INFLUENCE OF GUANO DEPOSITION ON PLANT COMMUNITY IN THE DUTCH WADDEN SEA

On the impact of nutrient influx by guano deposition by shore- and seabirds on the plant community of sandy barriers and dunes, and salt marshes of the Dutch Wadden islands

Abstract

The Wadden Sea offers migratory shore- and seabirds great ecological value. Its tidal flats and islands offer nourishment, nursery and resting availability. In return, these birds fertilise islands through guano deposition. These nutrient-poor islands may be dependent on this influx of marine-derived nutrients. This nutrient influx could support vegetation growth, on which the size and resilience of the island are strongly dependent. In this thesis, the effect of guano fertilization with respect to distance to colony distance and ecotope origin on the island vegetation is elucidated. The latter has been found to have the largest influence on island vegetation.

Camille Tuijnman – 5617375

First supervisor Valérie Reijers, second supervisor Floris van Rees

PREFACE

Before you lies the master thesis: "INFLUENCE OF GUANO DEPOSITION ON PLANT COMMUNITY IN THE DUTCH WADDEN SEA: On the impact of nutrient influx by guano deposition by shore- and seabirds on the plant community of sandy barriers and dunes, and salt marshes of the Dutch Wadden islands". It has been written to fulfil the graduation requirements of the Marine Science program at Utrecht University in Utrecht. I was engaged in researching and writing this thesis from August to March 2021.

I noticed during my previous studies that I craved a new challenge. I wanted to approach the thesis differently, by choosing a subject which required skills I did not yet have. I went on a large fieldwork campaign over the course of two months where I visited 10 Wadden islands and learned about 100 plant species by heart, and I have made myself familiar with programming in R. I have also gained more experience in a skill I was already familiar with, working in a laboratory. Like so many things in the world, writing this thesis was not without struggles and adversity. However, this has made finishing this thesis all the more rewarding and I have genuinely enjoyed working on and writing it.

I would like to thank my first supervisor Valérie Reijers for the inspiration and input she provided me with and for her fabulous DJ skills. After your talk during the Microbes and Biochemistry course, I knew you would provide me with a challenge that would genuinely pique my interest.

I would also like to thank my second supervisor Floris van Rees for his excellent guidance and support during the process. You have taught me many new valuable skills in the field and programming. I sincerely had a great time during the car rides and the fieldwork trips to some of the most beautiful locations in The Netherlands (not Schier).

I want to thank Maarten Zwarts as the ultimate fieldwork partner, and Nadia Hijner for the bento torch experience.

I also want to thank Loran Kleine Schaars and Evaline van Weerlee for a safe and efficient lab experience, and Leo Boogert for all the time he came in early to help me with the freeze dryer.

And I want to thank Solveig Höfer for showing me around the laboratory, around the NIOZ, helping me with programming and being an awesome person and friend.

And of course, my family, friends and partner for their love and support.

And finally, I would like to thank Arnold for sitting beside me every day I worked on this thesis. He is the best boy. See Appendix figure 1.

Camille Tuijnman

Utrecht, March 15, 2023

TABLE OF CONTENTS

1 INTRODUCTION

1.1 INTRODUCTION & HYPOTHESIS

The Dutch Wadden Sea islands play an invaluable role in the coastal protection of the mainland from flooding during storm surges. The islands can be divided into two categories, the barrier islands that separate the North Sea from the Wadden Sea, and the islands located behind those islands, the back-barrier islands (Govers & Reijers, 2021). At present, these islands are threatened by human disturbances, predator introduction, and anthropogenic greenhouse emissions causing accelerated sea level rise and increased storm surge frequencies (Trilateral Working Group on Coastal Protection and Sea Level Rise (CPSL), 2001; Veerman & Deltacommissie., 2008; Wang et al., 2012). These threats are reason for concern, as they endanger the survival of the islands and corresponding species.

The Dutch Wadden Sea islands play a central role in the global flyway networks for migratory shore- and seabirds (Boere & Piersma, 2012; Piersma et al., 2016). They offer feeding, breeding and roosting opportunities. In return, these birds increase ecosystem productivity through the provision of a marine derived nutrient influx, guano deposition (Anderson & Polis, 1999; Benkwitt et al., 2021; Buelow et al., 2018; Lundberg & Moberg, 2003). Guano is the accumulated excrement of migratory shore- or seabirds and contains high levels of nutrients such as nitrogen and phosphate phosphorus (Anderson & Polis, 1999; Ellis, 2005; García et al., 2002; Ryan & Watkins, 1989; Wait et al., 2005).

The size and resilience of the islands are dependent on vegetation growth (Durán & Moore, 2013). Yet, their sandy soil is often nutrient poor, constraining the growth of vegetation(V. C. Reijers et al., 2020). This leads to the question if the island's size and resilience are dependent on guano deposition by migratory shore- and seabirds.

To answer this question, the effect of guano deposition on island vegetation must be elucidated first. For example, it has been shown that excessive inputs of phosphorus and nitrogen can shift the community composition, resulting in a decrease in species diversity (Avolio et al., 2014; de Schrijver et al., 2011; Payne et al., 2013; Suding et al., 2005).

However, research on this topic is not always in agreement. On a community level, migratory shore- and seabirds have been shown to decrease the abundance of native species (Hogg & Morton, 1983; Vidal, Médail, Tatoni, Roche, et al., 1998; Vidal, Médail, Tatoni, Vidal, et al., 1998). However, they can also contribute to the persistence of rare native species (Dean et al., 1994; Norton et al., 1997).

Moreover, conflicting results have been published on the effect of migratory shore- and sea birds on species richness. Several studies reported that species richness was higher in areas that were unaffected by birds in comparison to colony areas (Ellis, 2005; Gillham, 1960; Ishida, 1996; Vidal et al., 2003), while other studies reported that the species richness was higher at intermediate levels of bird disturbance (Hogg & Morton, 1983; Vidal et al., 2003). Some reported that the effect of migratory shore- and sea birds on species richness was dependent on the island size (Hogg et al., 1989; Vidal et al., 2000; Vidal, Médail, Tatoni, Roche, et al., 1998) However, these results were also contradicting.

To close this knowledge gap, this thesis aims to investigate the effect of guano deposition on the plant community at the Dutch Wadden islands. It is proposed that the island plant community is dependent on guano deposition. The distance to colony will affect the species diversity, species richness, plant height, root depth and biomass. However, the magnitude of the effects will be dependent on the ecotope that the vegetation originates from.

The ecotopes reviewed here are sandy barriers and dunes and salt marshes. Sandy barriers and dunes are constantly changing due to wind and water action. In this highly dynamic environment, the flora and fauna are greatly affected by substrate mobility, extremely high temperatures, drought, flooding, salinity, and a scarcity of nutrients (Martínez & Vázquez, n.d.). Sandy barriers and dunes play an essential role in coastal protection. For example, coastal foredunes (the first dunes encountered from the sea land inwards) that can be found on the seaward side of the barrier islands, are the first line of defence for the barrier island, the back-barrier islands behind it, and the mainland from flooding during storm surges. The formation of foredunes takes place through feedback between dune grasses and sand transport processes (Mullins et al., 2019). The type of species and the vegetation density affect the dune width, height and growth rate through their influence on the rate of sand deposition (Godfrey, 1977; Zarnetske et al., 2012) A change in species composition could lead to, for example, changes in the dune building capacity of foredunes (Mullins et al., 2019; Zarnetske et al., 2012).

Salt marshes are organic matter rich, flat areas, located at low altitudes, that are flooded occasionally to daily by salt water. Therefore, the dominating vegetation is halophytic (Adam, 1990). The trapping and binding of sediment by these plants are essential for the stability of salt marshes. Salt marshes are not only invaluable for biodiversity and ecological productivity but function as carbon sequestration and provide coastal protection as well (Woodroffe, 2002).

The relation between bird colony presence and species diversity, species richness, plant height, root depth, and biomass will be investigated in detail. Three research questions will be answered step-by-step to unravel the effect of guano deposition on the island plant community. Assessing reciprocal interactions between bird and plant communities is key to understanding landscape development. Therefore, this research contributes to system understanding and policymaking for ecosystem management on soft sediment islands in the coastal realm.

1. **WHAT IS THE EFFECT OF DISTANCE FROM COLONY ON THE SPECIES COMPOSITION?**
    - **WHAT IS THE EFFECT OF DISTANCE TO COLONY ON THE SPECIES COMPOSITION WITH AN INTERACTION EFFECT OF DIFFERENT ECOTOPES?**

HYPOTHESIS 1: The species composition is affected by the distance to colony, but only in sandy barriers and dunes. Guano deposition in the colony area influences the various chemical soil parameters, such as the concentration of nitrogen and phosphorus (Anderson & Polis, 1999; Ellis, 2005; García et al., 2002; Ryan & Watkins, 1989; Wait et al., 2005). Guano fertilization will cause species with a high nutrient requirement to thrive. Whereas plants with a low nutrient uptake have a larger survival rate further away from a colony where nutrient limitation plays an increased role. The composition of the soil is much different in salt marshes in terms of salinity, humidity, grain size, organic matter, pH etc. so the distance from colony will have little to no effect at all (Hesp, 1991; Rezk, 1970). Additionally, the species composition will be greatly affected by the different ecotopes.

2. **WHAT IS THE EFFECT OF DISTANCE TO COLONY ON THE SPECIES RICHNESS?**
    - **WHAT IS THE EFFECT OF DISTANCE TO COLONY ON THE SPECIES RICHNESS WITH AN INTERACTION EFFECT OF DIFFERENT ECOTOPES?**

HYPOTHESIS 2: The species richness will decline further away from a colony, due to a lack of guano fertilization. However, this effect will be less noticeable in salt marshes with fertile soil containing high levels of organic matter. Ecotope will not affect the species richness.

3. WHAT IS THE EFFECT OF DISTANCE TO COLONY ON PLANT HEIGHT/ROOT DEPTH/BIOMASS?

- **WHAT IS THE EFFECT OF DISTANCE TO COLONY ON PLANT HEIGHT/ROOT DEPTH/BIOMASS WITH THE INTERACTION EFFECT OF DIFFERENT ECOTOPES?**

HYPOTHESIS 3: In sandy barriers and dunes, plant height will decrease further away from a colony due to less fertilization. For the same reason, root depth will increase, and biomass decline. However, there will be no such effect on the salt marsh vegetation, as the soil contains high levels of organic matter over all distances. The plant height, root depth and biomass will be equal over distance to colony in salt marshes. Plant height, root depth and biomass will be different between the ecotopes. Plants in salt marshes are smaller on average. Salt marsh soil has a fertile top layer; therefore, root depth will be shorter. Finally, plant coverage of salt marshes is lower, thus biomass will be lower.

1.2 LITERATURE STUDY

The Wadden Sea is the largest tidal flat system in the world (Simon, 2011). This sea is formed by a 500 km long barrier island chain along the Netherlands, Germany, and Denmark. The islands and tidal flats play a vital role in global flyway networks for migratory shore- and seabirds (Boere & Piersma, 2012; Piersma et al., 2016). Annually up to 12 million birds visit the Wadden Sea to participate in feeding, breeding, and roosting (Meltofte et al., 1994). According to the Rasmar convention on wetlands, the Wadden Sea is essential for 52 populations of 41 migratory bird species (Convention on Wetlands, n.d.). Seabirds come to the islands only to breed, while migratory shorebirds use the mudflats to stack up energy for their long-distance flights between the Arctic and the tropics.

The Dutch Wadden Sea is formed by its barrier islands, the largest islands are Texel, Vlieland Terschelling, Ameland and Schiermonnikoog. These waves-dominated islands protect fetch limited back-barrier islands, or Chenier islands, such as Griend and Zuiderduintjes (Govers & Reijers, 2021). The back-barrier islands are tide-dominated. Both barrier and Chenier Island provide brooding and roosting areas, high water refuge, and surrounding tidal mud flats offer feeding opportunities (Burger et al., 1997; Masero et al., 2000). Back barrier islands have great ecological value as they are often uninhabited by people or predators, and thus enjoy a unique feature of undisturbed opportunity for bird colonies to take refuge (Govers & Reijers, 2021; V. Reijers et al., 2020; US Department of Commerce, n.d.).

This unique tidal landscape offers important ecosystem services, for example, protection of the hinterland from flooding during extreme weather storm surges (Timmerman et al., 2021; Wang et al., 2018). Sandy dunes and salt marshes of the barrier islands attenuate the energy of waves before hitting the mainland, decreasing the chances of coastal flooding.

Despite their importance, the existence of this unique tidal landscape is under duress. The biggest threats are human interference such as disturbance and predator introduction (Lensink et al., 2015; Leyrer et al., 2019), and anthropogenic greenhouse emissions accelerating global climate change (Trilateral Working Group on Coastal Protection and Sea Level Rise (CPSL), 2001; Veerman & Deltacommissie., 2008; Wang et al., 2012). It has been shown that in general the introduction of invasive predator species, for example, rats or cats, can threaten an islands' ecosystem and cause a decline in the number of bird and bird colonies (Benkwitt et al., 2021; Blackburn et al., 2005; Iamond, 1989; Monteiro et al., 1996; Towns & Broome, 2010). Furthermore, global warming due to the enhanced greenhouse emission increases the frequency of storm surges and accelerates sea level rise (McInnes et al., 2003). This leads to more frequent flooding of the Wadden islands. Recent sea level rise predictions by the IPCC range from 0.43 m under RCP2.6 to 0.84 m under RCP8.5 by 2100 (IPCC, 2022). These predictions give a reason for concern, especially when considering that the recovery of island dunes after a storm surge can take several years or up to a decade (Houser et al., 2015). With the increasing frequency of storms, islands may not get the chance to recover and could irreversibly transition into a new, more unfavourable equilibrium state without

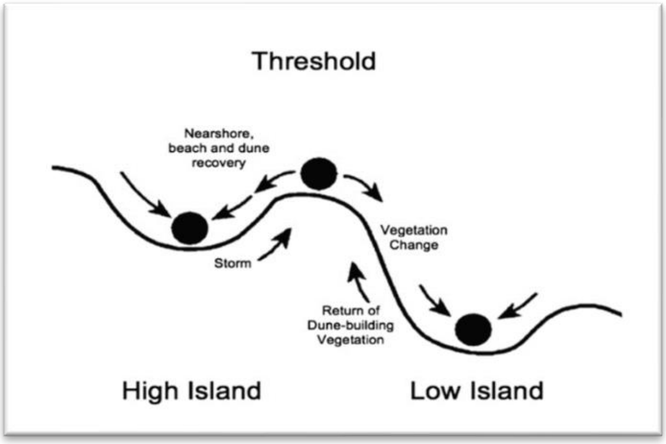


Figure 1 - Transition from a favourable equilibrium (high island) to an unfavourable equilibrium (low island) through increased storm surge frequency. Graph taken from (Houser et al., 2015).

dune-building vegetation (low islands) (Houser et al., 2015). This transition from islands where large dunes development is dependent on the recovery of beach vegetation and the recolonization of dune-building vegetation (high islands) (Durán & Moore, 2013; Houser et al., 2015), is schematically displayed in Figure 1. Whenever the tipping point is breached, returning to the favourable state requires much more energy.

Island size and resilience are thus strongly dependent on the vegetation cover (Durán & Moore, 2013; V. C. Reijers et al., 2020). Vegetation stabilizes islands by dampening hydrodynamic energy and limiting erosion by their root networks. The vegetation growth relies on nutrient influx, as nutrient availability is the most important factor in plant growth of ecosystems in temperate regions (Bedford et al., 1999). Yet, these islands have in general a nutrient-poor, sandy, and harsh environment, constraining vegetational growth (V. C. Reijers et al., 2020).

The fertilising effect of guano from seabirds has been understood for a long time, the so-called "white gold" sustained agricultural intensifications dating back to AD 1,000 (Santana-Sagredo et al., 2021). Guano is rich in nutrients such as nitrogen and phosphorus (Anderson & Polis, 1999; Ellis, 2005; García et al., 2002; Ryan & Watkins, 1989; Wait et al., 2005). The deposition of guano by migratory shore- and seabirds can provide these nutrient-poor islands with the nutrients necessary for vegetation growth, such as dune-building vegetation. It has been shown that ecosystem activity on islands grows with the increasing presence of shorebird deposition (Benkwitt et al., 2021; Buelow et al., 2018). The trophic and biogeomorphic interactions between migratory shore- and seabirds, and the island landscape are schematically represented in Figure 2.

