SEABIRD MEDIATED LINK BETWEEN MARINE AND TERRESTRIAL ECOSYSTEMS

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DECLARATION OF AUTHORSHIP

I hereby declare that this thesis has been composed by me and it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others.

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ABSTRACT

The meta-ecosystem concept describes spatial coupling of ecosystems through flows of energy material and organisms across ecosystem boundaries. Mobile species can act as biotic vectors to facilitate the movement of these items between ecosystems and can be essential to maintaining the meta-ecosystem. Global biodiversity and species movement are under increasing pressures of anthropogenic activity. A greater understanding of how mobile species influence the functioning of the meta-ecosystem will provide a better insight to how changes in one ecosystem may influence coupled ecosystems across landscapes. Throughout this thesis I use the marine-terrestrial meta-ecosystem connected by the seabird great skua as a model system to investigate this.

I use a combination of observational and manipulation experiments to determine the effects on plant nutrient assimilation, soil processes, plant community assemblage and dynamics and invertebrate community assemblage. I show that great skuas transport large quantities of essential plant nutrients into the terrestrial ecosystem through faeces and pellets. This feeds into plant nutrition regardless of species and life history traits and potentially reduces the reliance of heather and tormentil on mycorrhizae symbionts for nutrient acquisition. This nutrient deposition has little influence over the functioning of the soil biota: the increase in soil nutrient pools varied, mineralization was unaffected by great skua abundance and the rate of decomposition and nutrient release from litter was largely determined by the litter quality rather than where the litter was buried. This also indicates that plants are accessing nutrients rapidly and directly from faeces through abiotic pathways and the excess is lost through surface run-off or leached through the soil. Above ground I demonstrated that this increased nutrient availability and disturbance both play a role in rapidly shifting the plant community from dwarf shrub and tall acid grassland communities to short, ruderal, graminoid dominated communities. In addition, I demonstrate that in areas of elevated great skua abundance invertebrate communities are characterised by a greater abundance of detritivorous orders, a greater abundance of small predatory ground beetles and a lower abundance of predatory orders such as spiders and large immobile ground beetle relative to areas of low great skua abundance. I use joint species modelling to demonstrate that increases in great skua disturbance is associated with lower abundance of less mobile species, whist reductions in vegetation structure are associated with lower abundance or large mobile species, but greater abundance of small fast bodied species. Interestingly my work highlighted a temporal coupling of the marine and terrestrial ecosystem. Exposing plant communities to a lower abundance of great skuas caused a decline in leaf nitrogen concentration across all species, but phosphorus concentration did not change and increased in some species. In addition, plant communities did not change substantially over three years.

This work demonstrate how great skuas influence the key processes and functions in the terrestrial ecosystem. This is particularly relevant in light of recent changes to fisheries management in the EU, which is predicted to influence scavenging seabirds such as great skuas and negatively impact their ability to function as link species between the marine and terrestrial ecosystems. My results suggest that this will cause a reduced availability of inorganic nutrients in the soil. The plant community composition is will be slow to respond to this, and grass and ruderal species will remain dominant. Whilst there will be corresponding declines in nitrogen cycling in the terrestrial ecosystem, it is anticipated that phosphorus cycling will remain high. In addition, is predicted that the abundance of invertebrate species that were strongly influenced by direct disturbance will likely increase. However, those that are more influenced by vegetation structure such as spiders only recolonise once plant community composition recovers.

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CHAPTER 1

GENERAL INTRODUCTION

Coupled Ecosystems

Ecological studies primarily focus on interaction between species and their abiotic environment within ecosystems, however, there is growing recognition of the importance of processes over multiple temporal and spatial scales. An ecosystem is defined in the Convention of Biological Diversity as a dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit (United Nations, 1992). Boundaries between ecosystems occur where there is a gradual or abrupt change in environmental conditions and a related shift in biotic communities (Banks-Leite and Ewers, 2009). However, ecosystems are rarely closed, and organisms, materials and energy can flow across these boundaries, with potential consequences for the interactions within the recipient or host ecosystem. Inter-ecosystem interactions are usually weaker than intra-ecosystem interactions. The strength of these inter-ecosystem interactions are regulated by factors such as the size, shape and similarity of the ecosystems, the distance between them, and relative differences in productivity as well as permeability of the ecosystem boundaries to organisms, materials and energy (Polis, Anderson and Holt, 1997).

Ecosystems can interact through biogeochemical processes and the movement of species. Ecosystem boundaries are less of a barrier to mobile species, which can travel large distances in search of improved foraging, safety or reproductive opportunities (Alerstam, Hedenström and Åkesson, 2003). In doing so, they can directly interact with local trophic structures by increasing herbivory, providing supplementary prey or depredating local species. Furthermore, mobile species can act as biotic vectors, transporting parasites, propagules and nutrients from one ecosystem to another (Bauer and Hoye, 2014). The continuous movement of species between ecosystems can result in them becoming coupled whereby the functioning of recipient populations or ecosystems is regulated by frequent, predictable pulses of subsidies, disruption or services delivered by the mobile species. This has given rise to the concept of meta-ecosystems, where, similar to the idea of “meta-populations” and “meta-communities”, multiple ecosystems are considered in one functional unit (Loreau, Mouquet and Holt, 2003). Under this conceptual framework, sink ecosystems exist in an alternative stable state, that is reliant on the interaction with the source ecosystem (Beisner, Haydon and Cuddington, 2003) (see Figure 1.1).

Mobile species acting as a link to couple ecosystems have been identified in several environments around the world. Snow geese *Anser caerulescens antlanticus* L. (Kennard, 1927) couple farmland productivity in temperate regions and arctic fox *Vulpes lagopus* (Linnaeus, 1758) populations in the Arctic. Snow geese migrate between winter foraging grounds in temperate farmland and summer breeding grounds in arctic tundra. Eggs and chicks provide a secondary prey resource for resident arctic foxes, decreasing territory size and increasing reproductive success adjacent to the breeding colony. In addition, this food subsidy is particularly important in years when lemming (*Lemmus trimucronathus* (Kerr 1792) and *Dicrostonyx greoenlandicus* (Traill, 1823)) abundance (the primary prey source for Arctic foxes) is low, buffering the fox population from local declines in prey availability and coupling them to temperate farmland productivity (Giroux *et al.*, 2012). Herbivorous wildebeest *Connochaetes taurinus* (Burchell, 1823) couple grassland productivity. During the rainy season, wildebeest move from grazing wooded grasslands in the north of the Serengeti to calf and raise young on the highly nutritious but ephemeral short grass plains in the south. Theoretical modelling shows that this high intensity grazing, followed by low intensity grazing during the main growing season (the rainy season), is key to maintaining the wooded grassland productivity and ecosystem fertility, coupling this to the productivity of the short grassland plains via wildebeest (Holdo *et al.*, 2007). Migratory lesser long nosed bats *Leptonycteris yerbabuenae* (Martinez & Villa-R, 1940) couple discrete patches of desert vegetation. During their migration between southern USA and Mexico, lesser long nosed bats consume nectar from columnar cacti, agave and morning glory trees located near roosts. This provides them with energy and in doing so they pollinate the plants, mediating high levels of genetic diversity throughout their migration route. Cacti are key stone species in desert ecosystems, providing a water source and nutrients for many species, therefore, the bats facilitate the persistence of a large portion of the ecosystem (Nabhan, 2004; Hamerick et al. 2002). Finally, hippopotamus *Hippopotamus amphibius* (Linneaus, 1958) couple terrestrial productivity and aquatic systems. Hippos graze in the terrestrial ecosystem and use water bodies during the day to aid thermoregulation. In doing so they excrete large quantities of organic matter into the freshwater environment. The effect of this allochthonous nutrient subsidy is situation dependent. In flowing water, where organic matter becomes dilute it supports freshwater consumers (Masese *et al.*, 2015). However, in unconnected pools, the organic matter concentrates and enters water courses during flushing events which causes hypoxia, killing fish (Dutton *et al.*, 2018).

These examples demonstrate that the movement of species are be essential to maintaining populations, community composition, productivity and ecosystem functions and services. Global changes, from habitat destruction and invasive species to anthropogenic climate change as well as over exploitation of resources are posing increasing threats to biodiversity. These can directly impair the functioning of the mobile species in the meta-ecosystem by, for example, decreasing the population sizes of mobile species in source ecosystems, reducing their influence over sink ecosystems or by directly restricting the movement of populations and individuals between ecosystems (see figure 1.1) (Wilcove and Wikelski, 2008). These actions can also act indirectly on the function of mobile species. For example, red knot *Calidris canutus* (Linaeus, 1758) couple tropical winter foraging grounds and arctic summer breeding grounds, where chicks feed on arthropods emerging from defrosting tundra soil. Climate change is causing early snow melt at breeding grounds, which decreases arthropod body size and abundance as well as causing earlier emergence decoupling peak arthropod numbers from red knot hatching dates. This has negative effects on fledgling body size and, specifically, bill length. Juveniles are still able to make the migration, however, once they reach the winter coastal foraging grounds, they are unable to reach molluscs buried in inter-tidal sediments and switch to eating seagrass rhizomes (Van Gils *et al.*, 2016). The change in knot diet is likely to influence the mollusc and seagrass abundance with effects potentially cascading throughout the ecosystem. Therefore, studies that focus on how meta-ecosystems function and the role that mobile species play are vital to gaining a better insight to how actions in one ecosystem or at a local scale can cascade into coupled ecosystems and influence whole landscapes. Throughout this thesis I use the marine-terrestrial meta-ecosystem as a model system to investigate this.

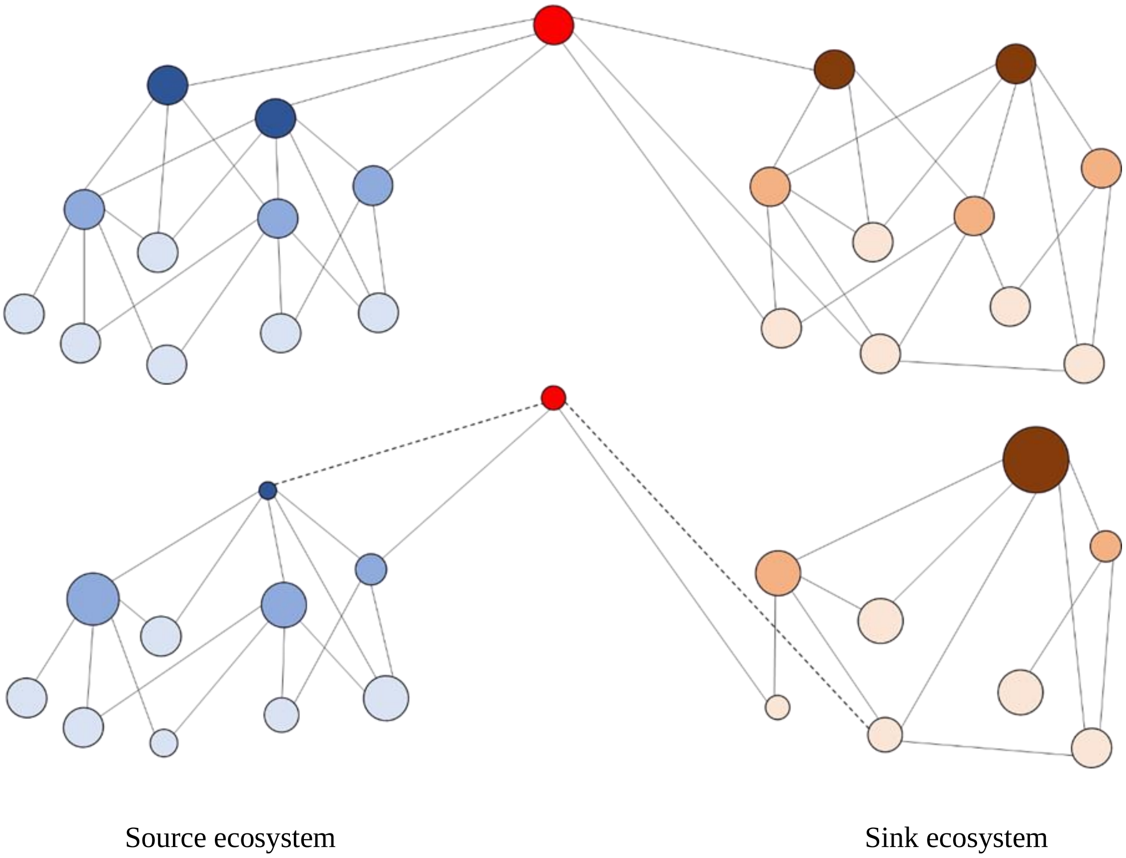


Figure 1.1. Ecosystems coupled by a mobile link species. Blue and brown circles represent biotic communities and environmental factors and the lines represent interactions between these. The two ecosystems are coupled by a mobile link species represented by the red circle. When there is a change in a resource availability in the source ecosystem which influences the mobile link species, there will be associated changes in sink ecosystem (adapted from Figure 5 Bauer and Hoye, 2014).

Links between the marine and terrestrial ecosystems

Globally, there is an estimated 594,000 km of coastline, where marine and terrestrial ecosystems abut (Polis and Hurd, 1996). Materials and nutrients can flow from the terrestrial to the marine ecosystem via geophysical processes such as the water cycle. As a result catchment-scale land management modifications in the terrestrial environment can influence marine ecosystems. For example, historical clearing and overstocking of farmland in eastern Australia caused increased nutrient and sediment loads in freshwater environments and contributed to the declining health of the Great Barrier Reef (McCulloch *et al.*, 2003). Abiotic exchanges of materials from marine to terrestrial ecosystems, however, are limited to windblown sea spray and seaweed and carrion deposited in the supralittoral zone (Polis and Hurd, 1996; Bokhorst *et al.*, 2007). Whilst decomposing seaweed can support a dense assemblage of arthropod consumers (up to 560 times that found in land), which in turn could influence species at higher trophic levels, neither of these process are likely to have far reaching effects in the terrestrial ecosystem (Polis and Hurd, 1996; Bokhorst *et al.*, 2007; Cross *et al.*, 2014).

