax in mud or forb-dominated communities in sand ( $\delta^{15}\text{N} \rightarrow \text{NMDS2}: -0.32$ ) and increases foliar nitrogen content independent of species composition ( $\delta^{15}\text{N} \rightarrow \text{PC2}_{\text{plant trait}}: 0.36$ ), (Figure 5c and S5 in the supplements).”

l. 325: is this posterior effect size reported on the z-standardised scale? Also, as per Bayesian convention, I suggest reporting posterior credible intervals, not standard deviation.

Reply:

Yes, it is reported on the z-standardized scale, we now clarify this. In a revised version we have reported the mean effect estimate along the 95% credible interval. This has been done in the entire 3.2 section.

l. 330: The terms “fixed effect” (and “random effect”) come from frequentist terminology but do not reflect the Bayesian thinking (e.g. all modelled parameters are probabilistic and not fixed), so I recommend using “population-level effect” or “main effect”

Reply:

All fixed-effects are changed into “main effect”.

l. 331: For better interpretability, could you un-z-standardise the posterior slope estimates?

Reply:

We appreciate the reviewer’s suggestion to un-z-standardise the posterior slope estimates to improve interpretability. In the current models, all continuous covariates were z-

standardised prior to fitting to ensure numerical stability and to facilitate comparison of effect sizes across predictors with very different units and ranges. Directly replotting all coefficients on the original scale would lead to considerable differences in magnitude between parameters, making a single coefficient plot with credible intervals difficult to interpret. This is especially true for the interaction terms between guano and  $\Delta\text{GI}$  or  $\Delta\text{NDVI}$ , whose interpretation on the original scale is inherently conditional on the value of the other predictor and therefore less straightforward.

To balance interpretability and numerical stability, we have retained the z-standardised coefficient plots (now explicitly described as “per 1 SD change” in the caption), and we have added a supplementary table (S8) reporting the mean and standard deviation of each covariate used for scaling. This allows readers to translate effect sizes back to the original units if desired, while keeping the visual comparison of coefficients clear and the model estimation numerically stable. Table for supplements:

S1: Scaling factors for the z-standardization for the INLA analysis.

Variable	Mean	SD
Log(Guano(g/m <sup>2</sup> /y)+1))	0.866	0.811
GI in 2021 (d <sup>-1</sup> )	0.002	0.001
NDVI in 2021 (-)	0.321	0.191
$\Delta\text{GI}$ (d <sup>-1</sup> )	0.000	0.001
$\Delta\text{NDVI}$ (-)	-0.029	0.082
Elevation (2021) (m)	1.829	1.044

l. 350: interaction with what?

Reply:

Interaction with the vegetation state change variable:  $\Delta\text{GI}$  or  $\Delta\text{NDVI}$ . We have added:

“Guano deposition, without interaction with  $\Delta\text{GI}$  or  $\Delta\text{NDVI}$ , had a positive effect on changes in sediment bed level in both models (Figure 6).”

l. 371–372: ‘lower areas experiencing more erosion or less accretion’ – this statement contradicts what you write earlier in the results section, line 358: ‘lower areas were more prone to accretion or less erosion’. Please check carefully for consistency.

Reply:

Thank you for pointing out this inconsistency. Indeed, the wording in L 371 was incorrect given the negative effect of elevation (z) on  $\Delta Z$ . We have revised the sentence to:

“At the landscape scale, elevation was the dominant predictor of elevation change, with

higher areas experiencing more erosion or less accretion in the years we analysed.”  
We have checked the results section for consistency to ensure that higher areas are now consistently described as more prone to erosion or reduced accretion.

l. 400: Vegetation tends to allocate biomass and productivity primarily in the compartment that is most limited (e.g. canopy-development in highly competitive, light-limited tropical rainforest conditions, root development under nutrient limitation). Couldn't you also argue that seabird guano input would ease the nutrient limitation for plant species, therefore reducing their allocation in root biomass (sensu 'optimal partitioning theory')?

Reply:

Correct, we have changed the word strengthening into modification, and added a sentence in the introduction:

“On the other hand, guano fertilization can also weaken erosion resistance by reducing the selective pressure for below-ground foraging, leading to lower investment in root biomass (Marin-Diaz et al., 2021; Poorter & Nagel, 2000).”

l. 408: missing word: 'might also HAVE limited us'?

Reply:

Correct, we added this.

l. 445: Rather than a discussion on model development, I would have wished to read a few sentences on the implications of your findings for seabird conservation / restorations. How can your findings be used to promote seabird conservation as a tool for enhancing sandy island ecosystem resilience? How should your findings be used and framed by conservation practitioners that seek to promote seabird protection and active restoration (e.g. through translocation, decoys, acoustic luring) as an ecosystem-based adaptation?

Reply:

At the end of the discussion we have added some sentences on the implications of this study, as suggested:

“Seabird restoration efforts, such as acoustic luring, decoys, or nest translocation, are increasingly used to re-establish colonies on coastal islands (Jones et al., 2025; Jones & Kress, 2012; Spatz et al., 2023). Our results show that such interventions will not only affect bird populations but could also transform plant communities through guano enrichment, with consequences for island morphodynamics resilience. Effective seabird restoration therefore requires a holistic approach that anticipates these vegetation shifts. Supporting nitrophilous, sediment-accreting plant species before or alongside seabird

restoration can help ensure that nutrient inputs strengthen, rather than weaken, the stability of restored islands.”

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