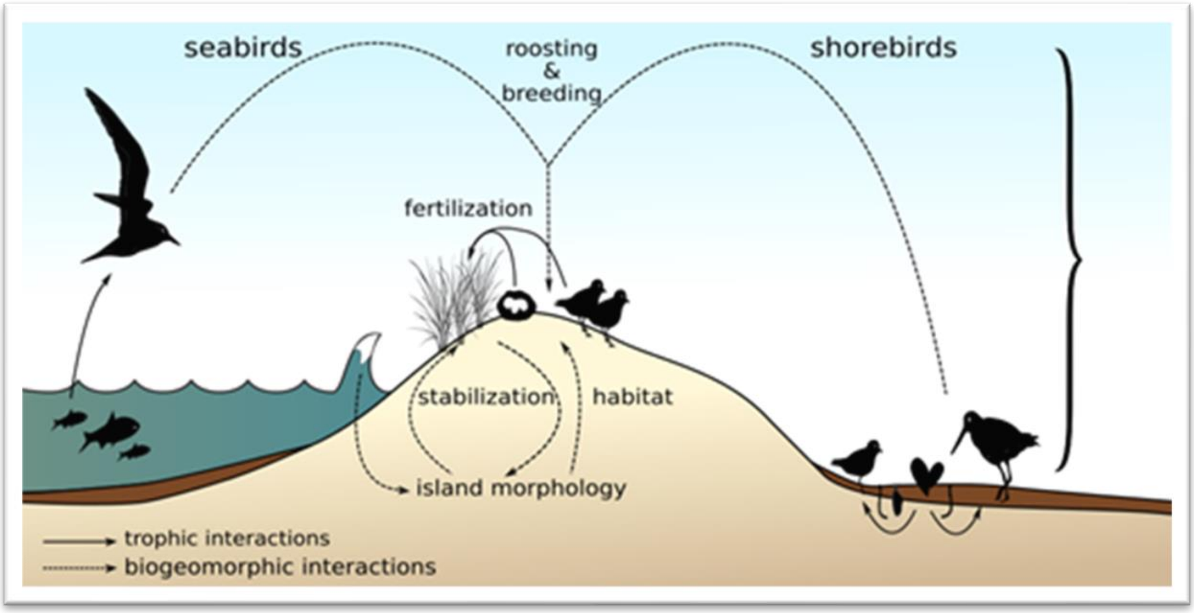


Figure 2 - Schematic representation of the marine derived nutrient influx brought by migratory shore- and seabirds. As birds breed and roost on the island, nutrients in form of guano are deposited on the island. This source of nutrients may be essential for the island's size and resilience. Image source: Avian Nutrient Pump - NIOZ, n.d.

This marine-derived nutrient transport is essential to these islands (Anderson & Polis, 1999; Lundberg & Moberg, 2003; Mulder & Keall, 2001; Polis & Hurd, 1995; Vidal et al., 2003). Island ecosystems can even be disproportional depending on the fertilization by birds due to their isolation from outside nutrient pools, as shown in a recent experiment by Buelow et al., 2018. However, with the decline in migratory shore- and seabird populations in the Wadden Sea (Lotze, 2005; van Roomen et al., 2012), this marine-derived nutrient transport and thus island resilience may be in danger.

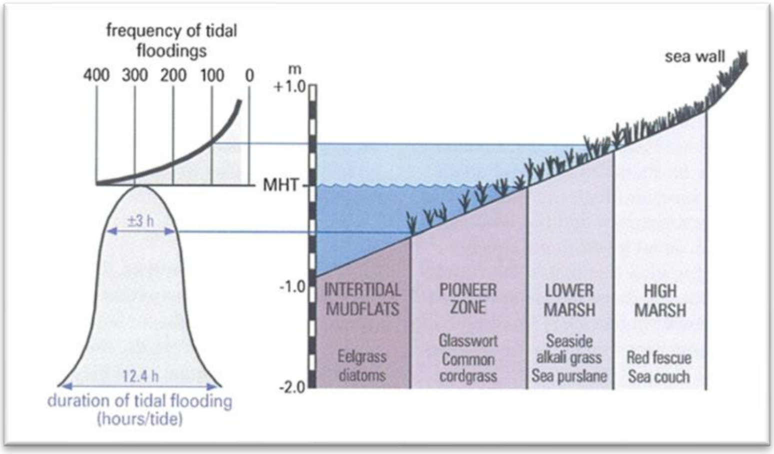


Figure 3 – Zonation of saltmarshes in relation to the duration and frequency of tidal flooding and march elevation for the Wadden sea, figure taken from Maciej Serda et al., 2016..

The Wadden islands have multiple ecotopes. Ecotopes are the smallest ecologically distinct landscape features in a landscape mapping and classification system. Different ecotopes have different vegetation covers. Here, sampling is carried out in three ecotopes: sandy barriers and dunes, salt marshes, and the sandy pioneers' zone. The type of ecotope is related to several factors. One important factor is altitude. Higher altitudes, where inundation does not frequently take place are an indication of sandy barriers and dunes. Sandy pioneers' zones and salt marshes are found at lower altitudes. For salt marsh to exist, the area must be flooded a certain times per year, see Figure 3. Inundation causes sediment deposition, which is necessary to maintain a salt marsh (Maciej Serda et al., 2016). Figure 3 distinguishes between lower salt marshes (flooded ≥ 100 times annually) and higher salt marshes (flooded ≥ 1 time(s) annually). Flooding more than once a year does not automatically indicate the presence of a salt marsh. Here is assumed that only the areas flooded at least one hundred times annually are salt marshes and sandy pioneers' zones. This requires tides above mean high tide. The average of the mean annual max surge and mean high tide can be used to distinguish sandy barriers and dunes from salt marshes and sandy pioneer zone. Another factor is the organic matter (OM) content in the sediment, which can be used to differentiate between salt marshes and sandy barriers. High OM content in the soil is a proxy for finer sediment structures (Buchanan & Longbottom, 1970; Mayer, 1994; Tyson, 1994) High OM concentration indicates clay sediment of salt marshes and lower concentrations indicate coarse sand in sandy pioneers' zones.

The islands can be divided into three classes. The first class are climax islands which have established dunes, and human activity. Climax islands are stable in terms of succession, and changes in habitat do not occur frequently (Cowles, 1899). The second class are bare islands. These islands are subjected to the elements and vegetation has little chance to grow here (de Groot et al., 2017). These first two classes are unlikely to be greatly affected by guano fertilization. The climax islands have already large and established dunes where the species composition is mainly uninfluenced. Meanwhile, the bare islands have neither vegetation nor bird colonies to fertilize them. The third class are biogeomorphologically active islands. Fauna here has a large influence on coastal geomorphic processes (Geyer et al., 2000). These biogeomorphologically active islands are the most likely to be influenced by guano deposition as the vegetation has not yet reached a climax, it is much more susceptible to large nutrient influx.

2 MATERIALS & METHODOLOGY

2.1 FIELD DATA LOCATION

2.1.1 Location and study design

The fieldwork survey of this study was conducted on eleven islands located in the Dutch Wadden Sea: the barrier islands Razende Bol, Texel, Vlieland, Richel, Engelsmanplaat, Het Rif, Schiermonnikoog, Rottumerplaat, and Rottumeroog as well as the fetch limited back barrier islands Griend and Zuiderduin, see Figure 4.

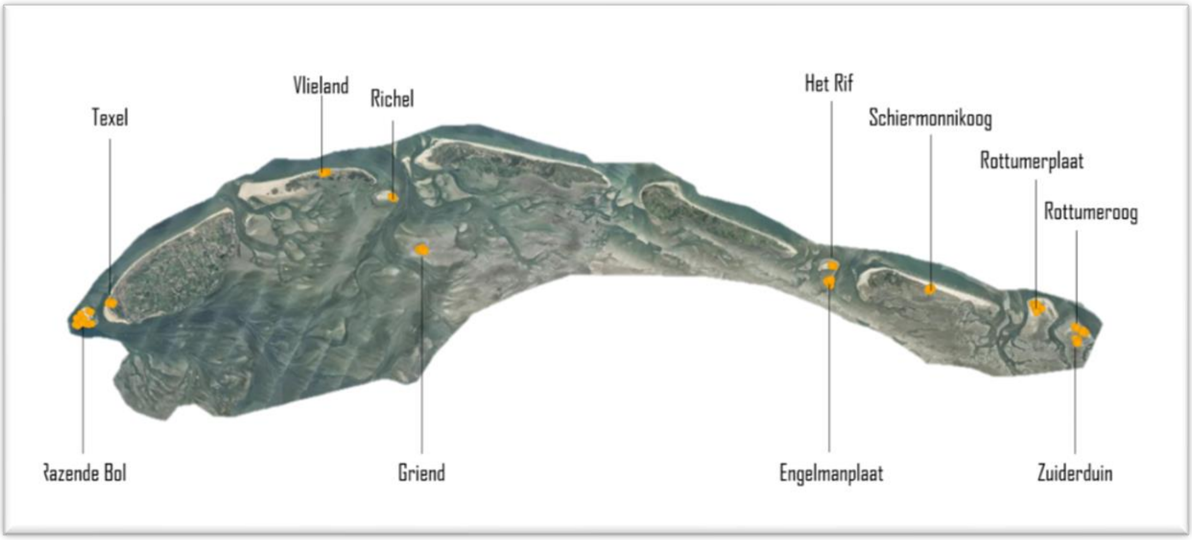


Figure 4 – Satellite view of the Dutch Wadden Sea with the eleven sampled islands. The orange markers indicate the sample locations. Satellite images are taken from Beeldmateriaal Nederland, n.d..

Islands were selected according to their bird colony presence or lack thereof and the island class:

- Climax islands: Texel, Vlieland, and Schiermonnikoog
- Bare islands, no bird colonies present: Engelmansplaat, Het Rif, and Razende Bol.
- Biogeomorphologically active islands: Griend, Rottumeroog, Rottumerplaat, Zuiderduintjes and Richel.

The sample locations were plotted over six guano zones. Guano zones are the zones around the colonies, see Figure 5. In each zone, five samples were taken. In the early stages of the fieldwork campaign, these samples were taken at random locations within the guano zones. However, later it was decided that walking five transects through the guano zones was more time efficient, as depicted in Figure 5.

The breeding season took place from March to July. Sampling during this period would cause great disturbance within colonies. Therefore, to minimize the disturbance and yet measure the maximum effect of a colony's presence, the sampling campaign took place immediately after the breeding season. To prevent large differences in data collection over time, sampling was conducted within a short and intense two months period in August and September.

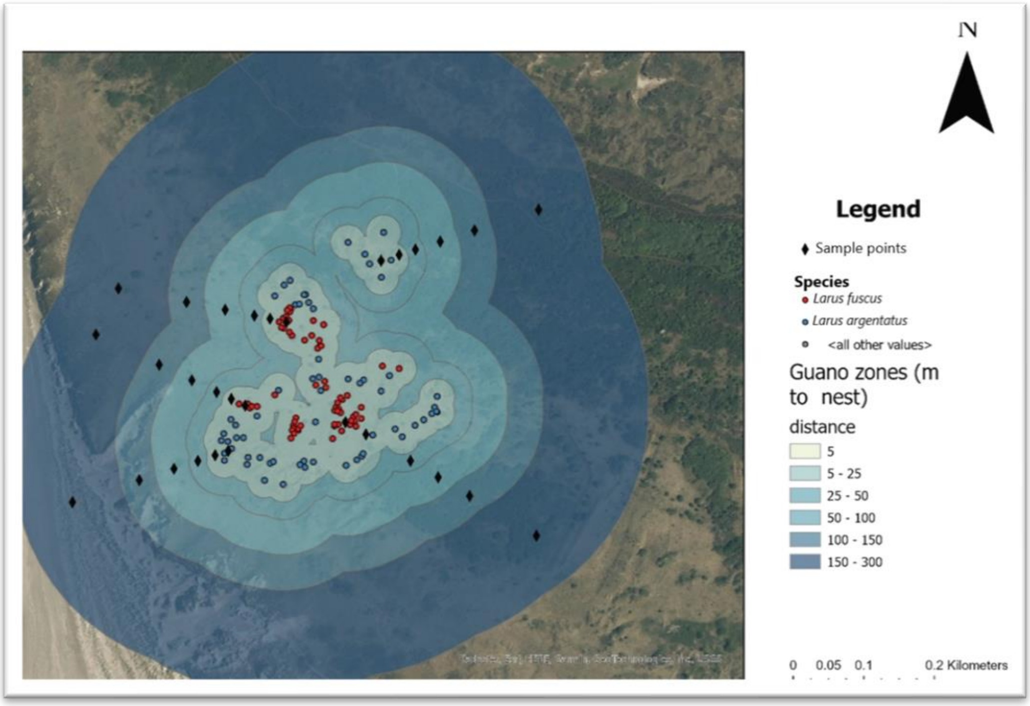


Figure 5 - Example of sample transects and guano zones. A guano zone is an area with a certain distance from a colony. The distance to the colony was divided into six guano zones. The centre zone is the zone within the colony. Nest locations in the colony are indicated with coloured dots. Here the colony mainly consisted of Larus fuscus (red dots) and Larus argentatus (blue dots). Five samples were taken per zone, indicated with diamonds. By F. van Rees (adapted).

Islands without colonies were sampled using a grid as a basis, see Figure 6. As was the case of Engelmansplaat, Het Rif, and Razende Bol. These types of islands asked for some flexibility, as some of the sample locations contained nothing but sand for multiple locations in a row or were located in the ocean.

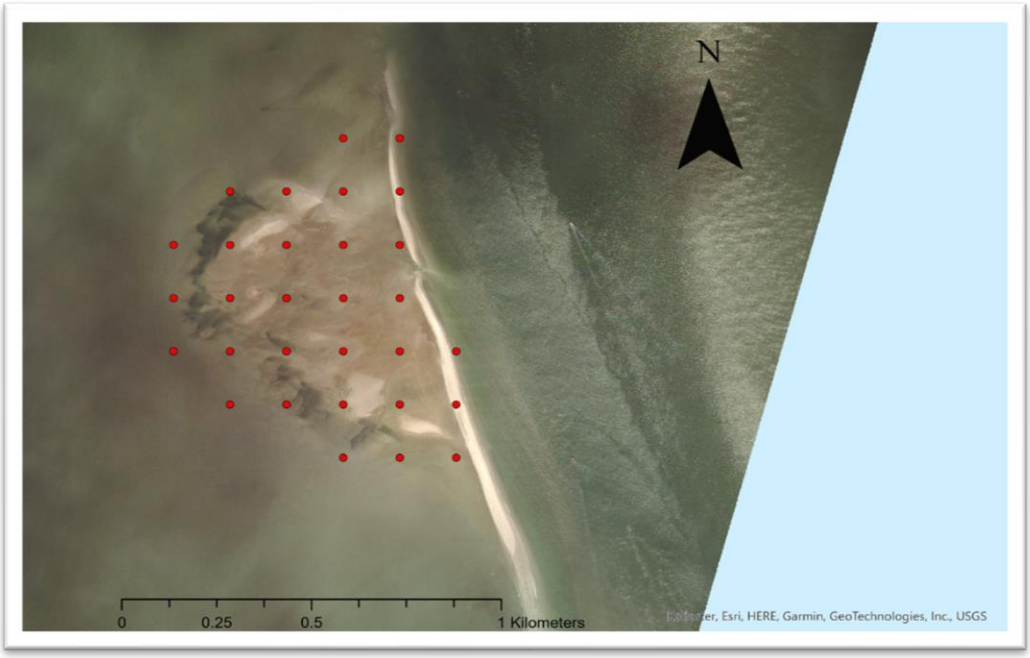


Figure 6 - Grid on Engelsmanplaat. Red dots indicate planned sample locations. Upon arrival, it was found that some of these locations were permanently submerged. By F. van Rees.

2.1.2 Sample method


Figure 7 - Example of typical plot layout. Zuiderduin sample location 11 in the saltmarsh. Photograph by F. van Rees.

At every sample location a 4 m^2 plot was laid out using folding rules, see Figure 7. First, an overview picture was taken for later reference.