Seabirds and anadromous fish (that migrate from freshwater to the sea) represent biotic links between marine and terrestrial ecosystems (Polis and Hurd, 1996; Ellis, 2005; Holtgrieve and Schindler, 2011 etc.). Both taxa spend a large part of their life cycles in the marine environment, feeding almost exclusively on marine resources and migrate to coastal terrestrial ecosystems to raise young and the heads of freshwater streams to spawn and die, respectively. In doing so they transport considerable amounts marine derived nutrients and energy, via excreta, reproductive materials (such as eggs) and carrion, across the marine-terrestrial interface, which can influence local terrestrial ecosystems.

Pacific salmon species have been shown to increase water nitrogen and phosphorus concentrations in spawning streams by 190% and 390%, respectively. Whilst in some freshwater systems this fertilization influences phytoplankton community composition, there is no corresponding increase primary productivity; rather migratory salmon shift stream metabolism from an autotrophic to a heterotrophic pathway (Chen *et al.*, 2011; Holtgrieve and Schindler, 2011). Salmon nest building activity reduces algal biomass and therefore primary productivity, but mobilizes sediment in the water column, which in combination with increased nutrients, promotes heterotrophs and secondary productivity (Moore and Schindler, 2008; Holtgrieve and Schindler, 2011). In addition, this disturbance has also been linked to shifts in stream invertebrate phenology (Moore and Schindler, 2010). Furthermore, by providing an abundant food source for American black bears *Ursus americanus* (Pallas, 1780) and brown bears *Ursus arctos* (Linnaeus, 1758), Pacific salmon species also influence the riparian ecosystem surrounding the stream. Marine derived nutrients promote terrestrial primary productivity and contribute approximately 20% of foliar nitrogen in shrubs and spruce trees up to 500 m from the stream and have been identified in herbivorous small mammals (Ben-David, Schell and Hanley, 1998; Hilderbrand *et al.*, 1999; Helfield and Naiman, 2001). Therefore, salmon couple marine and freshwater ecosystems and their influence on terrestrial riparian ecosystems is mediated by bear predation and activity. While the case of Pacific salmon linking marine and terrestrial environments, via freshwater ecosystems and bears, is one of the iconic examples of coupled ecosystems, seabirds are another prime example of how marine ecosystems can affect terrestrial ecosystems. Furthermore, because seabirds act as direct mobile link species (i.e. marine-terrestrial interactions via seabirds do not operate via freshwater ecosystems, nor a further species such as bears), seabirds provide a tighter, more controlled, test for how changes in one ecosystem than impact on another.

Seabirds as mobile link species

There are an estimated 261 million pairs of seabirds worldwide (Riddick *et al.*, 2012), all of which feed at sea but rear young on land. Seabirds are long-lived k-selected species with strong breeding site fidelity and high investment in rearing young (Furness, 2003), therefore, colonies are occupied for long periods within a year and used repeatedly over many years. This represents a potentially huge annual mobilization of marine derived nutrients onto the land via faeces, carrion, feathers, reproductive material and chick and adult carcasses (Ellis, 2005). The combination of marine derived nutrient depositions and disturbance in the terrestrial ecosystem have the potential to influence basal ecosystem functions such as nutrient cycling and plant nutrient assimilation as well as plant community composition, the effects of which can cascade through ecosystem to influence species at higher trophic levels. As such seabird can be considered mobile link species, connecting the marine and terrestrial ecosystems.

Bioenergetic models estimate that seabirds transport approximately 1,100 Gg of marine derived nitrogen per year into the terrestrial ecosystem worldwide through excreta alone (Riddick *et al.*, 2012). The level of marine derived nutrient deposition during the breeding season will in part determine the extent of the effect of seabirds on terrestrial ecosystems especially in remote coastal locations where there are few anthropogenic nutrient sources (Polis, Anderson and Holt, 1997; Wilson et al., 2004). Nutrient deposition is influenced by the species that is being studied as the concentration of nutrients in the faeces is determined by the size of the bird, individual metabolic rates and diet (Bryant and Furness, 1995; Wilson et al., 2004; Cross, 2014; Zwolicki et al., 2016). Furthermore, the amount of faeces deposited is by length of the breeding season and the amount of time spent in the terrestrial ecosystem (Wilson et al., 2004; Blackall et al., 2007; Riddick et al., 2012; Cross, 2014; Zwolicki et al., 2016). Bioenergetic models have been used to estimate the level of nutrient deposition in a year (e.g. Cross, 2014), however this has rarely been measured in the field. Accurate measures of species-specific seabird nutrient inputs in a system is essential to the interpretation of the role of seabirds in the functioning of the meta-ecosystem.

Marine nutrient deposition by seabirds can have major influences on the functioning and composition of terrestrial ecosystems (Lindeboom, 1984; Wilson et al., 2004). To influence terrestrial ecosystems, marine derived nutrients need to be retained in the bulk soil or assimilated by abiotic communities such as plants and soil microbes. In general, soils around seabird colonies are enriched with marine derived nutrients, which in turn increases leaf nutrient concentration (Hogg and Morton, 1983; Anderson and Polis, 1999; Croll, 2005; Ellis, Fariña and Witman, 2006; Maron et al., 2006; Callaham Jr. et al., 2012; Kolb, Palmborg and Hambäck, 2013; Kolb et al., 2015). However, several studies have identified species specific responses in leaf nutrient concentrations to seabird colonies, potentially relating to plant species growth forms, traits and life histories, which are known to influence nutrient acquisition, storage and use (Grime, 1977; Aerts and Chapin, 2000; Mulder and Keall, 2001; Havik, Catenazzi and Holmgren, 2014). Given that leaf nutrient concentrations are key determinants of a plant species functional role within the ecosystem, it is important to understand how individual plant species respond to marine nutrient deposition to determine the influence on terrestrial ecosystems (Grime et al., 1997; Aerts and Chapin, 2000; Wardle et al., 2004).

Plant and soil nutrient concentrations influence the speed of nutrient cycling (Wardle *et al.*, 2004). One way in which nutrients in living plant material are returned below ground is by the decomposition of dead plant material. The soil fauna, flora and microbes that comprise the decomposer community physically and chemically break down the litter to simple organic compounds and inorganic nutrients. These are either released into the environment (mineralization) or retained within the decomposer community (immobilization), depending on the individual organism’s nutritional requirements (BassiriRad, 2005; Moore *et al.*, 2006). In most terrestrial ecosystems the activity of the decomposer community and therefore the speed of decomposition is nutrient limited (Vitousek and Howarth, 1991). In theory, marine nutrient deposition by seabirds has the potential to subsidise the activity of the decomposer community through both elevated available nutrients in the soil and nutrients in the plant litter, enhancing decomposition and nutrient mineralization rates (Swift, Heal and Anderson, 1979; Bardgett *et al.*, 1999; Vesterdal, 1999; Wardle *et al.*, 2004; de Vries *et al.*, 2006; Parton *et al.*, 2007; Hobbie, 2008; Kobe, Lepczyk and Iyer, 2009). However, in seabird colonies there are currently few empirical studies to support this theory. Wardle et al. (2009) found that when rats reduced seabird abundance, the rate of nitrogen but not phosphorus cycling declined. Furthermore, Hawke and Vallance (2015) identified carbon limitation in the microbial community in seabird colonies and suggested that it was indicative of rapid decomposition and mineralization of fresh plant litter and mineralization of soil organic matter. However, neither Wright *et al.* (2010) nor Durrett *et al.*

(2014) identified any significant effect of marine derived nutrients on either ammonium or nitrate mineralization rates. There are therefore major gaps in our knowledge of how marine-derived nutrients impact these fundamental below-ground processes of decomposition, mineralisation and nutrient availability.

These below-ground processes and the rate of nutrient cycling can influence plant nutrient availability, which, in combination with the direct disturbance caused by seabirds in their colony, can influence plant species communities and productivity. In general, seabird colonies support plant communities at an early stage of succession, dominated by fast-growing, annual species (Croll, 2005; Ellis, Fariña and Witman, 2006; Baumberger et al., 2012; Zwolicki et al., 2016). Despite these studies demonstrating the link between seabirds and plant communities, the relative roles of nutrient deposition and disturbance in regulating the plant community composition is unclear. Several studies have focused on the effect of nutrient subsidies alone. Stable isotope analysis has identified the presence of marine derived nutrients in plant material; fertilization experiments resulted in a decline in dwarf shrub species in favour of graminoid species, similar to that observed in seabird colonies; and, phytomere experiments have identified toxic levels of ammonium in seabird colonies, restricting germination (Mulder and Keall, 2001; Croll, 2005; Ellis, Fariña and Witman, 2006; Maron *et al.*, 2006; Kolb, Jerling and Hambäck, 2010; Molina-Montenegro *et al.*, 2013; Zwolicki *et al.*, 2016). Others suggest that increases in species richness and plant cover at abandoned colonies and at intermediate distances from colonies highlights that disturbance and marine nutrient deposition interact to plant community composition (Hogg and Morton, 1983; Vidal et al., 2000; Ellis, Fariña and Witman, 2006). In addition, there are few studies that explore how changes in seabird abundance in the terrestrial ecosystem influence plant community dynamics. Plant community assemblage and dynamics regulate a number of key ecosystem processes and species at higher trophic levels, therefore, gaining a better insight of how specific seabird species influence these is key to understanding their function in linking the marine and terrestrial ecosystems.

Direct disturbance, carrion subsidies, and the effect of seabirds on plant communities, structure and nutrient concentrations have the potential to cascade through the terrestrial ecosystem and influence invertebrate community composition (e.g. Siemann *et al.*, 1998; Knops *et al.*, 1999; Wimp *et al.*, 2010; Hoekman *et al.*, 2011). The effects of seabirds on invertebrate communities appear to be dependent on the species of seabird, the geographical location and the effect on plants (Towns *et al.*, 2009; Kolb *et al.*, 2012; Bassett *et al.*, 2014). For example, increases in plant productivity, nutrient run-off into adjacent freshwater habitats and carrion subsidies in seabird colonies increase detritivores and scavenger invertebrate biomass (Sanchez-Pinero and Polis, 2000; Kolb, Jerling and Hambäck, 2010; Kolb *et al.*, 2012). This represents a large potential prey resource for predatory species. However, invertebrate predator abundance can be influenced by changes in plant communities and habitat complexity due to decreased predation efficiency and because they become more vulnerable to predation themselves (Langellotto and Denno, 2004). On arid islands, where seabirds promote vegetation cover, there is a corresponding increase in spider biomass (Polis and Hurd, 1995; Wait, Aubrey and Anderson, 2005). However, in a separate study, where high seabird nest densities inhibited plant growth, there was no corresponding increases in web building spider abundance and the abundance of Lycosid (wolf) spider declined (Kolb, Jerling and Hambäck, 2010; Kolb *et al.*, 2012). Although there is evidence that seabirds do influence the invertebrate communities more work is needed to identify the relative roles of direct disturbance, changes in vegetation structure and species composition and provision of food sources in regulating invertebrate community assemblage. This would provide a better understanding how seabirds function within the marine-terrestrial meta-ecosystem to influence the invertebrate community.

Shetland and great skuas as a model system

Great skuas are an ideal seabird species for testing the meta-ecosystem concept, linking marine and terrestrial ecosystems because, unlike the majority of seabirds in the UK, they form breeding colonies inland and nest on the ground. Consequently, faeces and carrion and therefore, marine derived nutrients are deposited directly into the terrestrial ecosystem. In addition, great skuas can cause considerable amounts of disturbance in areas of high use, through trampling and territorial fighting as well as actively ripping up vegetation.

In this study, I use three large great skua breeding colonies in Shetland, Lamb Hoga peninsula, Fetlar (Fetlar), Hermaness National Nature Reserve, Unst (Hermaness) and Isle of Noss National Nature Reserve (Noss), as model systems on which to test the hypotheses (see below) (see Figure 1.2).

Great skuas are opportunistic marine predators and scavengers and their diet reflect the availability of food resources in the marine ecosystem. In Shetland, in the 1970s, sandeel *Ammodytes* spp. were the most common prey items. However, following a collapse in sandeel stocks in the early 1980s and 1990s there was a shift to discarded whitefish species such as Atlantic herring *Clupea harengus* and whiting *Merlangius merlangus* and great skuas are now the dominant scavengers found at fishing vessels (Reeves and Furness, 2002; Votier, Furness, *et al.*, 2004; Church *et al.*, 2018). As in other scavenger seabirds, this superabundant food source resulted in rapid population growth and increased colony attendances (Furness and Hislop, 1981; Caldow and Furness, 2000; Bearhop *et al.*, 2001; Furness, 2003).