Then, within the plot, all plant species were identified. Supported by the application Obsidentify that is supported by Waarnemingen.Be. This application can identify over 22.000 species using artificial intelligence and machine learning (NRC, n.d.; Waarnemingen.Be, n.d.). Inconclusive results by the app are fact-checked by one of their 250 species experts, who would follow up with an accurate result within 24 hours. In addition, when in-field identification failed, an inhouse expert's opinion was used.

An indication of the coverage in percentages per species was made using the Brown-Blanquet method (Braun-Blanquet & others, 1932).

Thirdly, using a manual soil sample drill, the root depth was determined in duplicate. In some cases, the sand was too incohesive to use the gauge auger perpendicular to the ground and an angle of 45 ˚ approximately was used. The root depth was then calculated using the Pythagoras rule.

Fourthly, a sediment sample was obtained in duplicate. A standard volume of 100 mL sediment was taken for each sample using a 100 mL soil sample ring. These samples were stored within 24 hours* in a fridge (6 ˚C).

Fifthly, the height of the tallest plants on the corners from the 4 m^2 plot, and the highest plant within the plot were measured.

The sixth step was to choose a second smaller 0.16 m^2 plot within the 4 m^2 plot that was representable for the larger plot. Here, all vegetation was taken 2 cm above the sediment using an automated hedge trimmer (Makita or Gardena). This bulk vegetation was used to determine the average biomass of that area. Bulk vegetation samples were collected in large plastic sacks and either dried or frozen (-30 ˚C) within 24 hours*.

Finally, elevation measurements were done at every corner of the large plot and on two corners of the small plot using a dGPS.

**This was unfeasible for Schiermonnikoog and Griend vegetation samples because of the length of the expeditions.*

2.2 LABORATORY SECTION

2.2.1 Bulk vegetation

Samples were placed in paper bags in a forced air oven (60 ˚C) for 48 hours or until a constant weight was reached. Samples were then weighed within two hours of removal from the oven. The increase in weight over time due to the absorption of water was determined to be a maximum of 2%. This effect was neglected.

Paper bags were not removed to weigh dried samples. To correct this, the average weight of a paper bag was subtracted from the total weight. The paper bags had an average weight of 8.72 g, determined using the average weight of 20 bags that were dried for 48 hours.

Richel was weighed without paper bags, due to supply issues. Vlieland samples contained a large amount of sand due to the collection of mosses. Therefore, the sand was sieved out using a 500 µm stainless steel micron mesh sieve before weighing.

2.2.2 Sediment

Each sample was weighed after a freeze-drying cycle of 72 hours. The weight of the sample was then determined by subtracting the weight of the vessel the sample was stored in.

- 125 mL containers: 18.36 g (σ = 0.18 g, n = 547)
- 150 mL containers: 23.2 g (σ = 0.18 g, n = 25)
- Plastic bags: samples were transferred to 125 mL containers after drying and weighing. The empty plastic backs were then individually weighed and subtracted from the sample weight including the plastic bag.

After the freeze drying and weighing, the organic matter was determined using formula 1. A scoop of sediment was dried at 60 ° C for 48 hours, weighed, combusted at 575 ° C for 4 hours and weighed again.

$$[1] \qquad \frac{Mass\ after\ combustion}{Mass\ before\ combustion} * 100\ \% = OM\ \%$$

2.3 ANALYSIS IN R

2.3.1 Data selection

As this thesis was part of a larger research, many data points were taken. However, here the interest lies in samples taken within a colony (0 m from colony) the first guano zone and out of a colony (50 – 150 m from colony) the fourth and fifth guano zone, see Figure 5. Samples of other distances were not further included.

An OTU table, see 2.3.2, requires vegetation and coverage per sample. The islands Engelmansplaat, Het Rif and Razende Bol, with little to no vegetation, were thus not included in further calculations.

To compare ecotopes with roughly the same number of samples, the sandy pioneers' zone ecotope was not further investigated, see 2.3.3.

To answer the research question, the samples were divided into four groups, the first two groups are the sandy barriers and dunes (SBD), and salt marshes (SM) within the colony (0 m). The other two groups were the sandy barriers and dunes, and the salt marshes out of colony (50-150 m). The number of samples per group and in total can be found in Table 2-1. The number of samples per ecotope and distance to colony can be found in Table 2-2.

Table 2-1 – Total amount of samples taken per group.

	Total samples per group
SM (0 m)	7
SM (50-150 m)	21
SBD (0 m)	59
SBD (50-150 m)	46
Total samples	133

Table 2-2 – Number of samples per ecotope and per distance to colony.

Total SM samples	28
Number of species in SM	34
Total SBD samples	105
Number of species in SBD	93
Total in colony (0 m)	66
Total out of colony (50-150m)	67

2.3.2 NMDS – OTU table

For the visualisation of the species composition changing from one community to the next, non-metric multidimensional scaling (NMDS) plot was used. NMDS is often used in ecological research (Ciccarelli, 2015; Pickart et al., 2021; Rabinowitz, 1975). In preparation for this, an operational taxonomic units (OTU) table was created first.

2.3.3 Ecotope determination

All samples were assigned to one of the three ecotopes; sandy barriers and dunes, salt marshes, and sandy pioneers' zone.

Distinguishment between sandy barriers and dunes, salt marshes, and sandy pioneers' zone was based on altitude. This altitude was determined using the average of the mean high tide (MHT) and the mean annual max surge (MAMS), see Table 2-3. This average of MHT and MAMS (AMM) altitude separated the sandy barrier and dunes from the salt marshes and sandy pioneers' zone, see Figure 8. This was confirmed by observations of our data points plotted against satellite data, where salt marshes were exclusively found below 2 meters above NAP. The AMM was compared to the elevation measurements of the samples.

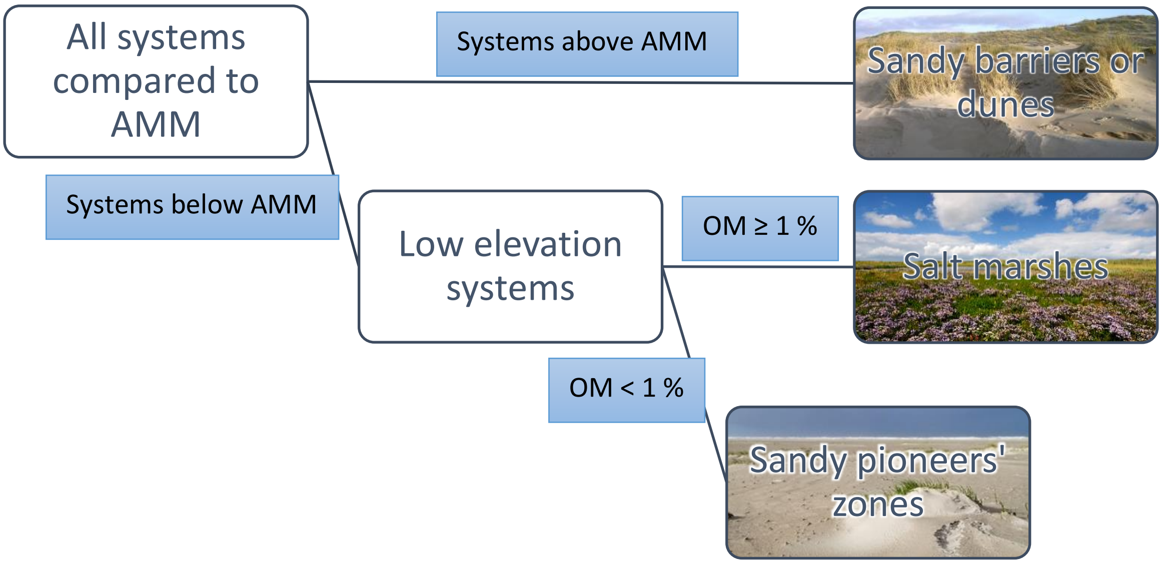


Figure 8 - Flowchart visualisation of ecotope separation based on the mean of MHT and MAMS, the AMM, and the organic matter percentage in the sediment. Picture credit from top to bottom; dunes on Texel Ecomare.nl, saltmarsh Rottumeroog R. van Wijk, embryo dune development Shutterstock.com ID: 745439923.

The MHT and MAMS are dependent on the location of the tidal inlet system (A.P. Oost et al., 2017). Towards the east, the tide is higher and thus the elevation until where salt marshes exist is also higher, see Table 2-3.

Table 2-3 – The mean high tide, mean annual surge and the average of both per relevant inlet system and corresponding islands A.P. Oost et al., 2017.

Inlet system	Corresponding islands	Mean high tide, or MHT (m)	Mean annual max surge, or MAMS (m)	Average of MHT and MAMS, or AMM (m)
Marsdiep	Razende Bol, Texel	0.61	2.4	1.51
Zeegat van het Vlie	Vlieland, Griend, Richel	0.85	2.48	1.67
Zoutkamperlaag	Engelmansplaat and Het Rif, Schiermonnikoog	0.93	2.55	1.74
Het Schild	Rottumeroog, Rottumerplaat, Zuiderduin	0.98	2.55	1.77

The ecotopes below AMM can be segmented into salt marshes and sandy pioneers' zones on basis of the organic matter (OM) content in the soil. High OM concentration indicates salt marshes. Here it is assumed that sediment samples taken below AMM and containing more than 1% of organic matter are taken in a salt marsh (Bai et al., 2016). However, it is possible that the sample originated from a young salt marsh with low deposition or a lower-located sandy barrier. Using outlier calculations, extreme outliers were identified and sorted with the correct ecotope.

Samples with less than 1 % organic matter in the sediment were assigned to the sandy pioneers' zone. After the distinction, 4.5 % of the total samples were found to be originated from the sandy pioneer's zone.

2.3.4 Data analysis

A linear mixed effect model (LMER) was used for continuous data (Bates et al., n.d.). The continuous data were NMDS1, plant height, root depth and biomass. For a count data outcome variable, a generalized linear mixed effect regression model (GLMER) was used (Barr, 2021). The fixed effects were distance to colony and ecotopes. The samples were taken within clustered groups, the islands. To account for this island-level variation, islands were added as random effect. The chosen level of significance, P = 0.05, is commonly used in ecology (Everitt, 1998).

For all outcome variables, two models were made. One with the mixed effects combined and one with the mixed effect interacting. The Akaike Information Criterion (AIC), was calculated to compare the different models and determine the best fit for the data (Burnham, 1998). However, the interacting model was used in all cases as this would offer more information to answer the research questions. The AIC values of the models approached each other, as they share the random effect, the island of origin. The intercept was significant in all models. All AIC values can be found in

Appendix table 1.

To check for normal distribution of the residuals, a Q-Q plot was made per model (Augustin et al., 2012). These plots can be found in the appendix.

2.3.5 Data analysis - ANOVA

An analysis of variance, or ANOVA (Fisher, 1936), was used to assess the differences between group means. Here two-way and three-way ANOVAs are performed (Millar & Holst, 1997), for LMER and GLMER respectively. The difference between these two is the number of independent variables. Two for a two-way ANOVA, and one more for a three-way ANOVA.

When an ANOVA resulted in statistical significance, this indicated that at least one of the means differed. A Tukey post hoc analysis was performed to identify which difference between pairs of means was significant (Tukey, 1949).

Extensive ANOVA result tables can be found in Appendix graph 8.

2.3.6 Beta diversity and dissimilarity percentage

To explain the difference in species composition in and out of colony per ecotope a dissimilarity percentage was calculated. The beta diversity of one ecotope from the two distances was divided by the total number of species in that ecotope to find the dissimilarity percentage, see formula 2.

$$[2] \qquad Dissimilarity\ percetage\ (SM\ or\ SBD) = \frac{\beta\ diversity\ (SM\ or\ SBD)}{Number\ of\ species\ in\ (SM\ or\ SBD)} * 100\%$$

3 RESULTS

3.1 SPECIES COMPOSITION

In sandy barriers and dunes, the most abundant species was *Ammophila arenaria*, with a presence of 45.7 % in all plots. In salt marshes, this was *Salicornia procumbens* with a 53,6% presence. These percentages were based on 228 field observations.

3.1.1 Visualisation of species composition using NMDS

Figure 9 Graphs A, B and C visualize different variables. Species composition was partially dependent on the island location, see graph A in Figure 9. The islands tend to 'clump' together.

The species composition seemed to be unrelated to the distance towards a colony, see graph B in Figure 9. In contrast, the ecotope shows an almost clean division between salt marshes and sandy dunes and barriers, see Figure 9, graph C.

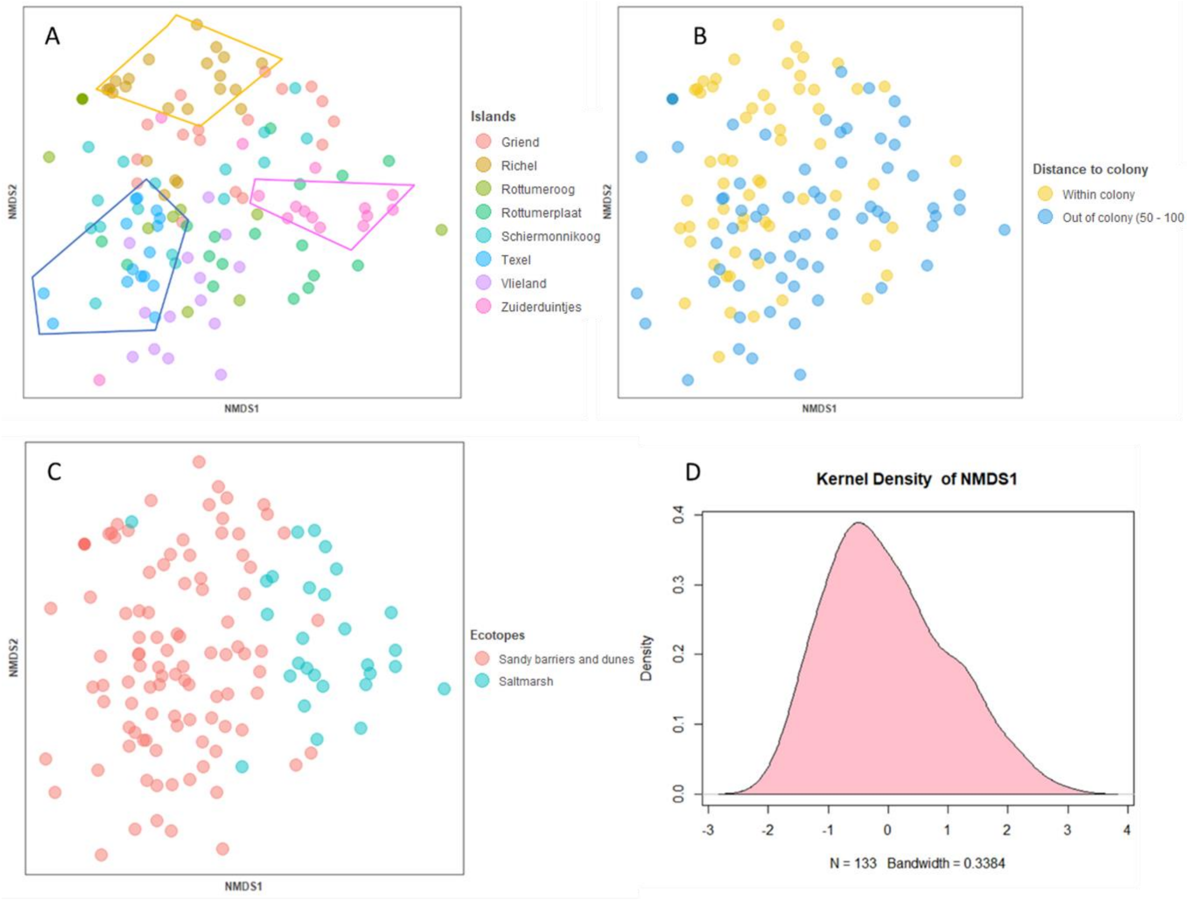


Figure 9 - Graph A visualizes the change of vegetation per island, grouping of islands is viable and for some highlighted. Richel with a yellow shape, Zuiderduintjes with a pink shape, and Texel with a blue shape. Graph B Indicates no change in vegetation in relation to distance to colony. Graph C shows a clear difference in vegetation per ecotope. Graph D shows the kernel density of NMDS 1.

These results were quantified by calculating the beta diversity per group, see Table 3-1 (Oksanen, 2022; Whittaker, 1960). The difference in species composition in the salt marshes within and out of the colony is low (18). Meanwhile, the differences in species composition between the ecotopes are large, in the colony 56 species and out of the colony 60 species. What stands out is that the species composition within the colony and out of the colony for sandy barriers and dunes differs a great amount, 52 species. This indicates that the species composition is dependent on the distance to colony in sandy barriers and dunes but not in salt marshes. This was found to be not significant in 3.3.2.

Table 3-1 – Beta diversity per group. SM = salt marsh, SBD = sandy barriers and dunes, 0 m is within the colony or guano zone 1, and 50-150 m is out of the colony or guano zone 4 and 5.

	SM (0 m)	SM (50-150 m)	SBD (0 m)	SBD (50-150 m)
SM (0 m)	0			
SM (50-150 m)	18	0		
SBD (0 m)	56	54	0	
SBD (50-150 m)	66	60	52	0

The dissimilarity percentage was calculated to be 53 % for the salt marshes and 56 % for sandy barriers and dunes. A similar number of species was unique per salt marsh groups and sandy barrier and dunes groups.

3.1.2 Species composition - NMDS1

Before an LMER model with outcome variable NMDS1 was made, a Shapiro-Wilk normality test was done to check for normality. The p-value, p = 4.96e-3, confirmed that the data was not normally distributed. An NMDS plot searches for the most variation within the data, therefore it will not be normally distributed. The kernel density graph of the histogram of NMDS 1 shows indeed a positive skew, see graph D in Figure 9.

ANOVA assumes that the data is normally distributed, the Q-Q plots of the residuals, Appendix graph 1, show that normal distribution is approached. The violation of the assumption has thus no serious consequences for the validity of the results (Glass et al., 1972).

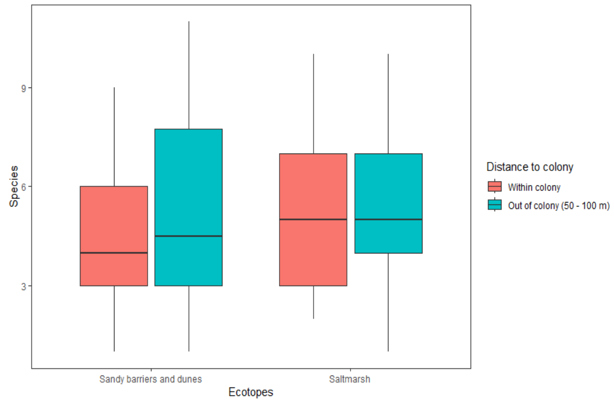
The fixed effect combination model with AIC = 281.66 was the most suitable. However, the LMER interaction model with AIC = 283.15 was used.

A two-way ANOVA was run on the interaction model to examine the effect of ecotope and distance to colony on the species composition. There was a statistical significance in species composition for the ecotope effect (F(3,129)= 69.96, $p << 0.05$) and no significant interaction.

A Tukey post-hoc test revealed that sandy barriers and dunes, and salt marsh groups differed significantly ($p << 0.05$).

3.2 SPECIES RICHNESS

The distance from colony does not seem to negatively influence the species richness, see the Graph 1 boxplot. On the contrary, the mean species richness was even greater out of colony of the sand barriers and dunes ecotope than within colony. However, this difference was found to be not significant.



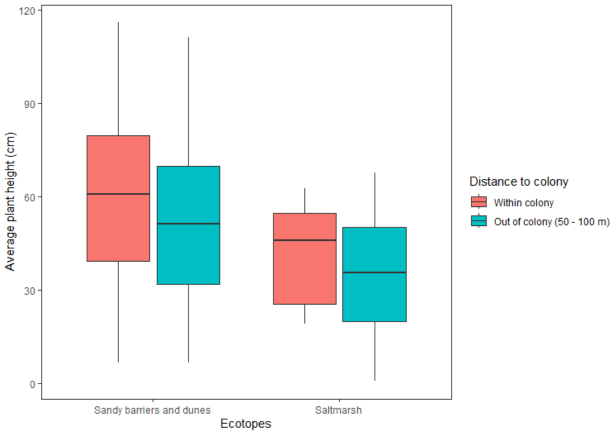
Graph 1 - Boxplot species richness per ecotope divided between within colony and out of colony.

The fixed effect combination GLMER model with AIC = 523.20 was the most suitable. However, the interaction model was used. A three-way ANOVA revealed that there was no statistically significant interaction between the effects or by one of the effects.

The Q-Q plots of the residuals can be found in Appendix graph 2 - Q-Q plots of glmer models with outcome variable species richness, the residuals are normally distributed.

3.3 AVERAGE PLANT HEIGHT

The average vegetation height in salt marshes was 33.82 cm height (σ = 18.25 cm), and the average in sandy barriers and dunes was 53.13 cm (σ = 26.22 cm), based on 228 field observations.



Graph 2 - Boxplot of the average plant height in centimetres per ecotope divided between within colony and out of colony.

Graph 2 indicates a difference in plant height within colony and out of colony, as well as between the ecotopes. The average plant height is lower within the salt marshes and lower out of the colony. However, only the first difference proved to be significant.

The LMER interaction model (AIC = 1128.75) was the most suitable. A two-way ANOVA showed significance for the ecotopes (F(3,129)= 6.94, p= 9.59e-3) and no significant interaction. A Tukey post-hoc revealed that sandy barriers and dunes, and saltmarshes groups differed significantly again p = 1.14e-2.

The Q-Q plots of the residuals can be found in Appendix graph 3.

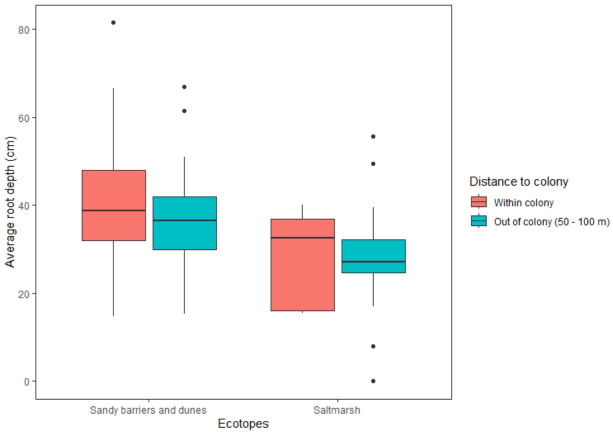
3.4 AVERAGE ROOT DEPTH

The boxplot gives reasons to believe that the average root depth within the salt marsh is lower than within sandy barriers and dunes, as suspected in hypothesis 3.

The interaction model (AIC = 926.39) was the most suitable.

A two-way ANOVA showed there was a significant main effect for ecotopes (F(3,129) = 10.13, p = 1.87e-3) and no significant interaction. A Tukey post-hoc found a significant difference between salt marshes and sandy barriers and dunes (p = 3.9e-3).

The Q-Q plots of the residuals can be found in Appendix graph 4.

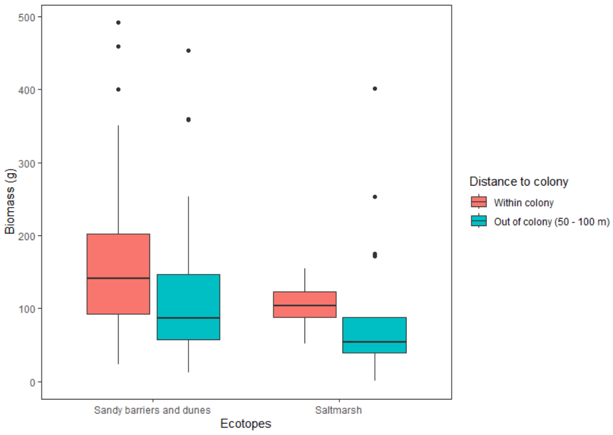


Graph 3 - Boxplot of the average root depth in centimetres per ecotope divided between within colony and out of colony. The average root depth is much more variable in Sandy barriers and dunes, and for ~75 % above 30 cm, whereas for salt marshes this is much less.

3.5 BIOMASS

Graph 4 indicates a difference in biomass per ecotope. The variation of vegetation mass is greater in sandy barriers and dunes. The biomass out of colony seems overall lower than within colony.

Using biomass as an outcome variable proved to be unfit to create a model. The initial Q-Q plots showed overdispersion. See Appendix graph 5. A histogram was used to indicate the diversion of data to normally distributed data with a bell curve. Appendix graph 6 - A) Histogram of the biomass, positively skewed. B) Histogram of the log of the biomass, normally distributed.



Graph 4 - Boxplot of the biomass in grams per ecotope divided between within colony and out of colony. ~ 75 % of the saltmarsh biomass within colony is heavier than the biomass out of colony.

A shows that the biomass histogram was positively skewed. To improve the data, creating a normally distributed outcome variable, the log of the biomass was obtained. The histogram, Appendix graph 6 - A) Histogram of the biomass, positively skewed. B) Histogram of the log of the biomass, normally distributed.

B, and Q-Q plot based on the two models' residuals using the log biomass, Appendix graph 7, show normal distribution.

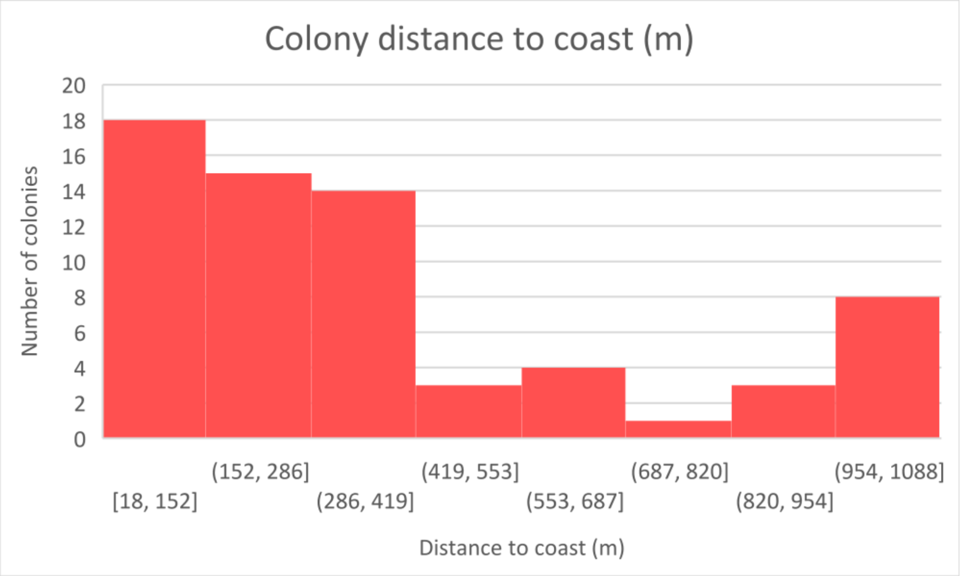
The initial AIC values were greatly reduced using the log of biomass. Initial combined fixed effects AIC = 1463.04, now AIC = 314.09. Initial interacting fixed effects AIC = 1455.16, now AIC = 317.63.

The LMER interaction model was used. A two-way ANOVA showed significance for the ecotope effect (F(3,129)= 5.07, p= 2.62e-2) and no significant interaction. A Tukey post-hoc found a significant difference between salt marshes and sandy barriers and dunes (p = 2.78e-2).

3.6 COLONY DISTANCE TO COAST

Almost 30 % of the colonies were located within 150 m of the coast, see Table 3-2.

Table 3-2 – Distance of colonies to the coast in meters.



4 DISCUSSION

In this thesis, the question of what the effect is of distance to colony on the plant species composition, the number of species, the average plant height/root depth, and the biomass and how this is influenced by ecotope origin is elucidated. The results indicate that most of the variation between in- and out of colony can be explained by the ecotope effect. Nonmetric multidimensional scaling shows a clear difference between sandy barriers and dunes, and salt marshes. This is confirmed by the beta diversity between the ecotopes. As well by the statistical significance that was found with an ANOVA for the ecotope fixed effect for the GLMER on species composition, and the LMERs on the average plant height, the average root depth, and the biomass. The effect of guano fertilization over the first 150 meters from the colony may be equal.

4.1 SPECIES COMPOSITION

Contrary to the hypothesised association that the species composition is dependent on the distance to colony, NMDS shows that the species composition is dependent on the island it originates from, as well as the ecotope, and not distance to colony. Yu et al., 2012 state that the island area and isolation are the main factors to influence the species composition. However, they did not look at the influence of guano fertilization. Further research would do well by investigating the effects of the area and the isolation effect on the species composition, as well as the influence of guano fertilization.

NMDS shows that the species composition is dependent on the originating ecotope. This is confirmed by the beta diversity that shows that the difference in species composition between ecotopes is large in the colony (56 species) and out of the colony (60 species), and by an ANOVA significant for the ecotope effect.

However, the species composition seemed unrelated to the distance to colony. This contradicts previous research that states that the composition is dependent on the distance to the colony (Vidal et al., 2003). The beta diversity however indicates that the distance does influence the species composition. Between the salt marshes in and out of colony, this is 18 and for sandy barriers and dunes 52. From this the dissimilarity percentage has been calculated, 53 % and 56 % respectively. The dissimilarity percentage emphasizes the difference in species composition within and out of colony per ecotope. These percentages are similar.

However, the number of samples taken in a salt marsh is 28 and in sandy dunes and barriers 105. A number approaching the latter for both ecotopes would provide a result that better reflects reality. Therefore, in future research, sampling between ecotopes should be equalized with a larger number of samples (n > 100 for both ecotopes).

4.2 SPECIES RICHNESS

An ANOVA revealed no significance for either ecotopes or distance to colony. This rejects the hypothesis that the number of species will decline further away from a colony. The answer to why the species richness is lower than anticipated may lie in the colony distance to the coast. 30 % of the colonies were located within 150 m of the coast. The foredunes where these colonies were often found are colonized by landscape-forming plants (V. C. Reijers et al., 2020). Only a few pioneer species, like *Elytrigia juncea* and *Ammophila arenaria*, can grow here. This could have an impact on the species diversity within the colony.

Other research has found that the species richness is greater at an intermediate level of disturbance. Disturbance being trampling and nutrient influx. The species richness was lower in active gull colonies than in undisturbed grassland, reported Hogg & Morton, 1983. However, more species could be found in a colony after it was abandoned. The abandoned colony became an intermediate area, with elevated nutrient levels but without the trampling.

Meanwhile, another study found that near king penguin colonies and further away the species richness were lower than in between (Vidal et al., 2003). The intermediate area experienced only moderate disturbance by seabirds.

Further research could investigate this nonlinear relationship in depth. For example, three zones (distances) should be considered. The first zone: within colony, the second zone: out of colony- or abandoned colony with intermediate disturbance, and a third zone: undisturbed area further away from the colony. This will provide an even more comprehensive view of the species diversity over distance than the approach chosen here. And the resampling of abandoned colonies would also offer more insight into the effect of the colonies on species richness over time.

4.3 PLANT HEIGHT

The plant height is statistically significant depending on the ecotope. Rejecting the hypothesis that in plant height will decrease further away from a colony for sandy barriers and dunes but remains equal for salt marshes. Although it has been shown that (organic) fertilization in agriculture causes plant height to increase (Purbajanti et al., 2019), plant fitness can also be negatively influenced by bird presence. Guano stains on island plants cause leaf dysfunction that may result in, among other things, asphyxiation (Alihussein et al., 2021). Moreover, the plant height is not only dependent on nutrient availability. Other important factors such as the burial rate (Qu et al., 2012), may affect the plant height stronger than the distance to colony.

Another reason that no significance was found for the distance to colony may be attributed to the fact that climax islands and biogeomorphologically active islands were not separated. This should be taken into consideration in future research, as biogeomorphologically active islands are more susceptible to the effects of guano fertilization.

The significant difference in ecotopes is explained by the different vegetation types commonly found within the ecotypes. The average vegetation height in salt marshes is lower than in sandy barriers and dunes and is largely affected by the most common species in an ecotope. In sandy barriers and dunes this is *A. arenaria*, an on average larger plant species than the most abundant salt marsh plant species *S. procumbent*, see Figure 10.