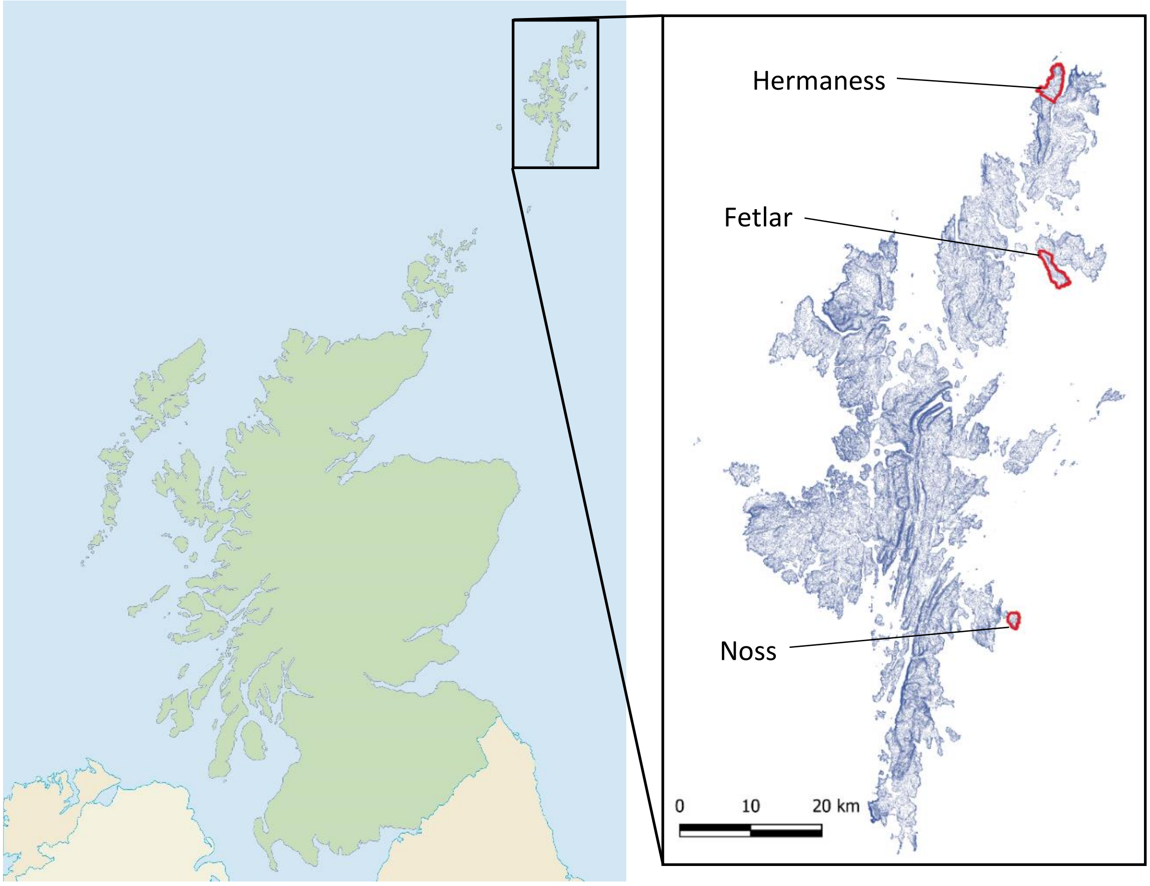


Figure 1.2. Location of Shetland in relation to UK. The red outlines indicate the locations of 3 large great skua colonies used throughout this thesis.

Great skuas are also ideal for testing the impact of different bird densities and different nutrient inputs and disturbance, because their abundance across the colony is not homogeneous. Instead, a skua colony comprises a loose collection of breeding territories, each one containing the nest and at least one raised "mound" on which the birds spend much of their time to observe their territory. In addition, within larger colonies, there are one or more discrete "club sites" where immature, non-breeding birds form large aggregations of between 10 and 200 individuals at very high density (Furness, 1987). Most of the land area of a colony away from nests, mounds and club sites is used infrequently by great skuas. This colony organisation of discrete areas of contrasting skua density (i.e. mounds and club sites represent high density, while most of the "intra-colony" space and completely separate control sites away from the skua colony represent low or no skua density) not only provides an ideal natural experimental system to test hypotheses on the effects of different levels of marine derived nutrients on the terrestrial ecosystem, but it also allows interpretation with respect to implications of the changes in the marine ecosystem that may affect seabird abundance. In addition to the large-scale observational experiment testing the effects of different skua densities at the three colonies, a manipulation experiment was undertaken at one colony by transplanting turfs between high and low skua density areas in a multifactorial design.

This was to expose turfs to a real-time temporal increase and decrease in nutrient input and disturbance *in situ*, and manipulate the level of association with the marine ecosystem, providing empirical evidence to support the findings of the observational study.

A final reason for using great skua populations in Shetland as a model system is restructuring of fisheries management policy currently underway in parts of Europe is expected to cause a significant shortfall in food availability for scavenging seabirds, specifically such as great skuas. The predicted impacts to great skua individuals and population will influence its role as mobile link species and therefore, provide an ideal case study for how changed in marine resource management can influence the terrestrial ecosystem.

The impact of marine ecosystem management on seabirds

As in the terrestrial environments, anthropogenic pressures have transformed a considerable number of marine ecosystems. Over the past 1,000 years coastal habitat alterations, exploitation of fish and marine mammal populations, pollution, eutrophication, species introductions and anthropogenic climate change have resulted in the simplification and homogenization of marine ecosystems, decreases in productivity, species decline, shifts in species distributions and altered food web dynamics (Jackson *et al.*, 2001; Lotze *et al.*, 2005; Halpern *et al.*, 2008; Hoegh-Guldberg and Bruno, 2010). Of all the forms of human disturbance, historic over-fishing has had the greatest impact on marine ecosystems (Jackson *et al.*, 2001) and over the last century global demand for protein has led to the expansion and industrialization of commercial fisheries, further accelerating this influence.

Commercial fisheries interact with seabird populations, with both negative and positive consequences. Entanglement in fishing gear, such as nets and hooks, can result in drowning; long line cod fisheries in Norway and Iceland are estimated to have a mortality rate of 1.75 birds per 1000 hooks set. In 1996, a Norwegian fleet set 476 million hooks, therefore, this annual mortality has the potential to have significant population level effects (Tasker *et al.*, 2000). Other interactions are through alterations in seabird prey resources through altering the structure of marine ecosystems. For example, increases in some diving seabird populations in the UK have in part been attributed to fisheries reducing the population of large predatory fish such as mackerel and herring, resulting in increased availability of the seabirds' small fish prey and reduced competition for this resource (Tasker *et al.*, 2000). Conversely, recent drastic reductions in some seabird species in some areas, e.g. kittiwakes *Rissa tridactyla* (Linnaeus, 1758) and Arctic terns *Sterna paradisaea* (Pontoppidan, 1763) in the northern North Sea, is attributed to the crash in lesser sand eels *Ammodytes marinus* (Raitt, 1934), thought to be partly due to overfishing in the 1980s and 1990s (see Church *et al.*, 2018). A particularly large and direct impact that commercial fisheries can have on seabirds is that fisheries discard huge quantities of dead or moribund fish and offal at sea. In the early to mid 1990s global discard was estimated at 27 million tonnes per year, with North Sea fisheries producing 575,000 t of fish and 60,000 t of offal discard per year, accounting for approximately 22% of all catches (Alverson *et al.*, 1994; Garthe, Camphuysen and Furness, 1996). This represents a superabundant and easy prey resource for scavenging seabird species such as great skuas *Catharacta skua* (Brunnich, 1764), northern fulmars *Fulmarus glacialis* (Linnaeus, 1761) , northern gannets *Morus bassanus* (Linnaeus 1758) and great black-backed gulls *Larus marinus* (Linnaeus, 1758), populations of which have increased considerably where discards are plentiful (Hudson and Furness, 1988; Garthe, Camphuysen and Furness, 1996; Garthe and Hüppop, 1998; Furness, 2003).

Fisheries management policy seeks to control the activities of commercial fisheries and increase the sustainability of the industry. Management practices can directly reduce fisheries impact on seabird populations, such as setting long lines at night to reduce by-catch (Tasker *et al.*, 2000), or influence seabirds indirectly, such as the European-wide discards ban. Fisheries within member states of the European Union are managed in accordance with the EU Common Fisheries Policy (CFP). In 2011 the European commission adopted major changes to the CFP with the aim of restoring European fisheries to a sustainable level. These reforms include the Landing Obligation, which requires all of the catch to be retained on the vessel, landed and counted against a quota; the aim is to essentially stop discarding and thus is also termed “the Discard Ban” (Regulation (EU) 2015/812 of the European Parliament and of the Council, 2015). Over the past 30 years, the quantity of fish discarded has been steadily declining (ICES, 2015; Church et al. 2019), however, the implementation of the Landing Obligation represents a major reduction in scavenging seabird prey availability. The Landing Obligation was a stepwise process, introducing the banning of discards of different fish species each year between 2015 and 2019. It began with banning discards of mackerel and herring in 2015, then haddock, whiting, plaice and other commercial white fish sequentially through 2016, 2017 and 2018 and the last major commercial whitefish discards banned were of cod in 2019.

Major changes to fisheries policy such as the EU’s Landing Obligation could have impacts on terrestrial ecosystems via impacts on the mobile link species: the reduced availability of discards as a food resource is predicted to decrease colony attendance due to longer foraging trips, shift demographics and cause population declines (Bearhop *et al.,* 2001; Oro *et al.,* 2004; Furness, 2007; Bartumeus *et al.,* 2010; Votier *et al.,* 2010; Bicknell *et al.*, 2013). Consequently, the discard ban has the potential to influence the function of these species as a mobile link species between marine and terrestrial ecosystems (fewer seabirds spending less time at the colony). Therefore, it is important to understand how these seabird species link the marine and terrestrial ecosystems and determine how the potential changes in abundance and attendance at colonies will change the marine nutrient inputs and influence ecosystem functioning and community composition dynamics. This PhD tests the impact of different seabird densities and different nutrient inputs, on a wide range of key parameters in a terrestrial ecosystem in the northern North Sea (soil processes in Chapter 3; plant communities in Chapter 4; invertebrate communities in Chapter 5). The region studied, Shetland, is where there is one of the largest fisheries in Europe, so that the implications for the Landing Obligation are likely to be considerable.

Thesis structure

The overarching aim of this thesis is to test the meta-ecosystem concept by identifying how great skuas are influencing the functioning of the terrestrial ecosystem and therefore determine their role in the meta-ecosystem. I test the impact of contrasting great skua abundance and therefore influence of the marine ecosystem, on essential ecosystem functions such as nutrient turnover, across multiple biological scales, from leaf to community levels and across multiple species communities (plants and invertebrates).

Specifically, I use a combination of observational, experimental and manipulation studies to quantify how great skuas influence the terrestrial ecosystem to infer how they function as a mobile link species between a marine and a terrestrial environment. The study design of contrasting skua densities and turf transplant manipulation ensures relevance for implications of how changes in marine resource management (especially the current EU Landing Obligation policy) is likely to influence this terrestrial ecosystem via changes in seabird nutrient input, both spatially and temporally.

Each chapter of this thesis addresses the effect of great skuas on a different part of the terrestrial ecosystem. However, as with any ecosystem-wide study the results do not exist in isolation and I have tried to link processes and results between chapters where possible. This thesis is set out to examine the effects of great skuas from the bottom up, i.e. from the nutrient inputs and soil and plant pools (Chapter 2), soil processes (Chapter 3), plant communities (Chapter 4) and invertebrate communities (Chapter 5). The hypotheses tested in each chapter are as follows:

The aim of Chapter 2 is to determine the amount of marine derived nutrients transported by great skuas, if these are incorporated into the terrestrial ecosystem and the effects on the nutrient status of soil and plants (Figure 1.3a). This not previously been studied in this system and it provides a background information for the rest of the thesis and aids in the interpretation of subsequent results. Initially, I combine nutrient concentrations within faecal and carrion samples with deposition rates to calculate an estimate of marine derived nutrients transported by great skuas. Then, test the hypothesis that increases in great skua abundance increases the nutrient status soils and plant tissue with different life histories. Four different plant species were used with contrasting life histories and abundance response to great skuas. It was anticipated that species were adapted to grow slowly in nutrient poor conditions such as heather would not respond to increased nutrient availability to the same extent as faster growing graminoid species such as sweet vernal grass. Finally, I use stable isotope analysis to determine test the hypothesis that marine derived nutrients were causing the observed changes in nutrient status.

The aim of chapter 3 is to determine how changes in the nutrient status of plants and soils influence rates of nutrient cycling (Figure 1.3 b). Hypotheses are divided into two main lines of enquiry: the effect on leaf litter decomposition and nutrient loss and the effect on nutrient mineralization. First, senescing plant material was used to test the hypothesis seabirds decrease the carbon to nutrient ratios by increasing the marine derived nitrogen and phosphorus in the fresh leaf litter. Subsequently, a fully factorial litter transplant experiment was established to test the hypotheses changes in litter chemistry by seabirds resulted in increases in decomposition rates and nutrient loss, and seabird guano could prime the decomposition of leaf litter. Finally, correlative and manipulative studies were used to test the hypothesis marine nutrient deposition by seabirds increases nitrogen and phosphorus mineralization rates within the soil.

The aim of Chapter 4 is to determine how great skuas influence plant community assemblage and dynamics and therefore, how the terrestrial plant community is coupled to marine ecosystems (Figure 1.3c). I used the pin-drop method to sample plant communities in an observational study to test the hypotheses local plant community composition is related to differences in great skua use and specifically, the abundance of dwarf shrub species is lower and graminoid species higher in areas of high great skua use. In addition I used the same methodology in a turf transplant experiment to measure changes in plant community composition over time and test the hypotheses: increases in great skua abundance would increase the proportion of graminoid species, at the expense of dwarf shrub species and decreases in great skua abundance would have the opposite effect. Finally, to infer the mechanisms driving plant community dynamics Grime’s C-S-R plant strategies were used to test the hypothesis that ruderal plant life strategies are associated with areas of high great skua use.

The aim of Chapter 5 is to determine how great skuas influence the invertebrate community and identify the relative roles of some of the key effects of great skua in regulating invertebrate community assemblage (Figure 1.3 d). I use pit-fall trapping to survey invertebrate community and test the hypotheses that the abundance of broad invertebrate orders and community assemblage is related to differences in great skua use within the colony. Specifically, it was anticipated that in areas of high great skua influence invertebrate orders that contained many detritivorous species would have a higher abundance and predatory species that require greater habitat structural complexity such as spiders would have a lower abundance. In addition, ground beetles were used to obtain a higher resolution data set to test the hypothesis that ground beetle species abundance and communities are influenced by great skua abundance. It was anticipated that these would follow a similar trend to invertebrate order communities, and large bodied predators would have a lower abundance in areas of high great skua influence. Finally, I test the hypothesis that carabid species abundances are specifically influenced by great skua density, soil nutrient concentration and great skua induced changes in vegetation structure, where great skua density is being used as a proxy for the level of direct disturbance.