Figure 10 - Left: A. arenaria on Ijmuiderstrand, average height 0.6 – 1.2 m. Photograph by Svdmolen, GNU Free Documentation License. Right: S. procumbent, average height of 2 – 40 cm. Photograph by Hugues Tinguy, Creative Commons Attribution-Share Alike 2.0 France.

4.4 ROOT DEPTH

The hypothesis that the root depth will increase, and biomass and plant height will decrease further away from the colony for sandy barriers and dunes while this will remain equal over distance for salt marshes was rejected. A statistical significance is found only for the ecotope effect, not for the distance to colony.

It has been shown that the root depth is dependent on multiple factors such as wind exposure and water availability (Hesp, 1991; Schat & van Beckhoven, 1991). The root depth may be stronger depending on these stress factors than nutrient availability.

The ecotope effect on root depth may be caused by the difference in wind-, water- and salt spray exposure, water availability, organic matter levels in the soil, and the grain size of the soil(Hesp, 1991; Huang et al., 2013; Rogers & Benfey, 2015; Schat & van Beckhoven, 1991; *Soil Organic Matter and Its Importance for Water Management | STOWA*, n.d.).

Root depth could only be measured as deep as the length of the manual soil sample drill, therefore deeper roots may have gone unnoticed.

4.5 BIOMASS

ANOVA showed that the biomass is only statistically significantly influenced by the ecotope effect. Previous research has found that the biomass outside of colony is lower than within (Vermeer & Berendse, 1983). The reason that here not the same results are found may be the draught period during most of the breeding season and the sampling campaign (*KNMI - Zomer 2022 (Juni, Juli, Augustus)*, n.d.). Summer 2022 had a nationwide average of 135 mm precipitation, in contrast to the usual 224 mm average. At the end of August, the nationwide precipitation shortage was about 300 mm.

This can affect plants in multiple ways. For one, draught can lead to a decrease in plant growth (Araus et al., 2002; Bradford & Hsiao, 1982). This would affect both plants within and outside of colony. However, nutrient uptake is decreased during periods of drought, also. The effect of guano fertilization is greatly dependent on precipitation (Bista et al., 2018; Ellis, 2005). A meta-study showed that plants have a decreased concentration of N and P in the plant tissue caused by drought stress (He & Dijkstra, 2014). Moreover, multiple studies show that drought stress can lead to a decrease in nutrient uptake from the soil (Ge et al., 2012; Pinkerton & Simpson, 1986; Sardans & Peñuelas, 2012). Here is hypothesised that the effect of guano fertilization increases plant height and biomass. However, if nutrient uptake was reduced the effect may not have been measurable. This could be confirmed by comparing N and P levels of annual plants within and outside colonies in a stable isotope experiment (Dawson et al., 2002).

4.6 ADDITIONAL FACTORS

The guano potency itself is dependent on the concerned bird species. Zwolicki et al., 2013, revealed that tundras in Spitsbergen were affected differently by a piscivorous colony than by a planktivorous colony. The piscivores increase the phosphate content and pH value of the soil more strongly than the planktivores. In this research, no discrimination is made between the different types of bird colonies. It would be interesting to establish the bird species of a sampled colony to indicate the nutrient influx into the soil.

The amount of guano deposition determines the quantity of nutrients introduced into the soil, as well. The quantity of guano deposition is dependent on the daily rate of excrement production, which is a function of the colony size (Zwolicki et al., 2013). The colony size should be taken into consideration as an indication of the amount of introduced nutrients and the level of effect this may have on the vegetation in future research.

For this thesis, the organic matter content of the soil was determined. The organic matter content can be used as an indication of the nitrogen level in the soil (Parton et al., 1987; Schulte & Hoskins, 1995). Future research can use this conversion to create a nitrogen gradient over increasing distance to colony. And so clearly visualize the maximum distance to colony that is affected by guano fertilization.

5 CONCLUSION

This thesis aimed to elucidate the effect of guano fertilizations on the vegetation of the Dutch Wadden islands. This was systematically approached by answering three questions on how the distance colony and ecotope origin affect (1) the plant species composition, (2) the number of species and (3) the average plant height/root depth, and biomass. It can be concluded that most variation can be explained only by the ecotope effect, not the distance to colony. The effect of guano fertilisation may be equal over the first 150 meters from a colony. The ecotope determines species composition, average plant height, average root depth and biomass.

This research clearly illustrates the effect of ecotopes on island vegetation, but it also raises questions about the reach of the guano fertilization effect. Further research is needed to more in-depth determine the effects of guano fertilization. Hereby, an increased distance should be considered, divided into three zones rather than two. Sample size should be increased and equalised over ecotopes, and the effect of precipitation further investigated through stable isotope experiments.

The Wadden islands play an important role in coastal protection. The island vegetation determines the size and resilience of the islands. Vegetation is dependent on nutrient availability. Migratory shore- and seabirds provide a marine derived nutrient influx that may positively affect island morphology. This research has shown that the effect of guano fertilization on island vegetation is most likely dependent on more than only the distance to colony. Precipitation may influence the effectiveness of guano fertilization, and an increased distance should be taken into consideration to further elucidate the effect of guano fertilization. Furthermore, this research proved that ecotope origin has a strong effect on the island vegetation. This thesis has shown that the here chosen distances to colony do not affect the island vegetation, thereby contributing to filling the knowledge gap of the effect of distance to colony on guano fertilization on island vegetation.

6 REFERENCES

Adam, P. (1990). *Saltmarsh ecology*. Cambridge University Press. http://www.loc.gov/catdir/toc/cam031/89022188.html

Alihussein, A., Baaloudj, A., Benhamiche-Hanifi, S., LASSOUANE, N., & Moulaï, R. (2021). Does seabird guano affect plant physiology in insular ecosystem? *Studia Universitatis Vasile Goldis Arad, Seria Stiintele Vietii*, *31*, 11–22.

Anderson, W. B., & Polis, G. A. (1999). Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia*, *118*(3), 324–332. https://doi.org/10.1007/S004420050733

A.P. Oost, R. van Buren, & A. Kieftenburg. (2017). *Overview of the hydromorphology of ebb-tidal delta of the trilateral Wadden Sea | Deltares*. 11200926-000. https://www.waddensea-worldheritage.org/resources/overview-hydromorphology-ebb-tidal-delta-trilateral-wadden-sea

Araus, J. L., Slafer, G. A., Reynolds, M. P., & Royo, C. (2002). Plant Breeding and Drought in C3 Cereals: What Should We Breed For? *Annals of Botany*, *89*(7), 925. https://doi.org/10.1093/AOB/MCF049

Augustin, N. H., Sauleau, E. A., & Wood, S. N. (2012). On quantile quantile plots for generalized linear models. *Computational Statistics & Data Analysis*, *56*(8), 2404–2409. https://doi.org/10.1016/J.CSDA.2012.01.026

Avian nutrient pump - NIOZ. (n.d.). Retrieved 27 January 2023, from https://www.nioz.nl/en/research/uu-nioz-projects/avian-nutrient-pump

Avolio, M. L., Koerner, S. E., la Pierre, K. J., Wilcox, K. R., Wilson, G. W. T., Smith, M. D., & Collins, S. L. (2014). Changes in plant community composition, not diversity, during a decade of nitrogen and phosphorus additions drive above-ground productivity in a tallgrass prairie. *Journal of Ecology*, *102*(6), 1649–1660. https://doi.org/10.1111/1365-2745.12312

Bai, J., Zhang, G., Zhao, Q., Lu, Q., Jia, J., Cui, B., & Liu, X. (2016). *Depth-distribution patterns and control of soil organic carbon in coastal salt marshes with different plant covers OPEN*. https://doi.org/10.1038/srep34835

Barr, D. (2021). *Learning statistical models through simulation in R: An interactive textbook*.

Bates, D., Mächler, M., Zurich, E., Bolker, B. M., & Walker, S. C. (n.d.). *Fitting Linear Mixed-Effects Models Using lme4*. https://doi.org/10.18637/jss.v067.i01

Bedford, B. L., Walbridge, M. R., & Aldous, A. (1999). PATTERNS IN NUTRIENT AVAILABILITY AND PLANT DIVERSITY OF TEMPERATE NORTH AMERICAN WETLANDS. *Special Feature Ecology*, *80*(7), 2151–2169. https://doi.org/10.1890/0012-9658(1999)080[2151:PINAAP]2.0.CO;2

Benkwitt, C. E., Gunn, R. L., Le Corre, M., Carr, P., & Graham, N. A. J. (2021). Rat eradication restores nutrient subsidies from seabirds across terrestrial and marine ecosystems. *Current Biology : CB*, *31*(12), 2704-2711.e4. https://doi.org/10.1016/J.CUB.2021.03.104

Bista, D. R., Heckathorn, S. A., Jayawardena, D. M., Mishra, S., & Boldt, J. K. (2018). Effects of drought on nutrient uptake and the levels of nutrient-uptake proteins in roots of drought-sensitive and -tolerant grasses. *Plants*, *7*(2). https://doi.org/10.3390/PLANTS7020028

Blackburn, T. M., Petchey, O. L., Cassey, P., & Gaston, K. J. (2005). *Functional Diversity of Mammalian Predators and Extinction in Island Birds*. *86*(11), 2916–2923.

Boere, G. C., & Piersma, T. (2012). Flyway protection and the predicament of our migrant birds: A critical look at international conservation policies and the Dutch Wadden Sea. *Ocean & Coastal Management*, *68*, 157–168. https://doi.org/10.1016/J.OCECOAMAN.2012.05.019

Bradford, K. J., & Hsiao, T. C. (1982). Physiological responses to moderate water stress. *Physiological Plant Ecology II: Water Relations and Carbon Assimilation*, 263–324.

Braun-Blanquet, J., & others. (1932). Plant sociology. The study of plant communities. *Plant Sociology. The Study of Plant Communities. First Ed.*

Buchanan, J. B., & Longbottom, M. R. (1970). The determination of organic matter in marine muds: The effect of the presence of coal and the routine determination of protein. *Journal of Experimental Marine Biology and Ecology*, *5*(2), 158–169. https://doi.org/https://doi.org/10.1016/0022-0981(70)90014-6

Buelow, C. A., Baker, R., Reside, A. E., & Sheaves, M. (2018). *Nutrient subsidy indicators predict the presence of an avian mobile-link species*. https://doi.org/10.1016/j.ecolind.2018.02.029

Burger, J., Niles, L., & Clark, K. E. (1997). IMPORTANCE OF BEACH, MUDFLAT AND MARSH HABITATS TO MIGRANT SHOREBIRDS ON DELAWARE BAY. *Biological Conservation*, *79*, 283–292.

Burnham, K. P. (1998). Model selection and multimodel inference. *A Practical Information-Theoretic Approach*.

Ciccarelli, D. (2015). Mediterranean coastal dune vegetation: Are disturbance and stress the key selective forces that drive the psammophilous succession? *Estuarine, Coastal and Shelf Science*, *165*, 247–253. https://doi.org/https://doi.org/10.1016/j.ecss.2015.05.023

Cowles, H. C. (1899). The ecological relations of the vegetation on the sand dunes of Lake Michigan [Continued]. *Botanical Gazette*, *27*(3), 167–202.

Dawson, T. E., Mambelli, S., Plamboeck, A. H., Templer, P. H., & Tu, K. P. (2002). Stable Isotopes in Plant Ecology. *Annual Review of Ecology and Systematics*, *33*(1), 507–559. https://doi.org/10.1146/annurev.ecolsys.33.020602.095451

de Groot, A. V, Oost, A. P., Veeneklaas, R. M., Lammerts, E. J., van Duin, W. E., & van Wesenbeeck, B. K. (2017). Tales of island tails: biogeomorphic development and management of barrier islands. *Journal of Coastal Conservation*, *21*, 409–419.

de Schrijver, A., de Frenne, P., Ampoorter, E., van Nevel, L., Demey, A., Wuyts, K., & Verheyen, K. (2011). Cumulative nitrogen input drives species loss in terrestrial ecosystems. *Global Ecology and Biogeography*, *20*(6), 803–816. https://doi.org/10.1111/J.1466-8238.2011.00652.X

Dean, W. R. J., Milton, S. J., Ryan, P. G., & Moloney, C. L. (1994). The role of disturbance in the establishment of indigenous and alien plants at Inaccessible and Nightingale Islands in the South Atlantic Ocean. *Vegetatio*, *113*(1), 13–23. https://doi.org/10.1007/BF00045460

Durán, O., & Moore, L. J. (2013). Vegetation controls on the maximum size of coastal dunes. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(43), 17217–17222. https://doi.org/10.1073/PNAS.1307580110/ASSET/19991A8E-35EC-49F3-B12A-7EBC1F89A8C8/ASSETS/GRAPHIC/PNAS.1307580110I88.GIF

Ellis, J. C. (2005). Marine Birds on Land: A Review of Plant Biomass, Species Richness, and Community Composition in Seabird Colonies. *Plant Ecology*, *181*(2), 227–241. http://www.jstor.org.proxy.library.uu.nl/stable/20146837

Everitt, B. (1998). The cambridge dictionary of statistics cambridge university press. *Cambridge, UK Google Scholar*.

Fisher, R. A. (1936). The use of multiple measurements in taxonomic problems. *Annals of Eugenics*, *7*(2), 179–188.

García, L. v., Marañón, T., Ojeda, F., Clemente, L., & Redondo, R. (2002). Seagull influence on soil properties, chenopod shrub distribution, and leaf nutrient status in semi-arid Mediterranean islands. *Oikos*, *98*(1), 75–86. https://doi.org/10.1034/J.1600-0706.2002.980108.X

Ge, T. da, Sun, N. B., Bai, L. P., Tong, C. L., & Sui, F. G. (2012). Effects of drought stress on phosphorus and potassium uptake dynamics in summer maize (Zea mays) throughout the growth cycle. *Acta Physiologiae Plantarum*, *34*(6), 2179–2186. https://doi.org/10.1007/S11738-012-1018-7

Geyer, W. R., Morris, J. T., Prahl, F. G., & Jay, D. A. (2000). Coastal biogeomorphology: an integrated approach to understanding the evolution, morphology, and sustainability of temperate coastal marshes. *Estuarine Science: A Synthetic Approach to Research and Practice*, 177–206.

Gillham, M. E. (1960). Destruction of indigenous heath vegetaion in Victorian sea-bird colonies. *Australian Journal of Botany*, *8*(3), 277–317. https://doi.org/10.1071/BT9600277

Glass, G. v, Peckham, P. D., & Sanders, J. R. (1972). Consequences of Failure to Meet Assumptions Underlying the Fixed Effects Analyses of Variance and Covariance. *Review of Educational Research*, *42*(3), 237–288. https://doi.org/10.3102/00346543042003237

Godfrey, P. J. (1977). Climate, Plant Response and Development of Dunes on Barrier Beaches along the U.S. East Coast by. *Int. J. Biometeor*, *21*(3), 203–215.

Govers, L., & Reijers, V. (2021). *Griend - Een bewogen eiland* (1st ed.). KNNV Uitgeverij, Zeist.

He, M., & Dijkstra, F. A. (2014). Drought effect on plant nitrogen and phosphorus: a meta-analysis. *New Phytologist*, *204*(4), 924–931. https://doi.org/10.1111/NPH.12952

Hesp, P. A. (1991). Ecological processes and plant adaptations on coastal dunes. *Journal of Arid Environments*, *21*(2), 165–191. https://doi.org/https://doi.org/10.1016/S0140-1963(18)30681-5

Hogg, E. H., & Morton, J. K. (1983). The effects of nesting gulls on the vegetation and soil of islands in the Great Lakes. *Canadian Journal of Botany*, *61*(12), 3240–3254. https://doi.org/10.1139/b83-361

Hogg, E. H., Morton, J. K., & Venn, J. M. (1989). Biogeography of island floras in the Great Lakes. I. Species richness and composition in relation to gull nesting activities. *Canadian Journal of Botany*, *67*(4), 961–969. https://doi.org/10.1139/b89-128

Home | Beeldmateriaal Nederland. (n.d.). Retrieved 15 March 2023, from https://www.beeldmateriaal.nl/

Homepage | Convention on Wetlands. (n.d.). Retrieved 17 January 2023, from https://www.ramsar.org/

Houser, C., Wernette, P., Rentschlar, E., Jones, H., Hammond, B., & Trimble, S. (2015). *Post-storm beach and dune recovery: Implications for barrier island resilience*. https://doi.org/10.1016/j.geomorph.2014.12.044

Huang, L., Dong, B. C., Xue, W., Peng, Y. K., Zhang, M. X., & Yu, F. H. (2013). Soil Particle Heterogeneity Affects the Growth of a Rhizomatous Wetland Plant. *PLoS ONE*, *8*(7). https://doi.org/10.1371/JOURNAL.PONE.0069836

Iamond, J. M. D. (1989). The present, past and future of human-caused extinctions. *Trans. R. Soc. Land. B*, *325*, 469–476. https://royalsocietypublishing.org/

Ishida, A. (1996). Effects of the common cormorant, Phalacrocorax carbo, on evergreen forests in two nest sites at Lake Biwa, Japan. *Ecological Research*, *11*(2), 193–200. https://doi.org/10.1007/BF02347685/METRICS

KNMI - Zomer 2022 (juni, juli, augustus). (n.d.). Retrieved 26 January 2023, from https://www.knmi.nl/nederland-nu/klimatologie/maand-en-seizoensoverzichten/2022/zomer

Lensink, R., van der Have, T. M., van der Haterd, R. J., Inberg, J. A., Soes, D. M., & Achterkamp, B. (2015). *Alien species on the Dutch Wadden Sea Islands*.

Leyrer, J., Frikke, J., Hälterlein, B., Koffijberg, K., Körber, P., & Reichert, G. (2019). *Managing Predation Risk for Breeding Birds in the Wadden Sea: Results from a Workshop in Tönning, Schleswig-Holstein, 7-8 March 2017*. Common Wadden Sea Secretariat.

Lotze, H. K. (2005). Radical changes in the Wadden Sea fauna and flora over the last 2,000 years. *Helgoland Marine Research*, *59*(1), 71–83. https://doi.org/10.1007/S10152-004-0208-0/FIGURES/9

Lundberg, J., & Moberg, F. (2003). Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. *Ecosystems*, *6*(1), 87–98. https://doi.org/10.1007/S10021-002-0150-4/METRICS

Maciej Serda, Becker, F. G., Cleary, M., Team, R. M., Holtermann, H., The, D., Agenda, N., Science, P., Sk, S. K., Hinnebusch, R., Hinnebusch A, R., Rabinovich, I., Olmert, Y., Uld, D. Q. G. L. Q., Ri, W. K. H. U., Lq, V., Frxqwu, W. K. H., Zklfk, E., Edvhg, L. v, … (2016). فاطمی, ح. Environmental impacts: Coastal ecosystems. *Uniwersytet Śląski*, *7*(1), 275–314. https://doi.org/10.2/JQUERY.MIN.JS

Martínez, M. L., & Vázquez, G. (n.d.). *COASTAL SAND DUNES AND BARRIER ISLANDS*.

Masero, J. A., Perez-Hurtado, A., Casas, M. C., & Arroyo, G. M. (2000). *Complementary use of intertidal mudflats and adjacent salinas by foraging waders The role of long-chain polyunsaturated fatty acids in animal migration (CGL2017-89009-P) View project Foraging ecology, body condition, and regulation of reproductive decisions in Seabirds View project*. https://www.researchgate.net/publication/258452260

Mayer, L. M. (1994). Relationships between mineral surfaces and organic carbon concentrations in soils and sediments. *Chemical Geology*, *114*(3), 347–363. https://doi.org/https://doi.org/10.1016/0009-2541(94)90063-9

McInnes, K. L., Walsh, K. J. E., Hubbert, G. D., & Beer, T. (2003). Impact of sea-level rise and storm surges in a coastal community. *Natural Hazards*, *30*(2), 187–207. https://doi.org/10.1023/A:1026118417752/METRICS

Meltofte, H., Blew, J., Frikke, J., Rosner, H.-U., & Smit, C. J. (1994). Numbers and distribution of waterbirds in the Wadden Sea. *Wader Study Group Bulletin, Special Issue*, *74*, 3–3.

Millar, R. B., & Holst, R. (1997). Estimation of gillnet and hook selectivity using log-linear models. *ICES Journal of Marine Science*, *54*(3), 471–477.

Monteiro, L. R., Ramos, J. A., & Furness, R. W. (1996). Past and present status and conservation of the seabirds breeding in the Azores Archipelago. *Biological Conservation*, *78*(3), 319–328. https://doi.org/10.1016/S0006-3207(96)00037-7

Mulder, C. P. H., & Keall, S. N. (2001). Burrowing Seabirds and Reptiles: Impacts on Seeds, Seedlings and Soils in an Island Forest in New Zealand. *Oecologia*, *127*(3), 350–360. http://www.jstor.org.proxy.library.uu.nl/stable/4222940

Mullins, E., Moore, L. J., Goldstein, E. B., Jass, T., Bruno, J., & Durán Vinent, O. (2019). Investigating dune-building feedback at the plant level: Insights from a multispecies field experiment. *Earth Surface Processes and Landforms*, *44*(9), 1734–1747. https://doi.org/https://doi.org/10.1002/esp.4607

Norton, D. A., Delange, P. J., Garnock-Jones, P. J., & Given, D. R. (1997). The role of seabirds and seals in the survival of coastal plants: lessons from New Zealand Lepidium (Brassicaceae). *Biodiversity & Conservation*, *6*(6), 765–785. https://doi.org/10.1023/B:BIOC.0000010401.93153.29

ObsIdentify is een app die al het leven kent - NRC. (n.d.). Retrieved 15 February 2023, from https://www.nrc.nl/nieuws/2022/02/10/obsidentify-is-een-app-die-al-het-leven-kent-a4087283

Oksanen, J. (2022, October 11). *Vegan: ecological diversity*. https://cran.r-project.org/web/packages/vegan/vignettes/diversity-vegan.pdf

Parton, W. J., Schimel, D. S., Cole, C. v., & Ojima, D. S. (1987). Analysis of Factors Controlling Soil Organic Matter Levels in Great Plains Grasslands. *Soil Science Society of America Journal*, *51*(5), 1173–1179. https://doi.org/10.2136/SSSAJ1987.03615995005100050015X

Payne, R. J., Dise, N. B., Stevens, C. J., Gowing, D. J., Duprè, C., Dorland, E., Gaudnik, C., Bleeker, A., Diekmann, M., Alard, D., Bobbink, R., Fowler, D., Corcket, E., Mountford, J. O., Vandvik, V., Aarrestad, P. A., & Muller, S. (2013). Impact of nitrogen deposition at the species level. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(3), 984–987. https://doi.org/10.1073/PNAS.1214299109/ASSET/F6100ED8-A25F-4944-8365-7EACAC40A187/ASSETS/GRAPHIC/PNAS.1214299109FIG02.JPEG

Pickart, A. J., Maslach, W. R., Parsons, L. S., Jules, E. S., Reynolds, C. M., & Goldsmith, L. M. (2021). Comparing Restoration Treatments and Time Intervals to Determine the Success of Invasive Species Removal at Three Coastal Dune Sites in Northern California, U.S.A. *Https://Doi-*

Org.Proxy.Library.Uu.Nl/10.2112/JCOASTRES-D-20-00085.1, *37*(3), 557–567. https://doi.org/10.2112/JCOASTRES-D-20-00085.1

Piersma, T., Lok, T., Chen, Y., Hassell, C. J., Yang, H. Y., Boyle, A., Slaymaker, M., Chan, Y. C., Melville, D. S., Zhang, Z. W., & Ma, Z. (2016). Simultaneous declines in summer survival of three shorebird species signals a flyway at risk. *Journal of Applied Ecology*, *53*(2), 479–490. https://doi.org/10.1111/1365-2664.12582

Pinkerton, A., & Simpson, J. R. (1986). Interactions of surface drying and subsurface nutrients affecting plant growth on acidic soil profiles from an old pasture. *Australian Journal of Experimental Agriculture*, *26*(6), 681–689. https://doi.org/10.1071/EA9860681

Polis, G. A., & Hurd, S. D. (1995). Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences of the United States of America*, *92*(10), 4382–4386. https://doi.org/10.1073/PNAS.92.10.4382

Purbajanti, E., Slamet, W., Fuskhah, E., & Rosyida, R. (2019). Effects of organic and inorganic fertilizers on growth, activity of nitrate reductase and chlorophyll contents of peanuts (Arachis hypogaea L.). *IOP Conference Series: Earth and Environmental Science*, *250*, 012048. https://doi.org/10.1088/1755-1315/250/1/012048

Qu, H., Zhao, H., Zhou, R., Zuo, X., Wang, J., Li, J., & Orr, B. J. (2012). Effects of sand burial stress on maize (’Zea mays’ L.) growth and physiological responses. *Australian Journal of Crop Science*, *6*(5), 869–876. https://search.informit.org/doi/10.3316/informit.733010698065679

Rabinowitz, G. B. (1975). An Introduction to Nonmetric Multidimensional Scaling. *American Journal of Political Science*, *19*(2), 343–390. https://doi.org/10.2307/2110441

Reijers, V. C., Lammers, C., de Rond, A. J. A., Hoetjes, S. C. S., Lamers, L. P. M., & van der Heide, T. (2020). Resilience of beach grasses along a biogeomorphic successive gradient: resource availability vs. clonal integration. *Oecologia*, *192*(1), 201–212. https://doi.org/10.1007/S00442-019-04568-W/FIGURES/4

Reijers, V., Govers, L., Heide, T., Temmink, R., Bouma, T., Luna Murillo, B., Nauta, J., Heusinkveld, J., Gräfnings, M., Hijner, N., Lamers, L., Christianen, M., Penning, E., fivash, greg, Smeele, Q., Zwarts, M., Hoeijmakers, D., Wiersema, H., Lengkeek, W., & Eijk, A. (2020, September 1). Op Griend gaat de natuur voor. *De Levende Natuur*, 156–175. https://www.researchgate.net/publication/344751181_Op_Griend_gaat_de_natuur_voor

Rezk, M. R. (1970). Vegetation Change from a Sand Dune Community to a Salt Marsh as Related to Soil Characters in Mariut District, Egypt. *Oikos*, *21*(2), 341–343. https://doi.org/10.2307/3543692

Rogers, E. D., & Benfey, P. N. (2015). Regulation of plant root system architecture: implications for crop advancement. *Current Opinion in Biotechnology*, *32*, 93–98. https://doi.org/10.1016/J.COPBIO.2014.11.015

Ryan, P. G., & Watkins, B. P. (1989). The Influence of Physical Factors and Ornithogenic Products on Plant and Arthropod Abundance at an Inland Nunatak Group in Antarctica. *Polar Biol*, *10*, 151–160.

Santana-Sagredo, F., Schulting, R. J., Méndez-Quiros, P., Vidal-Elgueta, A., Uribe, M., Loyola, R., Maturana-Fernández, A., Díaz, F. P., Latorre, C., McRostie, V. B., Santoro, C. M., Mandakovic, V., Harrod, C., & Lee-Thorp, J. (2021). 'White gold' guano fertilizer drove agricultural intensification in the Atacama Desert from ad 1000. *Nature Plants*, *7*(2), 152–158. https://doi.org/10.1038/s41477-020-00835-4

Sardans, J., & Peñuelas, J. (2012). Focus Issue on the Plant Physiology of Global Change: The Role of Plants in the Effects of Global Change on Nutrient Availability and Stoichiometry in the Plant-Soil System. *Plant Physiology*, *160*(4), 1741. https://doi.org/10.1104/PP.112.208785

Schat, H., & van Beckhoven, K. (1991). Water as a stress factor in the coastal dune system. In J. Rozema & J. A. C. Verkleij (Eds.), *Ecological responses to environmental stresses* (pp. 76–91). Springer Netherlands. https://doi.org/10.1007/978-94-009-0599-3_8

Schulte, E. E., & Hoskins, B. (1995). Recommended soil organic matter tests. *Recommended Soil Testing Procedures for the North Eastern USA. Northeastern Regional Publication*, *493*, 52–60.

Simon, M. (2011). Tidal Flats. In J. Reitner & V. Thiel (Eds.), *Encyclopedia of Geobiology* (pp. 880–883). Springer Netherlands. https://doi.org/10.1007/978-1-4020-9212-1_208

Soil Organic Matter and its Importance for Water Management | STOWA. (n.d.). Retrieved 12 March 2023, from https://www.stowa.nl/deltafacts/zoetwatervoorziening/delta-facts-english-versions/soil-organic-matter-and-its-importance

Suding, K. N., Collins, S. L., Gough, L., Clark, C., Cleland, E. E., Gross, K. L., Milchunas, D. G., & Pennings, S. (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(12), 4387–4392. https://doi.org/10.1073/PNAS.0408648102/SUPPL_FILE/08648TABLE3.HTML

Timmerman, A., Haasnoot, M., Middelkoop, H., Bouma, T., & Mcevoy, S. (2021). *NC-ND license Ecological consequences of sea level rise and flood protection strategies in shallow coastal systems: A quick-scan barcoding approach*. https://doi.org/10.1016/j.ocecoaman.2021.105674

Towns, D. R., & Broome, K. G. (2010). From small Maria to massive Campbell: Forty years of rat eradications from New Zealand islands. *Http://Dx.Doi.Org.Proxy.Library.Uu.Nl/10.1080/03014223.2003.9518348*, *30*(4), 377–398. https://doi.org/10.1080/03014223.2003.9518348

Trilateral Working Group on Coastal Protection and Sea Level Rise (CPSL). (2001). Coastal Protection and Sea Level Rise Final Report. *Wadden Sea Ecosystem*, *13*.

Tukey, J. W. (1949). One Degree of Freedom for Non-Additivity. *Biometrics*, *5*(3), 232. https://doi.org/10.2307/3001938

Tyson, R. (1994). *Sedimentary Organic Matter : Organic Facies and Palynofacies*. Springer Netherlands. http://ebookcentral.proquest.com/lib/uunl/detail.action?docID=3109077

US Department of Commerce, N. O. and A. A. (n.d.). *What is a barrier island?*

van Roomen, M., Laursen, K., van Turnhout, C., van Winden, E., Blew, J., Eskildsen, K., Günther, K., Hälterlein, B., Kleefstra, R., Potel, P., Schrader, S., Luerssen, G., & Ens, B. J. (2012). Signals from the Wadden sea: Population declines dominate among waterbirds depending on intertidal mudflats. *Ocean & Coastal Management*, *68*, 79–88. https://doi.org/10.1016/J.OCECOAMAN.2012.04.004

Veerman, C. P. (Cornelis P., & Deltacommissie. (2008). *Working together with water. A living land builds for its future. Findings of the Deltacommissie 2008*. http://inis.iaea.org/Search/search.aspx?orig_q=RN:40061497

Vermeer, J. G., & Berendse, F. (1983). The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. *Vegetatio*, *53*(2), 121–126. https://doi.org/10.1007/BF00043032

Vidal, E., Jouventin, P., & Frenot, Y. (2003). Contribution of alien and indigenous species to plant-community assemblages near penguin rookeries at Crozet archipelago. *Polar Biology*, *26*(7), 432–437. https://doi.org/10.1007/S00300-003-0500-5

Vidal, E., Médail, F., Tatoni, T., & Bonnet, V. (2000). Seabirds drive plant species turnover on small Mediterranean islands at the expense of native taxa. *Oecologia*, *122*, 427–434.

Vidal, E., Médail, F., Tatoni, T., Roche, P., & Vidal, P. (1998). Impact of gull colonies on the flora of the Riou archipelago (Mediterranean islands of south-east France). *Biological Conservation*, *84*(3), 235–243. https://doi.org/https://doi.org/10.1016/S0006-3207(97)00130-4

Vidal, E., Médail, F., Tatoni, T., Vidal, P., & Roche, P. (1998). Functional analysis of the newly established plants induced by nesting gulls on Riou archipelago (Marseille, France). *Acta Oecologica*, *19*(3), 241–250. https://doi.org/https://doi.org/10.1016/S1146-609X(98)80028-3

Wait, D. A., Aubrey, D. P., & Anderson, W. B. (2005). Seabird guano influences on desert islands: soil chemistry and herbaceous species richness and productivity. *Journal of Arid Environments*, *60*, 681–695. https://doi.org/10.1016/j.jaridenv.2004.07.001

Wang, Z. B., Elias, E. P. L., van der Spek, A. J. F., & Lodder, Q. J. (2018). Sediment budget and morphological development of the Dutch Wadden Sea: impact of accelerated sea-level rise and subsidence until 2100. *Netherlands Journal of Geosciences*, *97*(3), 183–214. https://doi.org/10.1017/NJG.2018.8

Wang, Z. B., Hoekstra, P., Burchard, H., Ridderinkhof, H., de Swart, H. E., & Stive, M. J. F. (2012). Morphodynamics of the Wadden Sea and its barrier island system. *Ocean & Coastal Management*, *68*, 39–57. https://doi.org/10.1016/J.OCECOAMAN.2011.12.022

Welkom - Waarnemingen.be. (n.d.). Retrieved 25 January 2023, from https://waarnemingen.be/

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563

Woodroffe, C. D. (2002). *Coasts: Form, Process and Evolution*.