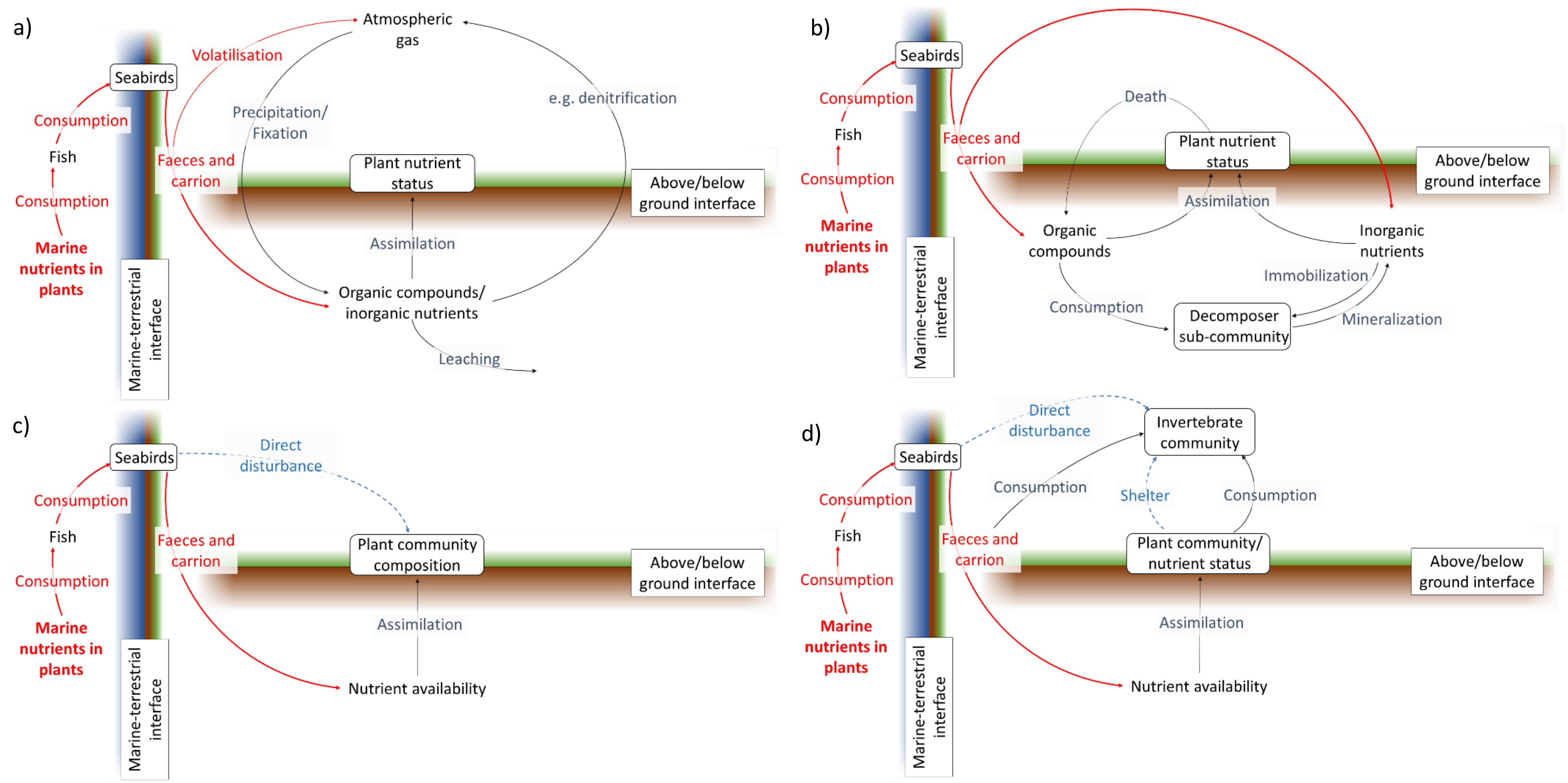
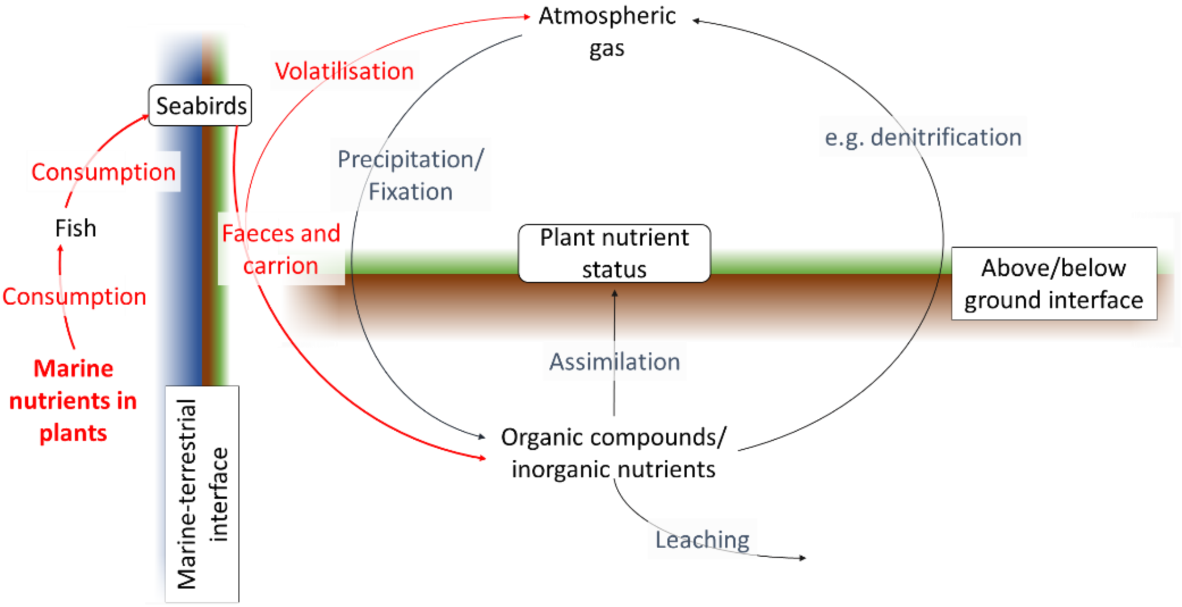


Figure 1.3. Conceptual diagrams of potential effects of seabirds on the terrestrial ecosystem/links to the marine ecosystem, broken down into four hypotheses addressed in the data chapters. In all the diagrams, red arrows indicate the directions of flow of marine nutrients and dark grey arrows indicate the flow of terrestrial and terrestrial/marine nutrients between nutrient pools. In addition, dashed blue arrows indicate other potential links between seabirds and taxonomic community of interest and between different taxa. (a) Seabird transport marine nutrients into the terrestrial ecosystem and they are incorporated into nutrient pools. (b) Marine resource input by seabirds influences terrestrial nutrient cycling. (c) Marine nutrient input and disturbance by great skuas influences plant community assemblage. And (d) seabirds influence the terrestrial invertebrate community assemblage.

CHAPTER 2

GREAT SKUAS TRANSPORT NUTRIENTS FROM THE MARINE ECOSYSTEMS TO THE TERRESTRIAL ECOSYSTEM.



ABSTRACT

The meta-ecosystem concept describes spatial coupling of ecosystems through flows of energy material and organisms across ecosystem boundaries. Mobile species can act as biotic vectors to facilitate the movement of these items between ecosystems and can be essential to maintaining the meta-ecosystem. Given the increasing threat to species movement and biodiversity in general from anthropogenic activity, a greater understanding of how meta-ecosystems function and the role that mobile species play can provide a better insight to how actions at a local scale can cascade into coupled ecosystems and influence whole landscapes. Throughout this thesis I use the marine-terrestrial meta-ecosystem connected by the seabird great skua as a model system to investigate this. In this chapter I address how these ecosystems are linked. I use a combination of observational and manipulative studies and nutrient concentration and stable isotope analysis to identify (1) the amount of marine derived nutrients transported by great skuas, (2) if these are incorporated into the terrestrial ecosystem and (3) how changes in great skua abundance influences the nutrient status of soil and four plant species with differing life histories. I show that great skuas facilitate the flow of nutrients from the marine ecosystem into terrestrial plants. Large quantities of essential plant nutrients are deposited into the terrestrial ecosystem by great skuas, in some areas up to 9 times more nitrogen than background deposition rates. This marine derived nutrient deposition feeds into plant nutrition, regardless of species and life history traits and potentially causes shifts in plant nutrient acquisition pathways in heather and tormentil. Exposing plant communities to a lower abundance of great skuas caused a decline in leaf nitrogen concentration across all species, but phosphorus concentration did not change and increased in some species. Greater marine derived nutrient deposition did not result in elevated soil nitrogen and phosphorus concentrations at all sampling locations, indicating that plants are rapidly assimilating the marine derived nutrients they require, and the excess is lost through surface run-off or leached through the soil. Plant nutrient status and acquisition influences several key ecosystem functions such as decomposition rates and plant community assemblage, therefore the changes identified here are likely to affect the entire terrestrial ecosystem. Restructuring of fisheries management policy currently underway in parts of Europe is expected to cause a significant shortfall in food availability for scavenging seabirds, such as great skuas. The predicted impacts will impair their function as a mobile link species, reducing marine derived nutrient inputs into the terrestrial ecosystem. My work suggests that, as a result, foliar $\delta^{15}N$ signatures and nitrogen but not phosphorus concentrations in plants will decline, with potential cascading consequences for the entire ecosystem.

INTRODUCTION

Mobile species can act as biotic vectors, transporting energy, nutrients and other organisms (e.g. seeds, parasites etc.) between ecosystems. This pathway can influence local ecosystem processes, taxonomic communities and trophic interactions and where the movement is frequent and predictable, mobile species can couple seemingly discrete ecosystems (Polis, Anderson and Holt, 1997; Bauer and Hoye, 2014). This occurrence has given rise to the concept of meta-ecosystems, whereby multiple connected ecosystems can be considered as one functioning unit (Loreau, Mouquet and Holt, 2003). Under this conceptual framework, sink ecosystems exist in an alternative stable state, that is reliant on the interaction with the source ecosystem and any perturbation in the source ecosystem is likely to also impact the recipient ecosystem (Loreau, Mouquet and Holt, 2003; Lundberg and Moberg, 2003). Given the increasing threat to species movement and biodiversity from anthropogenic actions such as habitat destruction and climate change (Wilcove and Wikelski, 2008; Van Gils *et al.*, 2016), a greater understanding of how meta-ecosystems function and the role that mobile species play can provide a better insight to how actions at a local scale can cascade into coupled ecosystems and influence whole landscapes.

Seabirds are highly mobile species, often covering large distances to forage on marine resources. During the breeding season, seabirds rear young in terrestrial nesting colonies, where they deposit large quantities of faeces and carrion, rich in marine derived nutrients (Furness, 1978; Bryant and Furness, 1995; Bancroft, Garkaklis and Roberts, 2005; Ellis, 2005). As a result, the soil and plants in and around seabird colonies are generally associated with high nitrogen and phosphorus concentrations (Hogg and Morton, 1983; Anderson and Polis, 1999; Ellis, Fariña and Witman, 2006; Kolb *et al.*, 2015), which influence local plant communities (Hogg and Morton, 1983; Vidal *et al.*, 2000; Croll, 2005; Ellis, Fariña and Witman, 2006; Baumberger *et al.*, 2012). Therefore, by regularly traversing the boundary between the marine and terrestrial ecosystems, seabirds act as a mobile link species, spatially coupling them into a meta-ecosystem. Despite these examples of seabird affecting the terrestrial ecosystem, there are few studies that have examined how this meta-ecosystem functions.

The level of marine derived nutrient deposition during the breeding season will in part determine the extent of the effect of seabirds on terrestrial ecosystems especially in remote coastal locations where there are few anthropogenic nutrient sources (Polis, Anderson and Holt, 1997; Wilson *et al.*, 2004). Nutrient deposition is influenced by the species that is being studied as the concentration of nutrients in the faeces is determined by the size of the bird, individual metabolic rates and diet (Bryant and Furness, 1995; Wilson *et al.*, 2004; Cross, 2014; Zwolicki *et al.*, 2016). Furthermore, the amount of faeces deposited is governed by factors such as the length of the breeding season and the amount of time spent at the colony during the breeding season (Wilson *et al.*, 2004; Blackall *et al.*, 2007; Riddick *et al.*, 2012; Cross, 2014; Zwolicki *et al.*, 2016). Bioenergetic models have been used to estimate the level of nutrient deposition in a year (e.g. Cross, 2014), however this has rarely been measured in the field. An accurate measure of the level of nutrient inputs in a model system, either by a single seabird species or an entire a seabird colony, will aid the interpretation of the role of seabirds in the functioning of the meta-ecosystem.

The incorporation of the marine derived nutrients into the terrestrial ecosystem will also affect the functioning of the meta-ecosystem. To influence terrestrial ecosystems, marine derived nutrients need to be retained in the bulk soil or assimilated by abiotic communities such as plants and soil microbes. However, nutrients can lost from faeces and carrion to the surrounding atmosphere through volatilization, leached to a soil depth inaccessible to terrestrial plant communities or transported back into the intertidal (Wootton, 1991) and inshore marine ecosystems through percolation or surface run-off (Lorrain *et al.*, 2017; Savage, 2019). The rate of nutrient loss is partly dependent on local soil conditions and prevailing weather systems. For example, ammonia emission modelling around seabird colonies demonstrates that volatilization rates are highest around cliff nesting species such as northern gannet and black guillemots *Cepphus grille* (Linnaeus, 1758), where faeces are deposited onto surrounding rocks (Wilson *et al.*, 2004; Blackall *et al.*, 2007). Conversely, volatilization at ground nesting and burrow nesting colonies such as great skuas and puffins is reduced by the overlaying vegetation more permeable soil (Misselbrook *et al.*, 2000; Wilson *et al.*, 2004; Blackall *et al.*, 2007).

The plant community assemblage in and around the seabird colony also influences the extent to which and rate that marine derived nutrients are incorporated into the terrestrial ecosystem. The acquisition, storage and utilization of nutrients in plants is associated with species specific growth forms, traits and life histories and therefore, individual species responses to elevated nutrient availability is likely to differ (Grime, 1977; Aerts and Chapin, 2000). For example, ruderal species, can exploit high nutrient availability by increasing growth rates, resulting in elevated tissue nutrient concentrations. This contrasts with slow growing plant species, which are well adapted to nutrient poor conditions as their growth rate matches nutrient availabity. When nutrient availability increases, nutrient assimilation can exceed utilization, therefore nutrients are either stored or assimilation rates reduced (Grime, 1977; Aerts and Chapin, 2000). Within seabird colonies, there have been few studies that have examined the relative differences in the response of different plant species. Havik, Catenazzi and Holmgren (2014) found that the mechanisms of nitrogen acquisition influenced the concentrations of marine derived nutrients in the plant tissues: nitrogen concentrations increased in non-nitrogen fixing species but were unaffected in nitrogen-fixing species. In other studies the reasons for different levels of plant nutrient acquisition in response to seabird colonies are less clear (Mulder and Keall, 2001). Given leaf nutrient concentrations are key determinants of how individual species function within the ecosystem (i.e. ecosystem processes and plant community assemblage) (Grime et al., 1997; Aerts and Chapin, 2000; Wardle et al., 2004; Kolb, Palmborg and Hambäck, 2013), tracing the marine derived nutrients within the different plant species will provide insight into the mechanisms influencing the function of the meta-ecosystem.

Stable isotopes are a useful tool for tracing the movement of nutrients through ecosystems (e.g. Staddon, 2004). Seabird faeces is naturally enriched in ^{15}N (rarer heavier isotope) relative to ^{14}N (abundant light isotope) because they are apex predators in long marine food chains (Schulting, 1998) and the lighter isotope is preferentially volatilized from faeces (Mizutani, Kabaya and Wada, 1985). Therefore, stable isotope analysis of bulk soil and plant tissue can be used to determine if marine derived nutrients are incorporated within the terrestrial ecosystem (Ben-David, Schell and Hanley, 1998; Hilderbrand *et al.*, 1999; Caut *et al.*, 2012; Cross *et al.*, 2014).

The meta-ecosystem concept predicts that any change in one ecosystem will influence the coupled ecosystems. A key driver of seabird populations are commercial fisheries, which in the past have both directly competed with and provided a superabundant food source for different seabird species (Furness, 2002, 2003; Votier, Furness, *et al.*, 2004; Cury *et al.*, 2011). In many parts of Europe changes in fisheries management policy are currently underway aimed at increasing the sustainability of the practice (Regulation (EU) 2015/812 of the European Parliament and of the Council, 2015). These changes are predicted to decrease food availability for many scavenging seabird species (Bicknell *et al.*, 2013), which is anticipated to increase foraging trip times, cause changes in diet preferences, alter population dynamics and cause long term declines in producitivty and population sizes (Furness, 1987, 2003, 2015; Klomp and Furness, 1992; Votier *et al.*, 2007). As seabirds act as a key link between the marine and terrestrial ecosystems these changed have the potential to alter the functioning of the meta-ecosystem.

Here and throughout this thesis I use great skua breeding colonies on blanket bog habitats as a model system to examine how seabirds influence the functioning of the meta-ecosystem. The aim of this chapter is to determine the amount of marine derived nutrients transported by great skuas, if these are incorporated into the terrestrial ecosystem and the effects on the nutrient status of soil and plants. Not only has this not previously been studied in this system, it provides a background information for the rest of the thesis and aids in the interpretation of subsequent results. Initially, I combine nutrient concentrations within faecal and carrion samples with deposition rates to calculate an estimate of marine derived nutrients transported by great skuas. Then, using a combination of correlative and manipulative experiments I tested the hypothesis that increases in great skua abundance increases the nutrient status of (1) soils and (2) plants with different life histories. Four different plant species were used with contrasting life histories and abundance response to great skuas (See Chapter 3). It was anticipated that species adapted to grow slowly in nutrient poor conditions such as heather would not respond to increased nutrient availability to the same extent as faster growing graminoid species such as sweet vernal grass. Finally, to determine if marine derived nutrients were driving the observed changes in nutrient status in the correlative study, I tested if (3) soil and plants growing in areas of high great skua abundance are enriched in ^{15}N.

METHODS

Study system

Data were collected over two great skua breeding seasons at three large great skua colonies in Shetland, comprising blanket peat bog: Lamb Hoga peninsula, Fetlar (Fetlar), Hermaness National Nature Reserve, Unst (Hermaness) and Isle of Noss National Nature Reserve (Noss) (centred at 60° 34' 39.77"N, 0° 53' 33.63"W, 60° 49' 0.15"N, 0° 53' 32.40"W and 60° 8' 22.94"N, 1° 1' 2.40"W, respectively, see Figure 2.1). The vegetation communities at Fetlar and Hermaness have affinities to National Vegetation Classification (NVC) community M19 *Calluna vulgaris – Eriophorum vaginatum* blanket mire blanket mire vegetation, whereas that at Noss has a greater affinity to NVC community M17 *Trichophorum cespitosus – Eriophorum vaginatum* blanket mire and M15 *Trichophorum cespitosus – Erica tetralix* wet heath, as there is a reduced abundance of *Calluna vulgaris* largely due to historic land use (Rodwell, 1991).

Great skua abundance across the colony is not homogeneous, but comprises a loose collection of breeding territories, each one containing the nest and at least one raised mound on which the birds stand to observe their territory. In addition, within larger colonies, there are one or more discrete areas called "club sites" where immature, non-breeding birds form large aggregations of between 10 and 200 individuals (Furness, 1987). Most of the land area of a colony away from nests, mounds and club sites is used infrequently by great skuas and is referred to here as the "intra-colony". This colony organisation of different areas of contrasting skua usage (and therefore contrasting marine nutrient input) provides an ideal system in which to test the hypotheses.

Nutrient deposition by great skuas

Study design

In order to calculate the amount of marine derived nutrients introduced into the terrestrial ecosystem by great skuas, rates of faecal and pellet deposition were measured at club, mound and intra-colony control sites at all three colonies. In addition, faecal and pellet samples were collected to measure the nutrient content. Five club sites were selected across the three colonies: two at Hermaness (Fild and North), two at Noss (East and West) and one on Fetlar. Within each club site, sampling locations were established in a grid formation, each one separated by at least 5 m. The number of sampling locations within each club site was determined by the size and use if the site (see Table 2.1 in results section). Within colonies, mound sampling sites were selected at random from all breeding territories identified within approximately a 1 km radius of the club sites (methodology adapted from Walsh *et al.*, 1995) (n = 30). The exception to this was at Hermaness, where several mound sites are approximately 2 km south of the nearest club site.

Intra-colony sample locations were established 20-30 m from each mound site on a random bearing (n = 30). Figure 2.1 shows the location of the great skua colonies and the sampling strategy.

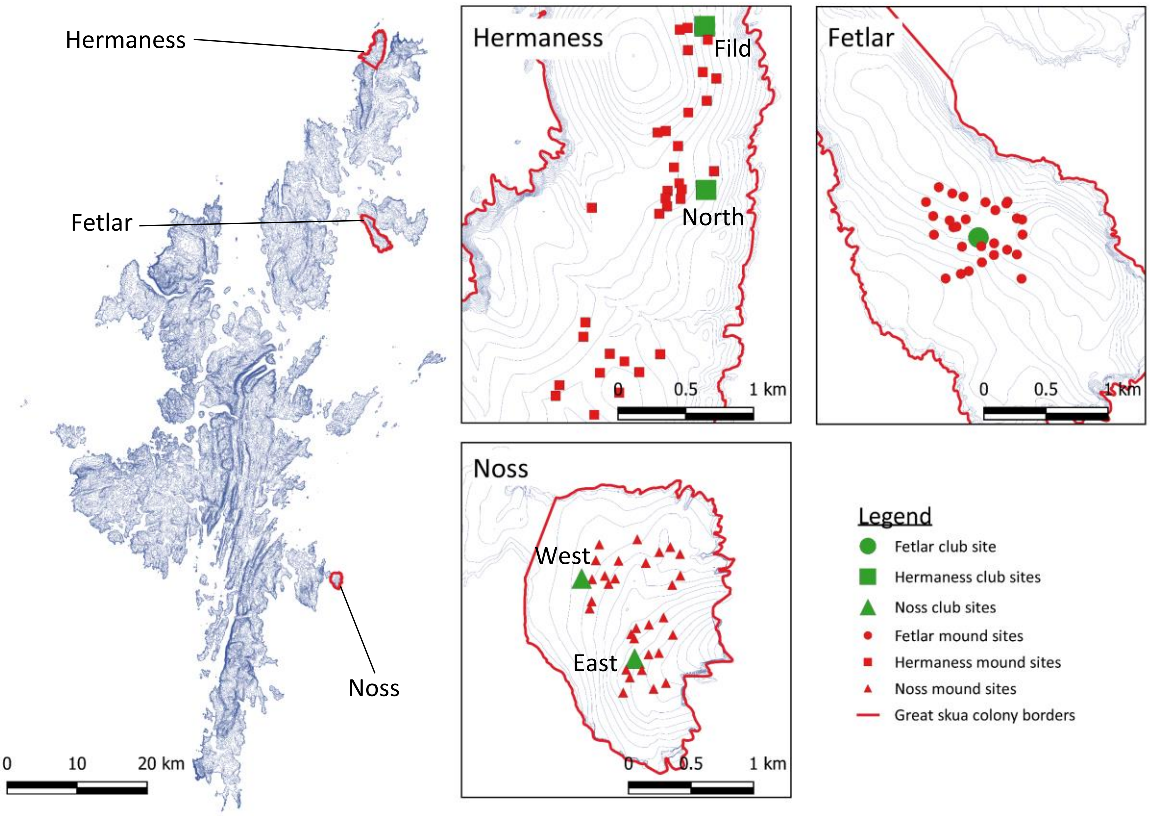


Figure 2.1. A map of the study design used to determine the amount of nutrients deposited by great skua into the terrestrial ecosystem. The large green symbols identify the location of each club site, with the name of that club sites appear in the text adjacent, where there is more than one. The small red symbols identify the location of the mound sampling sites. Intra-colony control sampling sites not shown due to the scale of the maps.

Faecal and pellet deposition rates

To determine the rates of faecal and pellet disposition, in June 2016, $1m^2$ and $4m^2$ quadrats were cleared of all signs of faeces and pellets, respectively. After a period of 15 days, faeces and pellets within the quadrats were counted. Where faeces overlapped, a count was approximated based on size, shape and orientation of the outline.

Chemical analysis of samples

To determine the chemical composition of faeces and pellets a total of 12 samples of each were collected at random from within the quadrats. All additional material, such as grass and soil, were removed from the samples by hand, before each sample was air dried, weighed, and ball-milled into a fine homogenous powder. Nitrogen concentration were quantified using an automated elemental analyser (FlashSmart, Thermo Scientific). Phosphorus, potassium, calcium and magnesium concentrations was determined using a nitric acid microwave digest (MARS 6, CEM) and subsequent analysis using ICP-OES (iCAP 6000, Thermo Scientific).

Calculating nutrient deposition rates

Nutrient deposition is expressed as mean kg of nutrient per hectare per year. Concentrations of nutrients were converted into grams per dry weight, averaged across the samples and multiplied by respective deposition and scaled up rates to calculate kg of nutrient deposited per Ha per day. Great skuas, spend most of the year at sea and only use the terrestrial environment to breed and raise young. The length of time spent at the breeding colony in a season by breeding pairs and non-breeding individuals was calculated using dates of arrival and departure in Furness (1978).

To calculate a measure of variation around the final nutrient deposition rate, standard errors of individual means (mean g of nutrient in faeces/pellets and mean deposition rate) were converted into percent uncertainty (i.e. a mean of 10 and a standard error of 0.5 would equate to 5% uncertainty), added together and converted back to a single standard error.

In addition, the total amount of marine nitrogen and phosphorus transferred in a breeding season by great skuas was estimated. The area of all club sites were measured using aerial photographs in Geographical Information System (GIS) and the area of a sub-set of 12 mounds were measured at each colony. In order to estimate the total area of mounds at each colony, mean mound areas were multiplied by the number of breeding pairs recorded during the Seabird 2000 census of the UK (Mitchell *et al.*, 2004). This figure was then used to convert deposition rates into total deposition.

The effect of great skuas on soil and plant nutrient status

Study design

To test the hypothesis that marine nutrient deposition by great skuas increases nitrogen and phosphorus concentrations in soil and plants (hypothesis 1 and 2) a correlative study and manipulation experiment were undertaken. The correlative study was established at all three great skua breeding colonies and used natural variation in great skua abundance across the colonies to identify three different treatments: club sites, mound sites and intra-colony (control) sites. At each colony, a single club site was selected at random and sampling areas were established in a grid formation, each one separated by at least 5 m (n = 12). The club sites at Fetlar and Noss were the same as those used in the previous study, however, a different club site was used at Hermaness. Within colonies, mound sampling areas were selected at random from all breeding territories identified within approximately a 0.5 km radius of the club sites (methodology adapted from Walsh et al., 1995) (n = 12). Intra-colony sample locations were established 20-30m from each mound site on a random bearing (n = 12). In addition, to determine if there was a colony scale effect of great skuas on nutrient inputs, each colony had a paired extra-colony control site. These were defined as sites without an established great skua breeding colony (Mitchell *et al.*, 2004) but which had similar soil type, plant communities, underlying bedrock and distance and orientation to the sea. At each site, sampling sites were established in a grid formation separated by at least 15m (n = 12). See Figure 2.2 for a map of sampling sites.