Yu, M., Hu, G., Feeley, K. J., Wu, J., & Ding, P. (2012). Richness and composition of plants and birds on land-bridge islands: Effects of island attributes and differential responses of species groups. *Journal of Biogeography*, *39*(6), 1124–1133. https://doi.org/10.1111/J.1365-2699.2011.02676.X

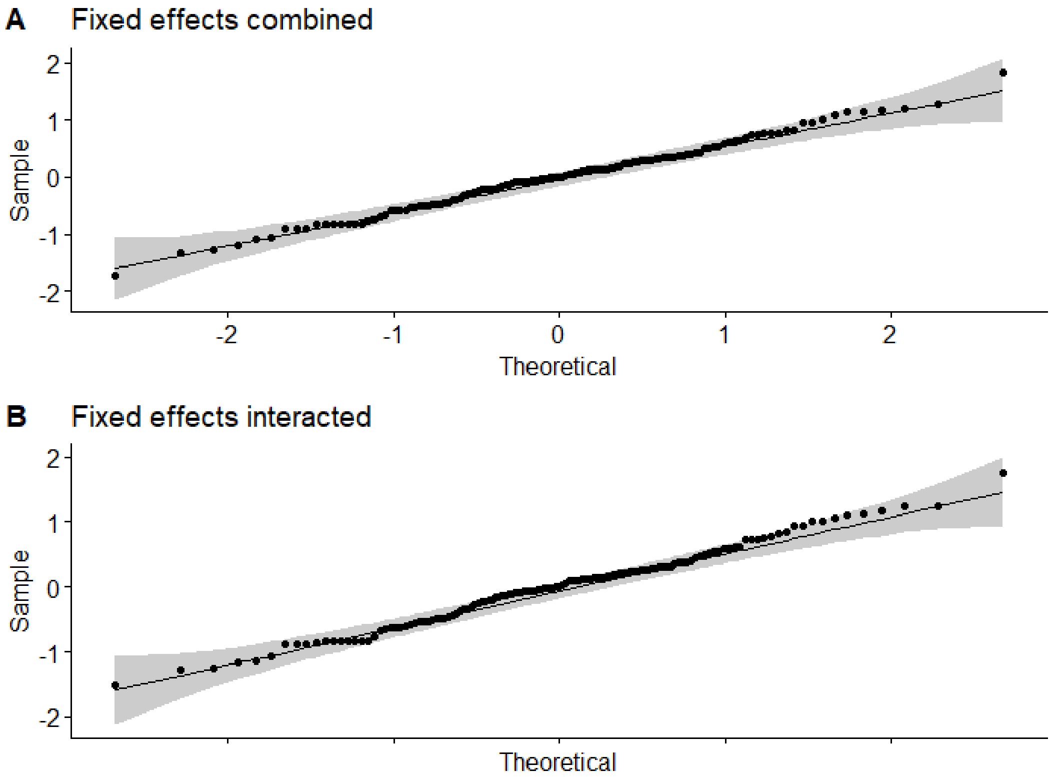
Zarnetske, P. L., Hacker, S. D., Seabloom, E. W., Ruggiero, P., Killian, J. R., Maddux, T. B., & Cox, D. (2012). Biophysical feedback mediates effects of invasive grasses on coastal dune shape. *Ecology*, *93*(6), 1439–1450. https://doi.org/10.1890/11-1112.1

Zwolicki, A., Zmudczyńska-Skarbek, K. M., Iliszko, L., & Stempniewicz, L. (2013). Guano deposition and nutrient enrichment in the vicinity of planktivorous and piscivorous seabird colonies in Spitsbergen. *Polar Biology*, *36*(3), 363–372. https://doi.org/10.1007/S00300-012-1265-5/TABLES/3

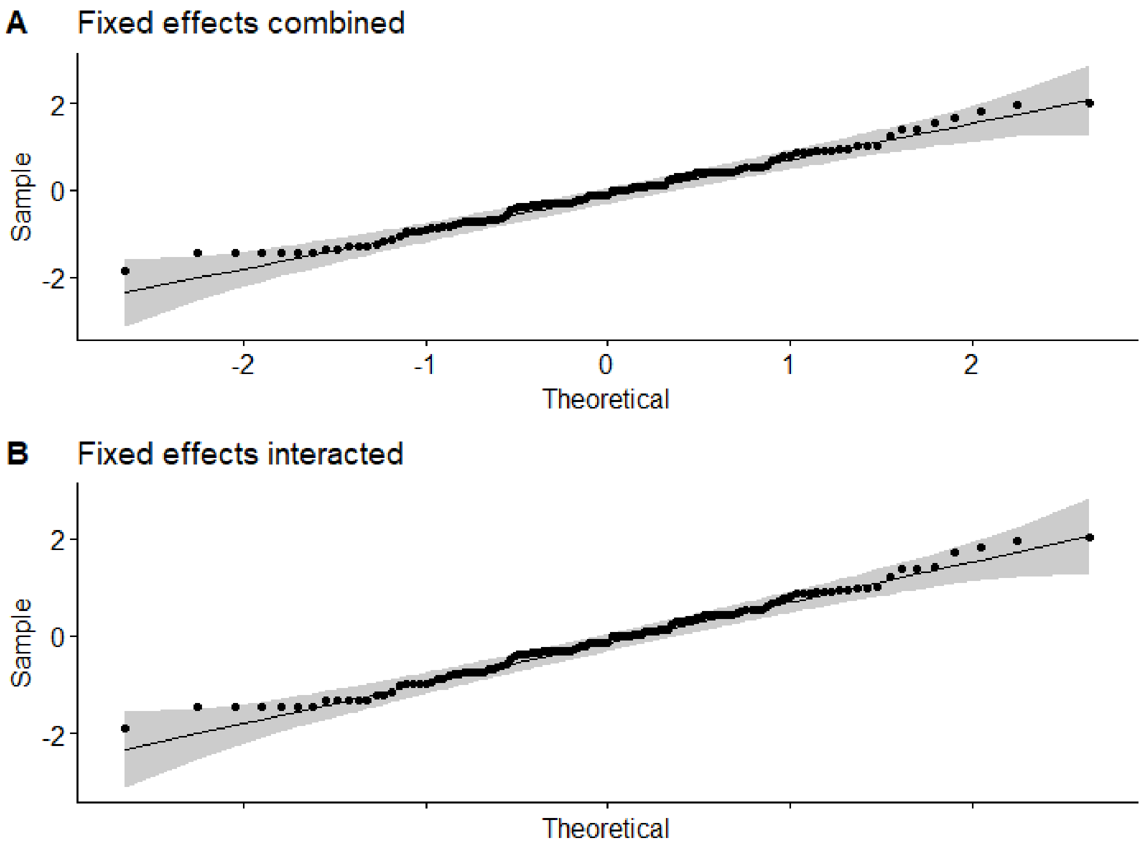
7 APPENDIX

Appendix table 1 - The AIC values of all outcome variables per model type, combined or interacting fixed effects. The lowest AIC value represents the most fitting model. The values are similar due to the random effect.

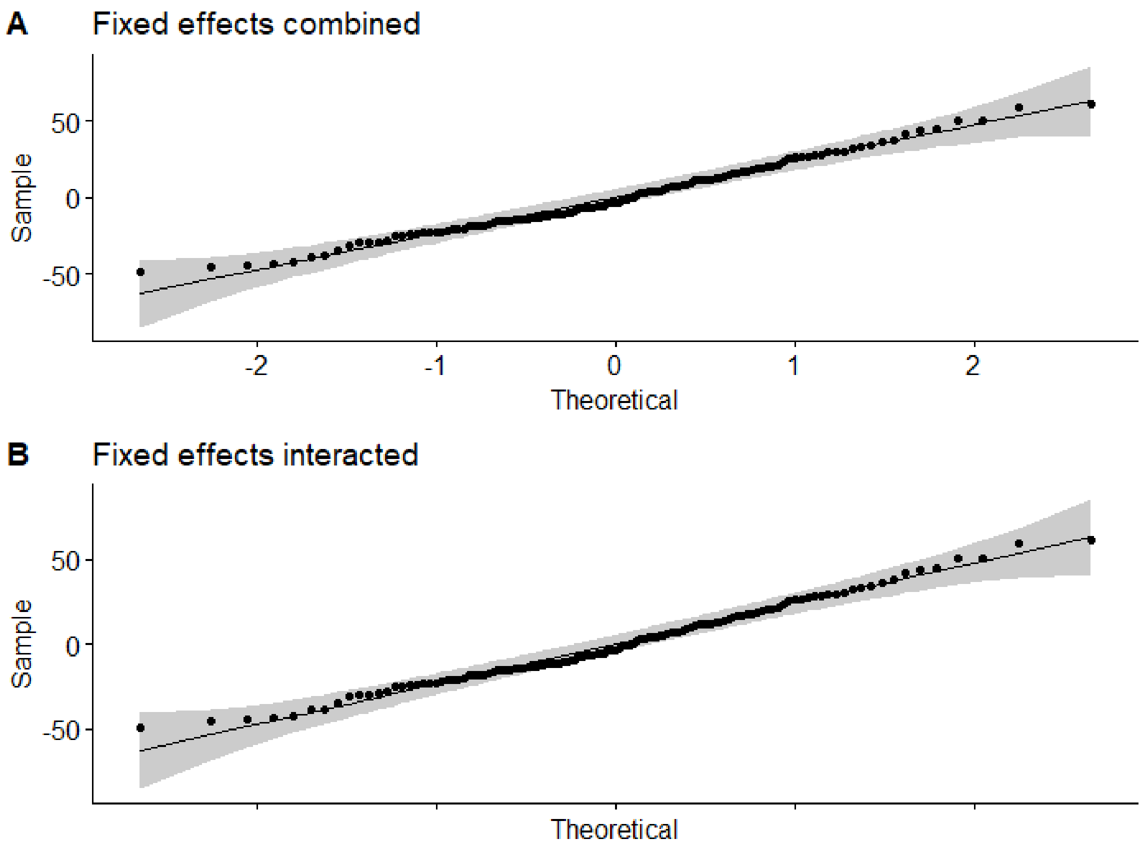
		AIC values				
Fixed effect(s) ↓	**outcome variable ⟶**	**NMDS1**	**Species richness**	**Average plant height**	**Average root depth**	**Biomass**
Combined fixed effects		316.92	523.20	1133.41	926.9	316.92
Interacting fixed effects		317.63	525.25	1128.75	930.58	317.63



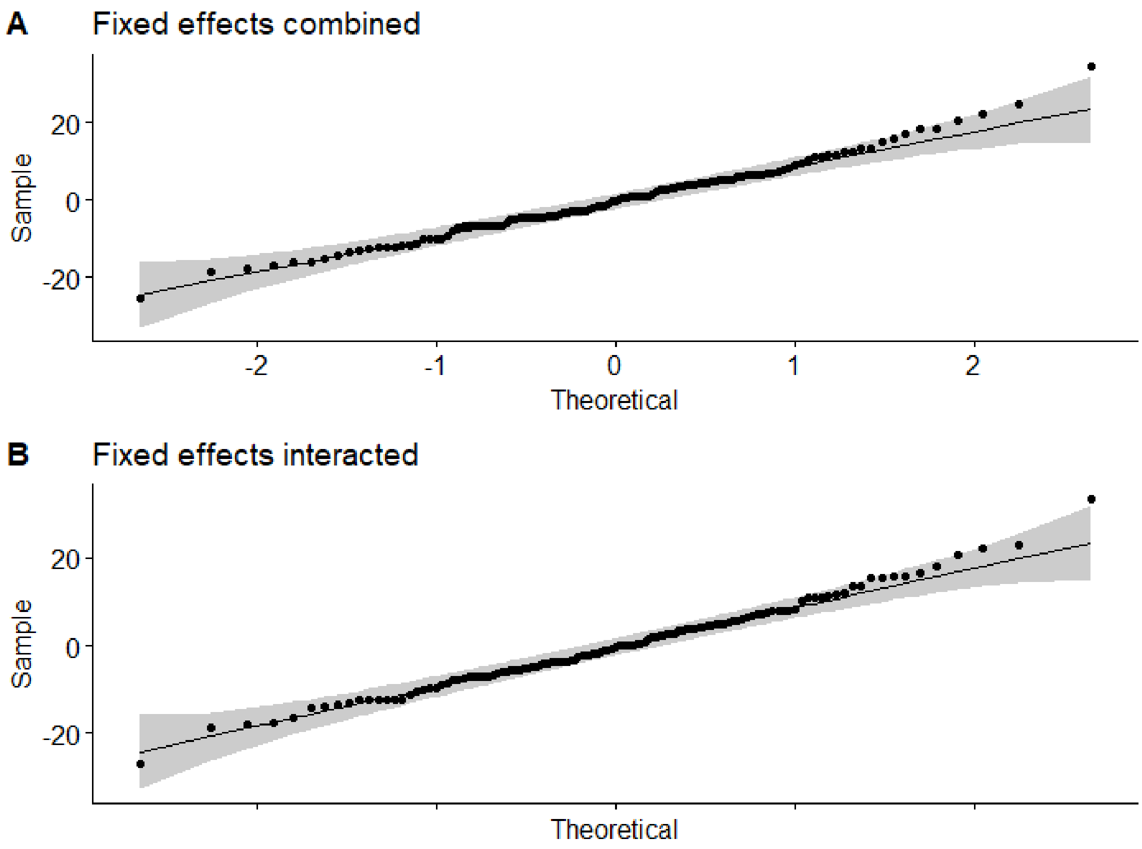
Appendix graph 1 - Q-Q plot of LMER residual with outcome variable NMDS1, the residuals are normally distributed, although the distance to colony fixed effect shows a deviation at the end.



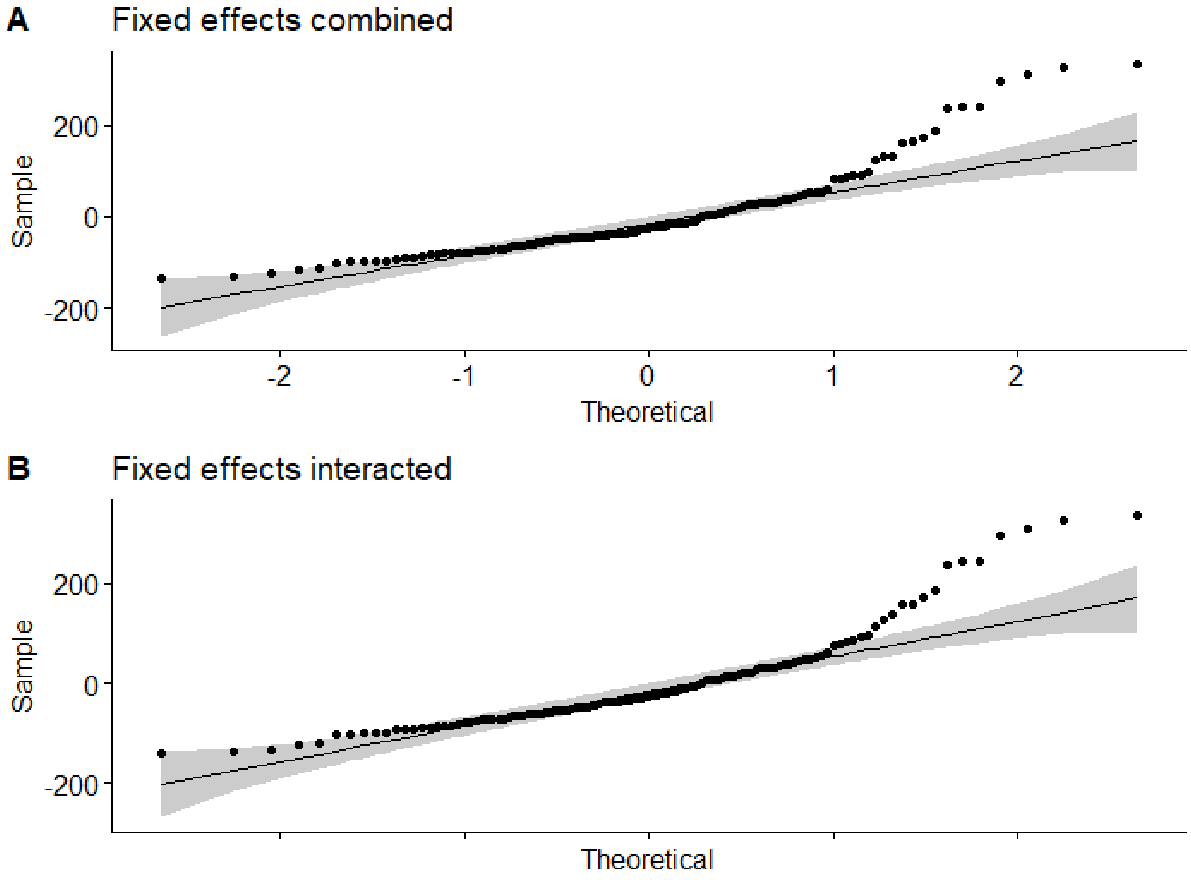
Appendix graph 2 - Q-Q plots of glmer models with outcome variable species richness, the residuals are normally distributed.