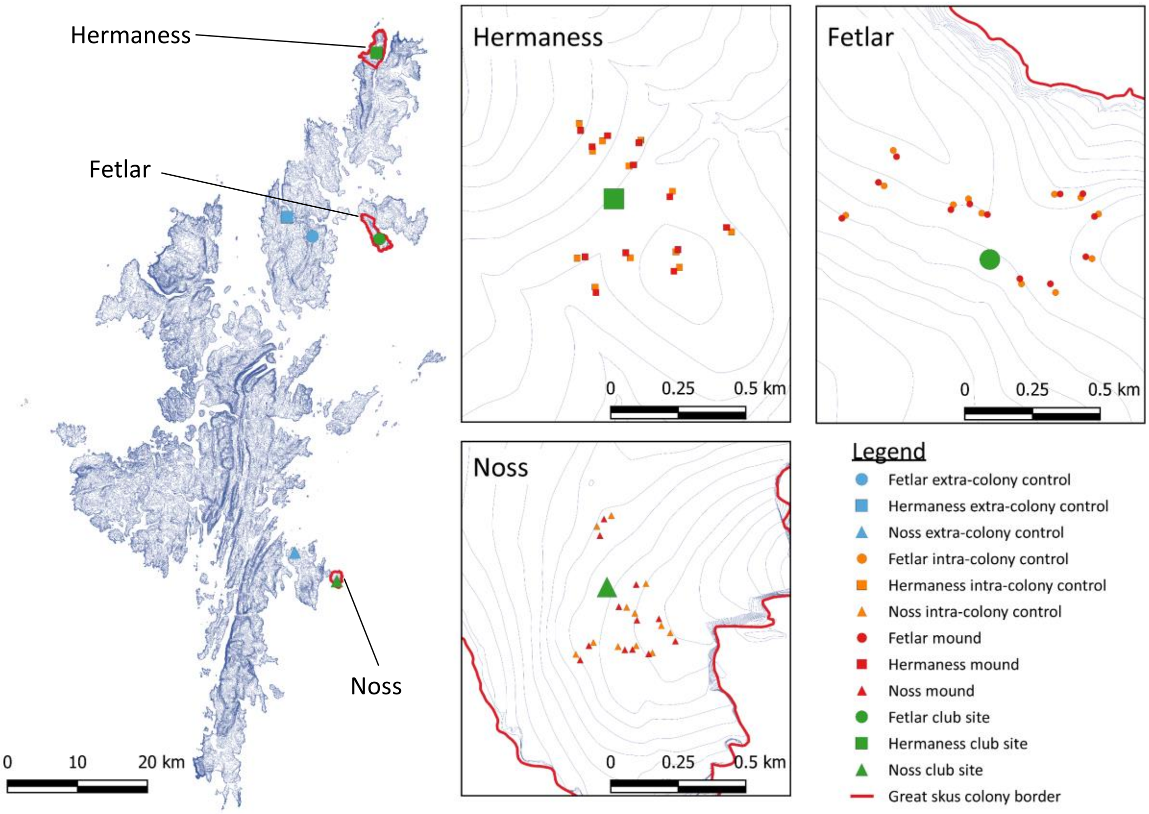


Figure 2.2 The corelative study design. In the map of Shetland (left) the large green and blue points represent the club and extra colony control sites, respectively. In the individual colony maps the small red and orange points represent mound and intra-colony sample locations and the large green points represent the club site location and shape represents the three separate sampling colonies (circle – Fetlar, square – Hermaness and triangle – Noss).

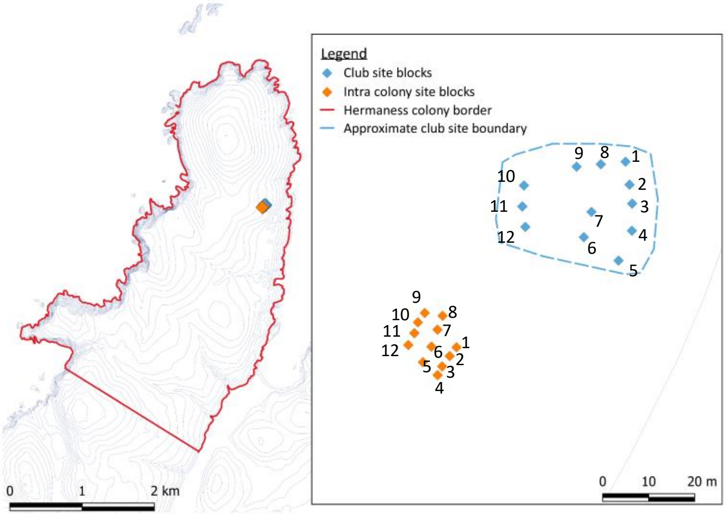


Figure 2.3. The reciprocal turf transplant study design and location at the Hermaness great skua colony. In the map on the right, the blue points represent the blocks in the club site and the orange points represent blocks in the intra colony site. At each block, two turfs were dug, one of which was transplanted to the paired block (same numbers) in the opposing site (Club or Intra) and the other was placed back into the site of origin.

The manipulation experiment comprised reciprocal turf transplants, used to artificially increase and decrease great skua abundance. The experiment was established at the North club site and an adjacent area of intra-colony control at Hermaness, in a separate area of the colony used for the correlative study. In March 2016, pairs of turfs in a block design (n =12) (block locations are shown in Figure 2.3) were cut from the club site and intra-colony control site and placed into freely draining plastic boxes of the same size (35cm x 53cm x 15cm (depth)). One of the pair was reciprocally transplanted with the corresponding block in the club or intra-colony control site, while the other was placed back into the hole it was cut, establishing four different treatments:

1. Club site to club site (high to high great skua abundance),
2. Club site to Intra-colony control site (high to low),
3. Intra colony control site to club site (low to high), and,
4. Intra-colony control site to Intra-colony control site (low to low)

Sample collection

In June 2017 and July 2018, a single soil core (diameter = 4cm, depth = 10cm) was taken at each sample location in the corelative study and from each turf in the manipulation study, respectively. The soil cores were returned to the laboratory, where they were air dried, ground using a pestle and mortar and sieved to 2mm before being stored in dry dark conditions prior to chemical analysis. At each sample location in the corelative study, a second core was taken using a bulk density sampler (diameter = 5.4cm, depth = 5.9cm). Soil was air-dried and weighed to determine dry weight per volume of soil. This allows for nutrient concentration in the soil to be converted from mg of nutrient per g of soil to mg of nutrient per m^2 of soil. This conversion corrects for any influence the physical soil properties may have on resource availability allowing for accurate comparison of samples over a large geographical area. This was not considered necessary for the manipulation experiment as it occurred within the same geographical location.

In July 2017 and August 2018, plant samples were collected from half of the sample location used in the corelative survey (n = 6; sample locations selected randomly), and from all turfs in the manipulation study where the species occurred. Plant samples comprised fresh, above ground vegetative tissue (i.e. not flowering stem) of two graminoid species: common cotton sedge *Eriophorum angustifolium* and sweet vernal grass *Anthoxanthum odoratum*, a forb species: tormentil *Potentilla erecta*, and a dwarf shrub: heather *Calluna vulgaris*. These species were selected because they are fairly ubiquitous across the study area and have contrasting life histories. In addition, heather and common cotton sedge abundance declined, and tormentil and sweet vernal grass abundance increased in response to great skuas (see Chapter 3). Heather was not collected from sample locations at Noss, as it is uncommon in the intra-colony sward. The plant samples were returned to the laboratory, where they were air dried, and ball-milled to a fine homogenous power before being stored in dry dark conditions prior to chemical analysis.

Nutrient analysis

The same methodology was used to measure the concentration of nitrogen and phosphorus in soil samples and plant samples in the corelative study and manipulation study. Nitrogen concentrations were quantified using an automated elemental analyser (FlashSmart, Thermo Scientific). Phosphorus concentration was determined using a nitric acid microwave digest (MARS 6, CEM) and subsequent analysis using ICP-OES (iCAP 6000, Thermo Scientific).

Extractable nutrients were also measured in the soil samples from both studies. Ammonium and nitrate, and phosphate were extracted by shaking soil in 1M KCl for 1 hour and 2.5% Acetic acid for 2 hours, respectively. Nitrogen extracts were stored at --20°C, while phosphate extracts were stored at 4°C, prior to analysis on a SEAL AutoAnalyzer 3 constant flow analyser system (Seal Analytical, UK).

All nutrient concentrations in the correlative study were converted to weight per unit area using the soil bulk density, for the reason identified above.

Marine derived nutrients in the terrestrial ecosystem

Stable isotope analysis was used to determine if the nitrogen in the soil and plant tissue was marine-derived. A sub-sample of the faecal and pellet samples used in the previous study and plant and corresponding sample locations soil samples (n = 6) were analysed for the ratio of ^{14}N

and ^{15}N using continuous-flow isotope ratio mass spectrometry (CF-IRMS, Costech ECS 4010 elemental analyser and Thermo Finnigan Delta Plus XP mass spectrometer). Three internal laboratory standards (Sigma-Aldrich gelatine and two Sigma-Aldrich alanine solutions, one of which is labelled with ^{15}N) were included in the analysis to allow for any instrument drift to be corrected. Results are expressed in $\delta^{15}N$ parts per thousand (‰) deviations from the international standard AIR.

Statistical analysis

The effect of great skua use on nitrogen and phosphorus concentrations in the soil and plant material (hypotheses 1 and 2) in the correlative and manipulation experiments were assessed using linear and linear mixed effects models, respectively. In all cases the concentrations of nutrient was the response variable. In the correlative study, great skua use (extra-colony control, intra-colony control, mound and club), colony and their interaction were used as fixed effects and the significance of the predictor was determined using ANOVA. Where the interaction between great skua use and colony was significant, colonies were reanalysed separately and Tukey's post-hoc analysis was carried out to aid interpretation of interactive effects. It was considered inappropriate to use colony as a random effect as there too few to colonies to accurately estimate the variation of the population of the effect (i.e. less than 5).

In the manipulation experiment great skua abundance at the turf location (two levels - high or low), great skua abundance at turf origin (high or low) and their interaction were used as fixed effects, and to account for non-independence of these samples block origin and location were used as random effects. The significance of the predictors was estimated using bootstrapped likelihood ratio tests, with the relevant predictor removed. A graphical interpretation of the hypothetical outcomes of this analysis is shown in Figure 2.4. A biological interpretation is as follows: no significant effect of turf origin or location indicates that great skuas are not influencing nutrient concentrations (Figure 2.4a); a significant effect of turf origin only would indicate that historic great skua abundance determines nutrient concentrations (Figure 2.4b); a significant effect of turf location only indicates that great skuas directly influence nutrient concentrations (Figure 2.4c); a significant effect of turf location and origin suggests that nutrient concentrations is influenced by short-term changes in great skuas abundance and historical abundance (Figure 2.4d); and, a significant interaction term suggests that the short-term effect of changes in great skua abundances on nutrient concentrations is dependent on the historical great skua abundance (Figure 2.4e). Marginal R^2 and conditional R^2 of each model were calculated to assess the goodness of fit.

The effect of great skua use on $\delta^{15}N$ signature in soil and plant (hypotheses 3) was assessed using linear models. In these models, great skua use (extra-colony control, intra-colony control, mound and club), colony and their interaction were used as fixed effects and the significance of the predictor was determined using ANOVA.

All models were checked and validated following Zuur, Ieno and Elphick (2010) and data were transformed to meet assumptions of statistical model or test where appropriate.

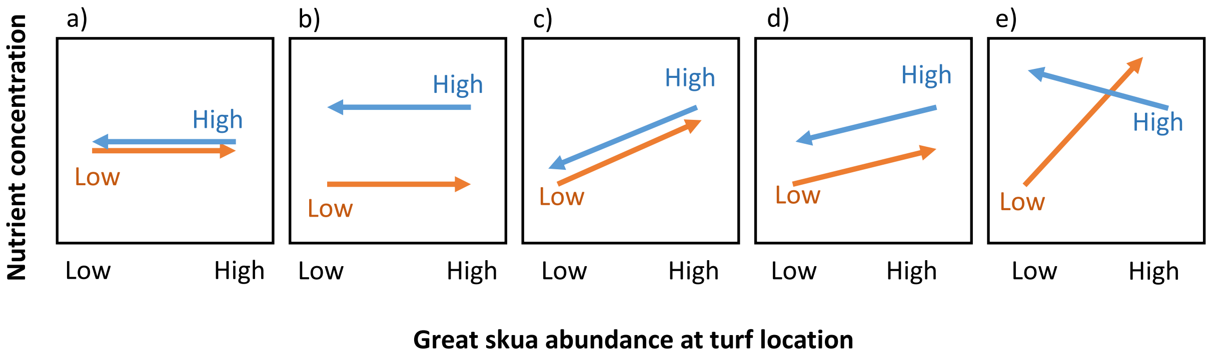


Figure 2.4 Hypothetical effects of nutrient concentrations in soil and plants in response to reciprocal turf transplants. Blue arrows represent turf that started in areas of high great skua abundance and were moved to areas of low great skua abundance, orange arrows represent turf that started in areas of low great skua abundance and moved to areas of high great skua abundance. (a) No significant effects; (b) significant effect of turf origin; (c) Significant effect of turf location; (d) Significant effect of turf location and turf origin; and, (e) Significant interaction term.

RESULTS

Nutrient deposition by great skuas

The rates of nutrient deposition were calculated separately for each club site and averaged across mound sites for each colony. Therefore, the data presented in Tables 2.1 and 2.2 is the quantity of nutrient deposited at club sites by the aggregation of non-breeding birds and at mound sites by a pair of breeding birds rather than per individual bird. On average, across all colonies, non-breeding great skuas transport 91.81 (±42.04) kg of nitrogen, 49.34 (±23.90) kg of phosphorus, 5.07 (±2.44) kg potassium, 96.41 (±48.32) kg calcium and 2.31 (±1.01) kg magnesium per hectare per year into club sites through faeces and pellets. In addition, across all colonies, breeding pairs deposit an average of 34.95 (±11.77) kg of nitrogen, 17.50 (±6.76) kg of phosphorus, 1.95 (±0.70) kg of potassium, 33.72 (±13.79) kg of calcium and 0.86 (±0.28) kg of magnesium per hectare per year into each mound site through faeces and pellets. Great skuas were occasionally noted utilising intra-colony control areas, however, no faeces or pellets were recorded in either the intra-colony.

The area of club sites varied from just over 200 m^2 in the northern extent of Noss, to just over 500m^2 at the Fild club site in Hermaness. The size of mound sites also varied considerably but on average measured 5.94 m^2 at Fetler, 5.05 m^2 at Hermaness and 7.23 m^2 at Noss. Therefore, in total great skuas deposited an estimated 22.65 kg N and 11.37 kg P at Fetlar, 19.81 kg N and 10.70 kg P at Hermaness and 13.33 kg of N and 6.73 kg of P at Noss from the marine ecosystem to the terrestrial ecosystem during the breeding season.

Table 2.1. Mean (+/- se) nutrient deposition rates from faeces by great skuas at 3 different colonies (kg of nutrient ha^{-1} $year^{-1}$). n represents the number of sampling sites that deposition of faeces was recorded at.

	n	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Club						
Fetlar	15	107.07 (54.4)	49.71 (27.3)	6.03 (3.2)	94.25 (54.0)	2.60 (1.3)
Hermaness, Fild	12	61.90 (20.5)	28.74 (10.7)	3.48 (1.2)	54.49 (21.6)	1.51 (0.5)
Hermaness, North	12	95.65 (48.1)	44.41 (24.2)	5.38 (2.8)	84.19 (47.8)	2.33 (1.1)
Noss, East	12	73.05 (29.3)	33.92 (15.0)	4.11 (1.7)	64.30 (29.9)	1.78 (0.7)
Noss, West	11	107.70 (52.4)	50.01 (26.4)	6.06 (3.1)	94.80 (52.3)	2.62 (1.2)
Mound						
Fetlar	30	55.73 (18.0)	25.87 (9.5)	3.14 (1.1)	49.05 (19.1)	1.36 (0.4)
Hermaness	30	23.38 (8.9)	10.85 (4. 6)	1.32 (0.5)	20.58 (9.1)	0.57 (0.2)
Noss	30	24.20 (7.7)	11.24 (4.0)	1.36 (0.5)	21.30 (8.1)	0.59 (0.2)

Table 2.2. Mean (+/- se) nutrient deposition rates from pellets by great skuas at 3 different colonies (kg of nutrient Ha^{-1} $year^{-1}$). n represents the number of sampling sites that deposition of faeces was recorded at.

	n	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Club						
Fetlar	15	2.74 (1.7)	7.99 (5.0)	0.06 (0.0)	18.01 (11.2)	0.14 (0.1)
Hermaness, Fild	12	3.54 (1.1)	10.32 (3.2)	0.08 (0.0)	23.27 (7.2)	0.18 (0.1)
Hermaness, North	12	3.00 (1.0)	8.74 (2.9)	0.07 (0.0)	19.71 (6.6)	0.16 (0.1)
Noss, East	12	3.12 (1.1)	9.11 (3.3)	0.07 (0.0)	20.53 (7.5)	0.16 (0.1)
Noss, West	11	1.29 (0.5)	3.77 (1.6)	0.03 (0.0)	8.50 (3.5)	0.07 (0.0)
Mound						
Fetlar	30	0.80 (0.3)	2.33 (0.9)	0.02 (0.0)	5.24 (2.0)	0.04 (0.0)
Hermaness	30	0.25 (0.2)	0.72 (0.5)	0.01 (0.0)	1.63 (1.1)	0.01 (0.0)
Noss	30	0.51 (0.3)	1.49 (0. 9)	0.01 (0.0)	3.37 (2.0)	0.03 (0.0)

There is a considerable amount of error in the calculated nutrient deposition rates, especially at club sites, where the standard errors are almost 50% of the means. As a percentage around the means, the amount of error in the mean nutrient concentration in faeces and pellets accounted for between 20 and 25% and 14 and 23 %, respectively depending on the nutrient. At club sites the amount of error in the mean faecal and pellet deposition rates accounted for between 13 and 30% and 17 and 48%, respectively, depending on the club site and at mound sites, between 11 and 17% and 23 and 53%, respectively, depending on the colony.

The effect of great skuas on soil nutrient status

In general, soils in the correlative study from mounds and club sites had the greatest concentrations of total and extractable nitrogen and phosphorus (Figure 2.5 and top row of Figure 2.6). The analysis indicated that the concentration of all the nutrients measured was significantly influenced by great skua use and the colony, except for ammonium concentration, which was consistent across colonies (see Table 2.3). Furthermore, the effect of great skua use was significantly different at each colony for all nutrients. At Noss, total nitrogen and phosphorus concentration was greatest at high great skua use (mounds and club site). By contrast, at Fetlar, club site nitrogen and phosphorus concentration were not different from intra-colony control sites, while at Hermaness club site, soil nitrogen was significantly less than intra colony controls samples, and soil phosphorus no different from intra colony controls samples. Soil ammonium concentration was greatest at Fetlar and Hermaness at extra-colony control sites and not significantly different from mound or club sites, but this as not true for Noss. Soil nitrate was largely unaffected by great skuas, apart from at Noss, where nitrate concentrations were significantly elevated at club sites. Soil phosphate concentrations were least at control sites and greatest at mound and club sites, although concentrations at club sites varied with respect to mound sites: the Fetlar club site was significantly higher, whereas the club site Hermaness was significantly lower and the club site at Noss was not different.

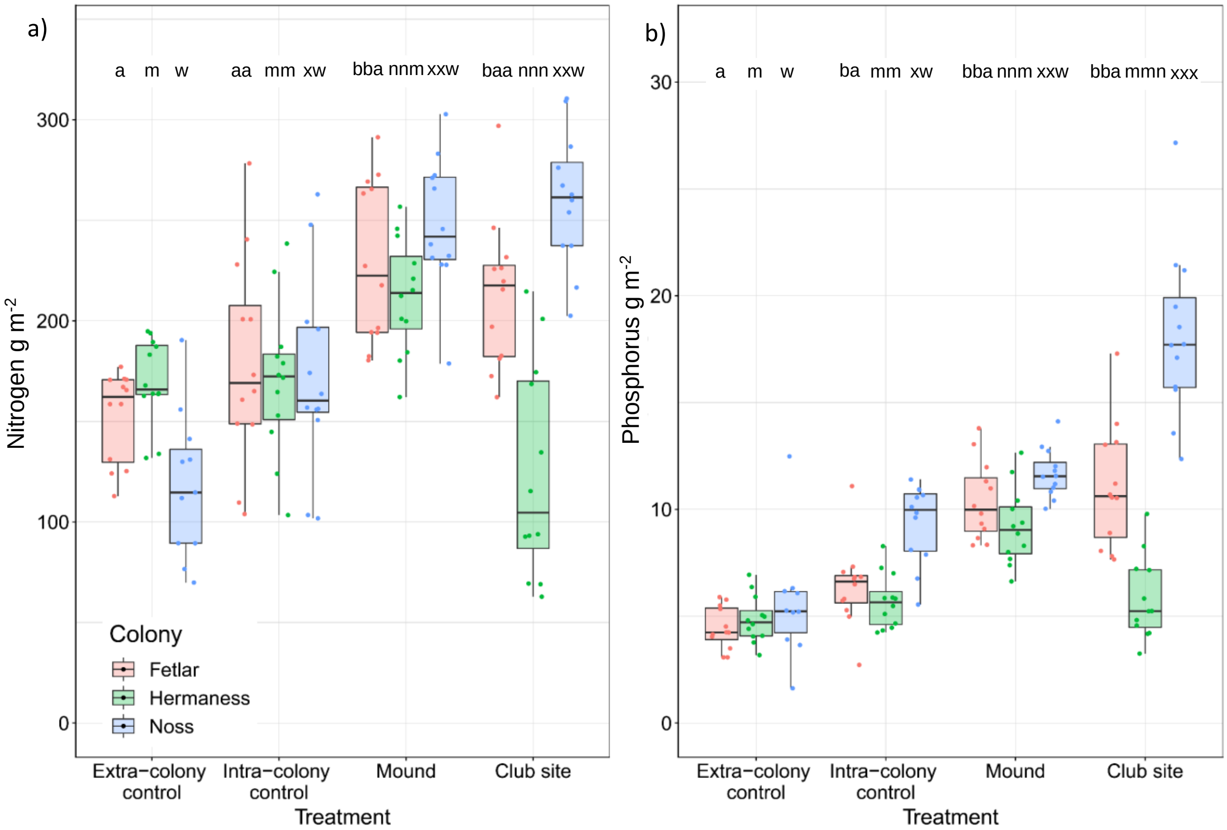


Figure 2.5 The relationship between total soil (a) nitrogen and (b) phosphorus and great skua use and colony. Each boxplot represents a colony within treatment (boxplot in style of Tukey) and each point represents a sample location. Letter codes are results from Tukey's Post-Hoc analysis, where each colony was analysed separately: the 1st letter represents sig. difference from extra-colony control sites, the 2nd from intra-colony control sites and the third from mound sites.

Table 2.3. The significance of great skua use, colony and the interaction between the two in predicting soil nutrient concentrations in the corelative study according to ANOVA. ($p > 0.1$. = ns, $p < 0.1$ = number, $p < 0.05$ = bold,)

		Great skua use			**Colony**			**Interaction**		
	Resid. df	df	F	p	df	F	p	df	F	p
Total nitrogen	131	3	29.72	**<0.001**	2	8.81	**<0.001**	6	12.66	**<0.001**
Ammonium	128	3	28.65	**<0.001**	2	2.05	ns	6	7.52	**<0.001**
Nitrate	127	3	41.17	**<0.001**	2	41.91	**<0.001**	6	18.52	**<0.001**
Total phosphorus	130	3	79.03	**<0.001**	2	58.46	**<0.001**	6	14.55	**<0.001**
Phosphate	130	3	134.8	**<0.001**	2	6.50	**<0.01**	6	16.92	**<0.001**

Table 2.4. The significance of great skua abundance at turf origin, turf location and the interaction between the two in predicting extractable soil nutrient concentrations in the manipulative study according to bootstrapped likelihood ratio tests and the how well the model fits the data without (R^2_{marg}) and accounting for (R^2_{cond}) the random effects. ($p > 0.1.$ = ns, $p < 0.1$ = number, $p < 0.05$ = bold,)

	Location		**Origin**		**Interaction**			
	LRT	p	LRT	p	LRT	p	R^2_{marg}	R^2_{cond}
Ammonium	1.35	ns	1.55	ns	2.08	ns	0.07	0.67
Nitrate	15.52	**<0.001**	4.47	**<0.05**	0.07	ns	0.37	0.55
Phosphate	11.98	**<0.001**	5.70	**<0.05**	1.20	ns	0.33	0.56

Unlike the correlative study, in the manipulation study soil ammonium concentration was not different between the club site and the intra-colony are and was unaffected by the transplant (Figure 2.6 and Table 2.4). Nitrate and phosphate concentrations were influenced by both the translocation and the origin of the turf. However, contrary to expectations, nitrate concentrations decreased when the turf was moved into the club site and increased when moved out of the club site. Whereas, phosphate concentrations increased when the turf was moved into the club site and decreased when the turf was removed from the club site. In addition, when removed from the club site the phosphate concentration was less than the intra-colony control sites (significant effect of turf origin).

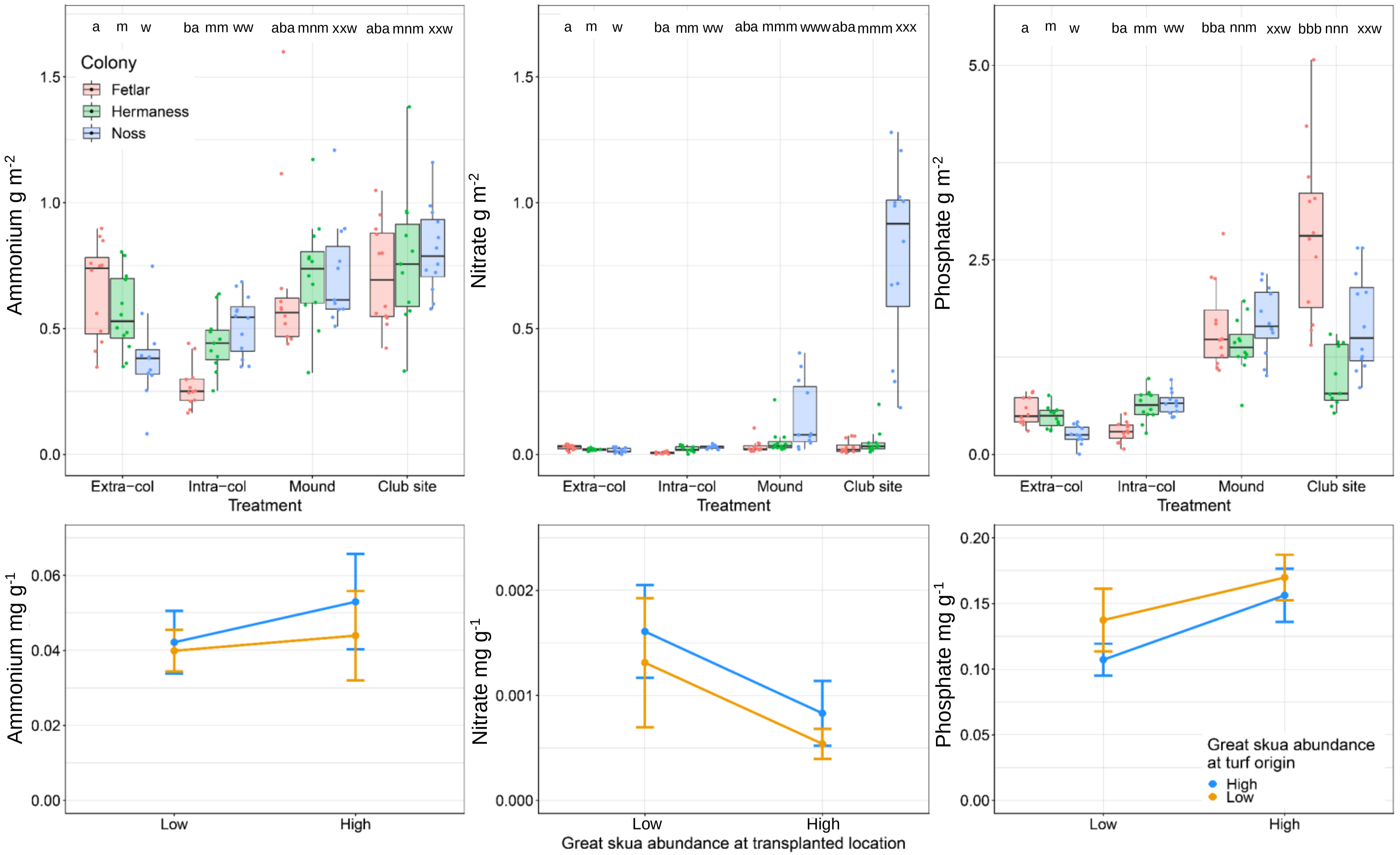


Figure 2.6. The relationship between extractable nitrogen and phosphorus concentrations in soil and great skua use in the observational study (top row) and manipulative study (bottom row). In the observational study, each boxplot represents a colony within treatment (boxplot in style of Tukey) and each point represents a sample location. Letter codes are results from Tukey's Post-Hoc analysis, where each colony was analysed separately: the 1st letter represents sig. difference from extra-colony control sites, the 2nd from intra-colony control sites and the third from mound sites. In the manipulation study, blue represents turfs that originated from areas of high great skua abundance (high to high on the right and high to low on the left), and orange represents turfs that originated from areas of low great skua abundance (Low to low on the left and Low to high on the right). Points represent sample means and error bars are 95% CI around means. Note that nutrient concentrations are expressed in different units in the corelative study (top row) and manipulation experiment (bottom row).