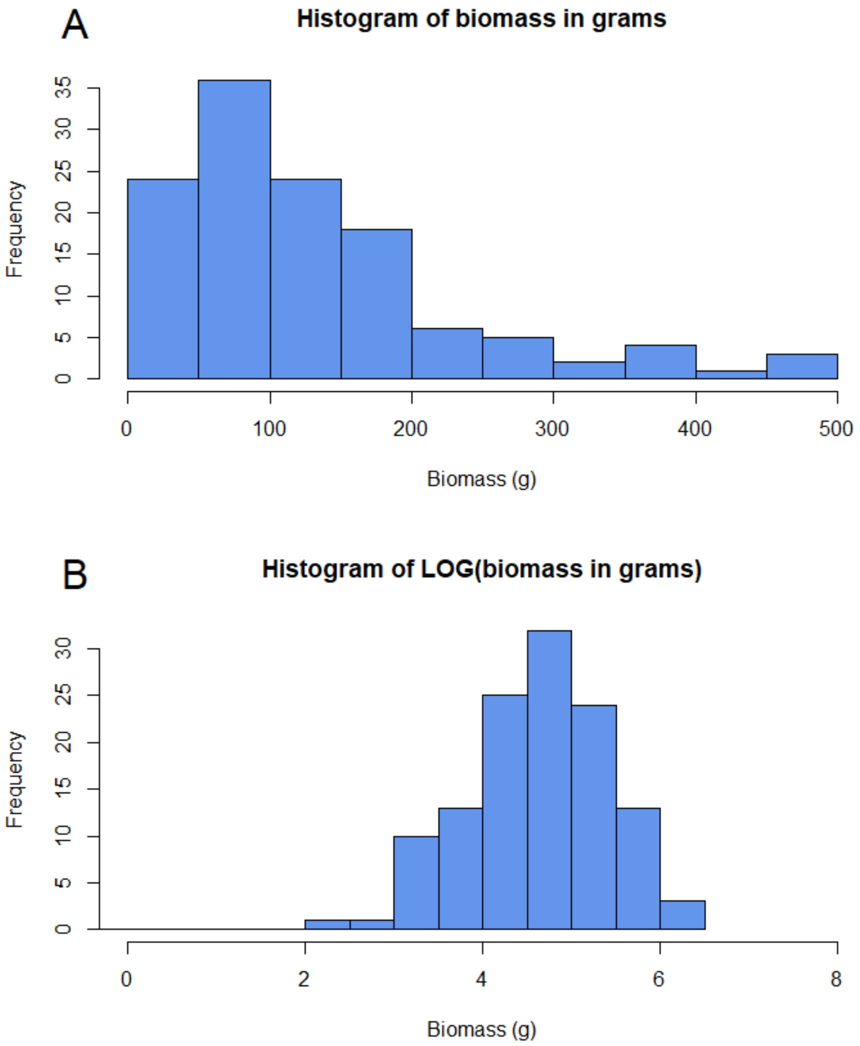
Appendix graph 3 - Q-Q plots of LMER models with outcome variable average plant height, the residuals are normally distributed.



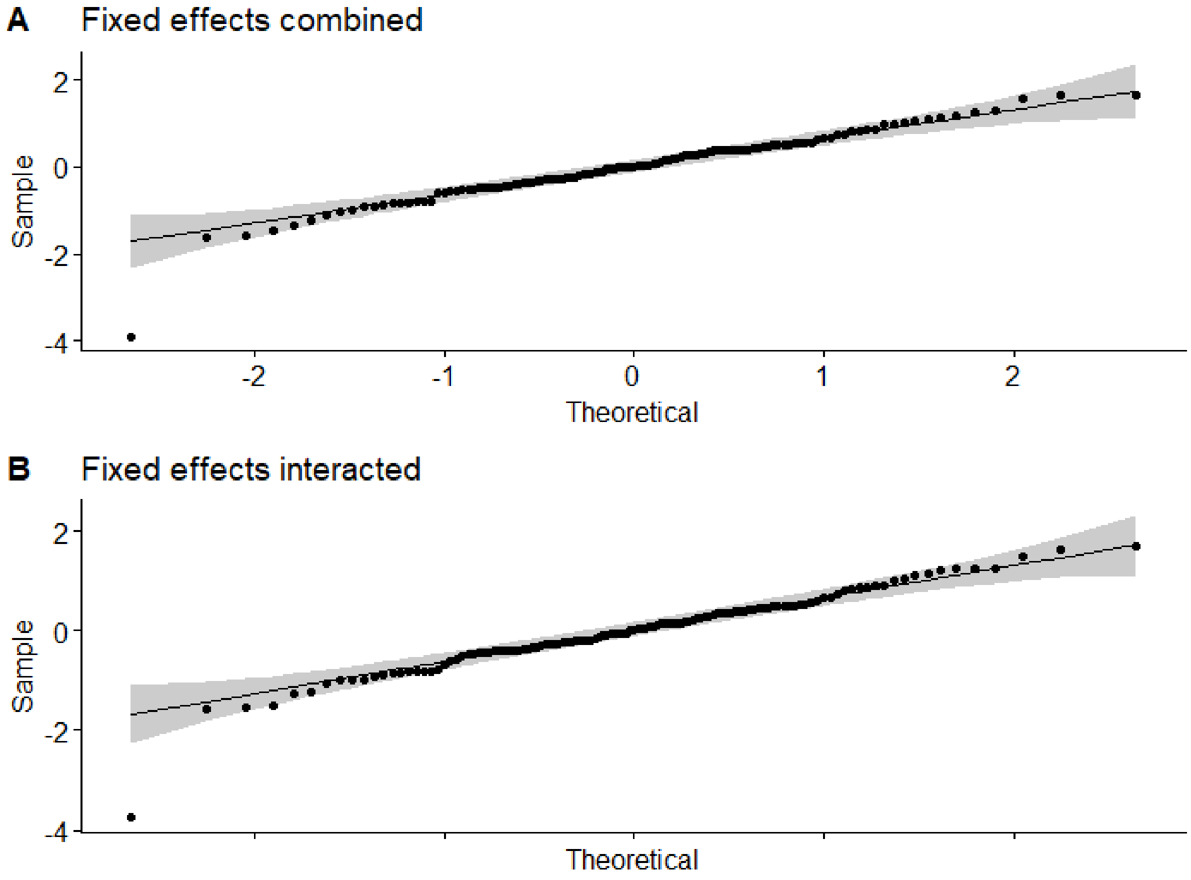
Appendix graph 4 - Q-Q plots of LMER models with the outcome variable average root length, the residuals are normally distributed.



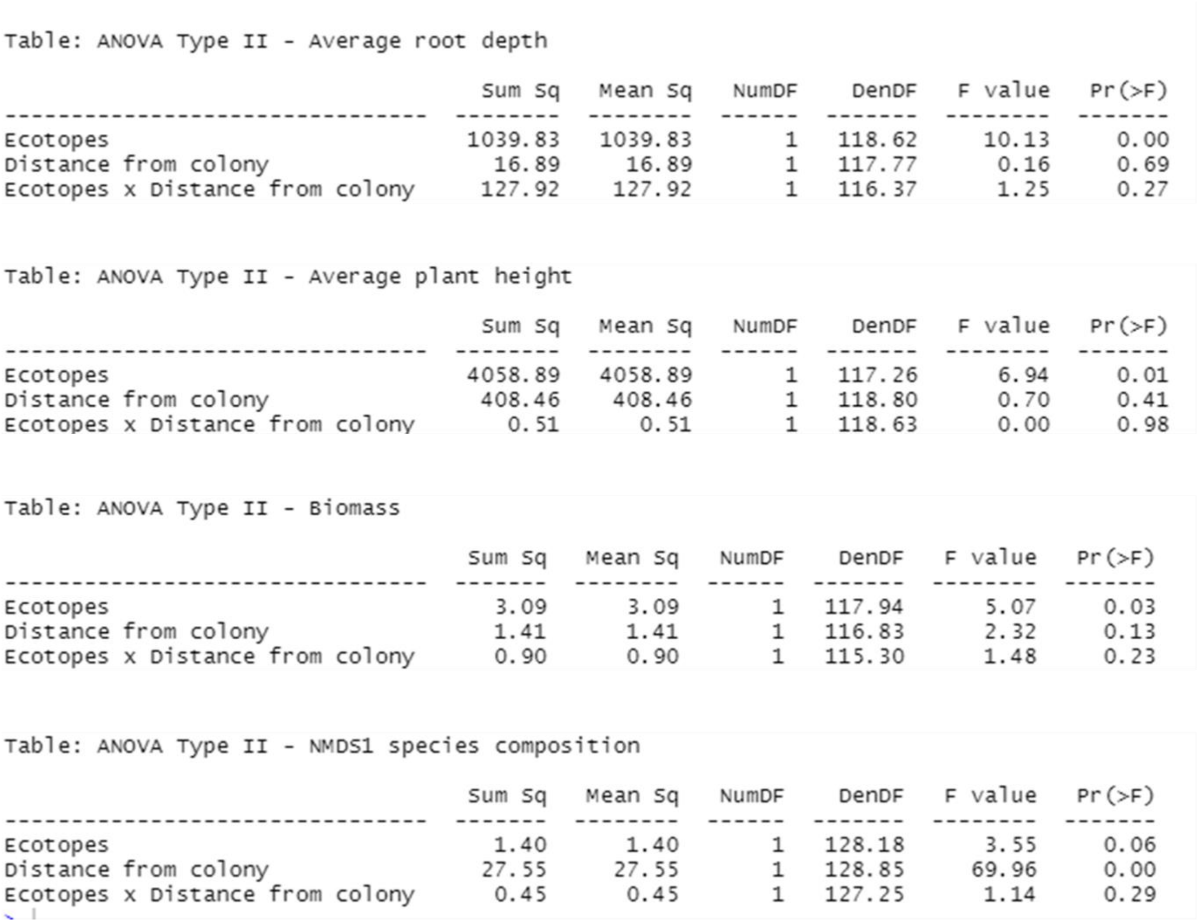
Appendix graph 5 - Q-Q plots of LMER models with outcome variable biomass, the residuals are not normally distributed.



Appendix graph 6 - A) Histogram of the biomass, positively skewed. B) Histogram of the log of the biomass, normally distributed.

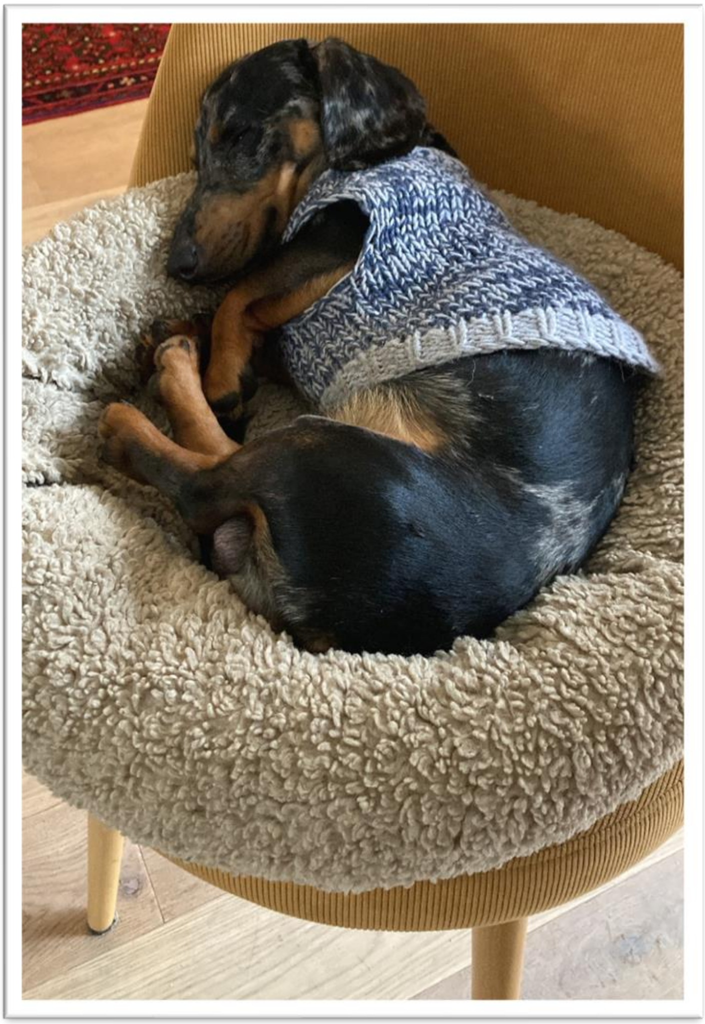


Appendix graph 7 - Q-Q plots of LMER models with outcome variable LOG(biomass), the residuals are normally distributed.



```
Table: ANOVA Type II - Average root depth

                                    Sum Sq   Mean Sq   NumDF     DenDF   F value    Pr(>F)
--------------------------------  --------  --------  ------   -------  --------   -------
Ecotopes                           1039.83   1039.83       1    118.62     10.13      0.00
Distance from colony                 16.89     16.89       1    117.77      0.16      0.69
Ecotopes x Distance from colony     127.92    127.92       1    116.37      1.25      0.27


Table: ANOVA Type II - Average plant height

                                    Sum Sq   Mean Sq   NumDF     DenDF   F value    Pr(>F)
--------------------------------  --------  --------  ------   -------  --------   -------
Ecotopes                           4058.89   4058.89       1    117.26      6.94      0.01
Distance from colony                408.46    408.46       1    118.80      0.70      0.41
Ecotopes x Distance from colony       0.51      0.51       1    118.63      0.00      0.98


Table: ANOVA Type II - Biomass

                                   Sum Sq   Mean Sq   NumDF     DenDF   F value    Pr(>F)
--------------------------------  -------  --------  ------   -------  --------   -------
Ecotopes                             3.09      3.09       1    117.94      5.07      0.03
Distance from colony                 1.41      1.41       1    116.83      2.32      0.13
Ecotopes x Distance from colony      0.90      0.90       1    115.30      1.48      0.23


Table: ANOVA Type II - NMDS1 species composition

                                   Sum Sq   Mean Sq   NumDF     DenDF   F value    Pr(>F)
--------------------------------  -------  --------  ------   -------  --------   -------
Ecotopes                             1.40      1.40       1    128.18      3.55      0.06
Distance from colony                27.55     27.55       1    128.85     69.96      0.00
Ecotopes x Distance from colony      0.45      0.45       1    127.25      1.14      0.29
```

Appendix graph 8 – A compilation of the ANOVA results of average root depth, average plant height, biomass and NMDS1 – species composition.



Appendix figure 1 – Arnold Tuijnman, companion of the author. Here asleep on his chair, a common sight during the creation of this thesis.