The effect of great skuas on plant nutrient status

A total of 264 specimens were measured for both nitrogen and phosphorus concentrations in the corelative study. Nitrogen measurements in sweet vernal grass from Hermaness were considered unreliable due to an error with the mass spectrometer and were removed from analysis. Furthermore, two extreme heather nitrogen measurements from Hermaness samples were removed from analysis (but remain in Figure 2.7). Plant nitrogen and phosphorus concentration were elevated at mound and club sites regardless of species (Table 2.5 and Figure 2.7). Both nitrogen and phosphorus concentrations were significantly influenced by great skua use in all species. Nitrogen concentration in sweet vernal grass was significantly more elevated at Noss than at Fetlar. In addition, the effect of great skuas on species nitrogen concentration was fairly consistent between colonies, with the exception of tormentil, where high nitrogen concentrations in extra-colony control sites samples likely influenced the significant interaction. Phosphorus concentration in sweet vernal grass and heather was not consistent between colonies. Furthermore, the effect of great skua use on phosphorus concentration in common cotton sedge, sweet vernal grass and tormentil was significantly influenced by colony. This finding was probably driven largely by data from Fetlar, where plants from mounds had elevated concentrations and plants from club sites had lower concentrations.

Table 2.5 The significance of great skua use, colony and the interaction between the two in predicting plant nutrient concentrations in the corelative study according to ANOVA. ($p > 0.1$. = ns, $p < 0.1$ = number, $p < 0.05$ = bold,).

		Great skua use			**Colony**			**Interaction**		
	Resid. df	df	F	p	df	F	p	df	F	p
Nitrogen										
Common cotton sedge	60	3	58.95	**<0.001**	2	3.04	0.06	6	1.79	ns
Sweet vernal grass	40	3	27.49	**<0.001**	1	15.25	**<0.001**	3	0.64	ns
Tormentil	60	3	44.76	**<0.001**	2	0.22	ns	6	2.74	**<0.05**
Heather	38	3	90.19	**<0.001**	1	0.25	ns	3	1.81	ns
Phosphorus										
Common cotton sedge	60	3	113.54	**<0.001**	2	2.61	0.08	3	2.59	**<0.05**
Sweet vernal grass	60	3	51.75	**<0.001**	2	8.13	**<0.001**	6	3.46	**<0.01**
Tormentil	60	3	49.54	**<0.001**	2	0.85	ns	6	3.54	**<0.01**
Heather	35	3	160.71	**<0.001**	1	6.67	**<0.05**	3	0.10	ns

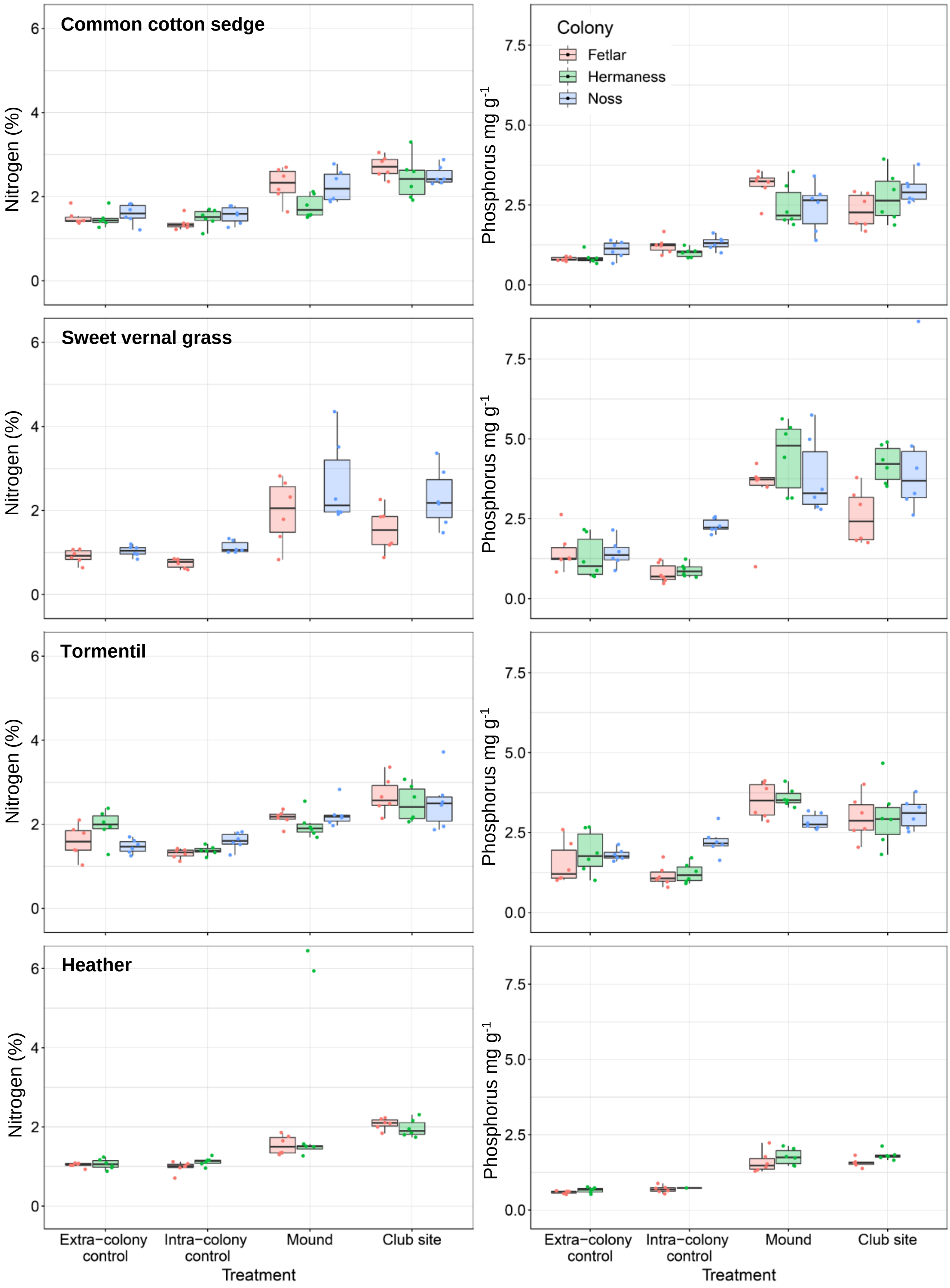


Figure 2.7 The relationship between great skuas and the concentration of nitrogen (left hand column) and phosphorus (right hand column) in common cotton sedge (top row), sweet vernal grass (2nd row), tormentil (3rd row) and heather (bottom row). Each boxplot represents a colony within treatment (boxplot in style of Tukey) and each point represents a sample location. Missing boxes (i.e heather at Noss) represent no data.

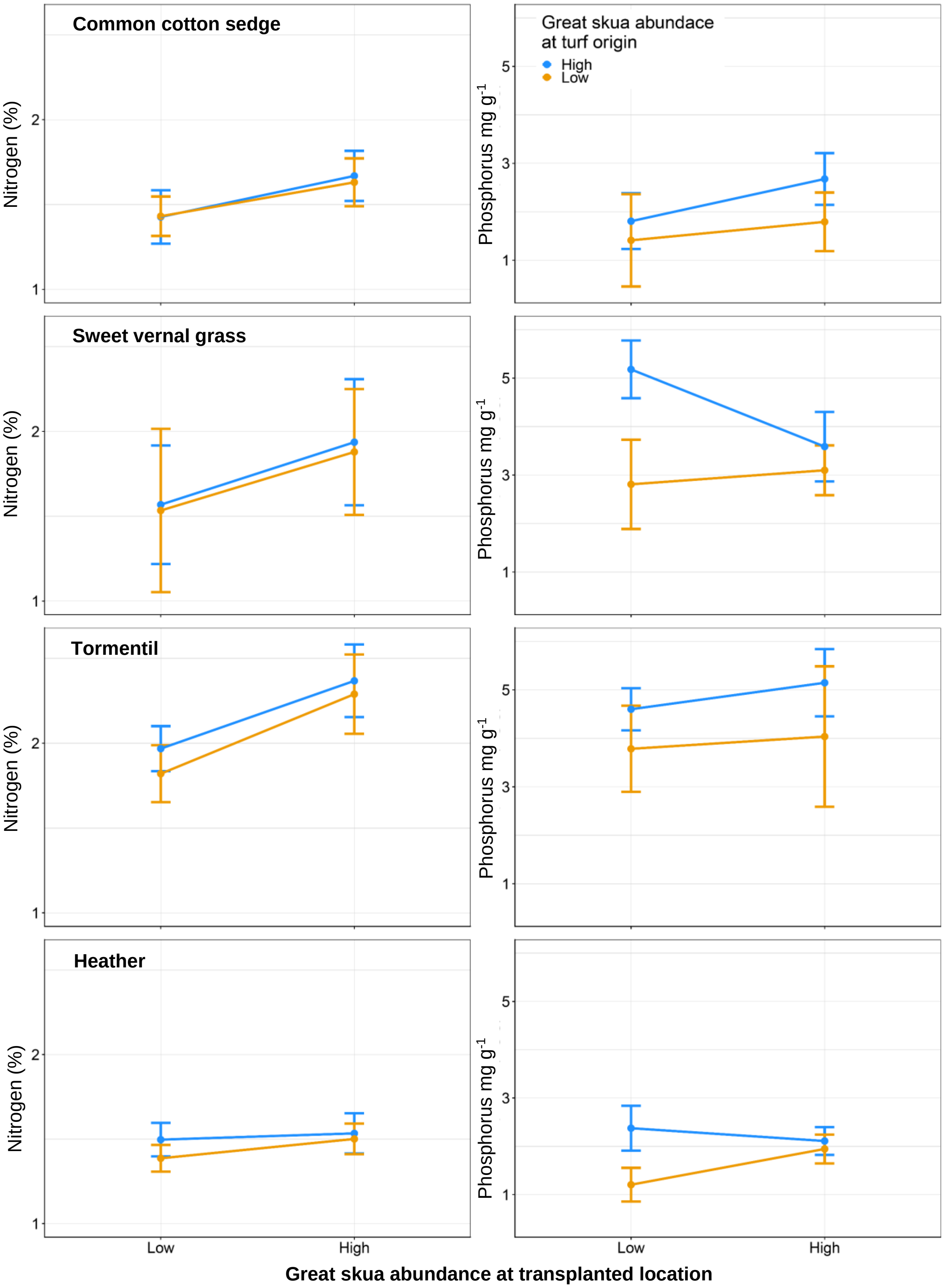


Figure 2.8 The relationship between great skuas and the mean concentration of nitrogen (left hand column) and phosphorus (right hand column) (± 95% CIs) in common cotton sedge (top row), sweet vernal grass (2nd row), tormentil (3rd row) and heather (bottom row) in the turf transplant experiments.

Table 2.6. The significance of great skua abundance at turf origin, turf location and the interaction between the two in predicting extractable soil nutrient concentrations in the manipulative study according to bootstrapped likelihood ratio tests and the how well the model fits the data without (R^2_{marg}) and accounting for (R^2_{cond}) the random effects ($p > 0.1.$ = ns, $p < 0.1$ = number, $p < 0.05$ = bold,)

	Location		**Origin**		**Interaction**			
	LRT	p	LRT	p	LRT	p	R^2_{marg}	R^2_{cond}
Nitrogen								
Common cotton sedge	5.30	**<0.05**	0.05	ns	0.02	ns	0.17	0.50
Sweet vernal grass	3.68	0.05	0.27	ns	0.23	ns	0.12	0.82
Tormentil	12.96	**<0.001**	1.74	ns	0.54	ns	0.33	0.65
Heather	3.33	0.07	1.22	ns	0.56	ns	0.13	0.21
Phosphorus								
Common cotton sedge	2.51	ns	2.36	ns	1.04	ns	0.11	0.48
Sweet vernal grass	3.66	0.06	10.87	**<0.001**	11.02	**<0.001**	0.37	0.85
Tormentil	0.81	ns	3.55	0.06	0.19	ns	0.10	0.28
Heather	3.69	0.05	7.99	**<0.01**	9.07	**<0.01**	0.41	0.63

In the manipulation experiment, plant nitrogen concentration was significantly or marginally non-significantly influenced by the translocation in all species (Figure 2.8 and Table 2.6). The nitrogen concentrations increased in plants growing in turfs that were moved into the club site and decreased in turfs moved away from club sites, to similar levels to control turfs that were not moved (high to high and low to low, respectively). Plant phosphorus concentrations, however, had a more complex relationship with the changes in great skua abundance in the turf transplant experiments, which was dependent on the plant species. There was no effect of the transplant on phosphorus concentration, and there were no significant differences between the club or intra-colony control samples in common cotton sedge. There was a marginally insignificant (P=0.06) effect of soil origin on tormentil phosphorus concentration, indicating samples from club site turfs had higher concentrations the intra-colony control turfs, and this was unaffected by the translocation. Phosphorus concentration in sweet vernal grass and heather, was significantly influenced by the origin of the turf and marginally non-significantly (P=0.05 for heather and 0.06 for sweet vernal grass) influenced by the translocation. In addition, the effect of the translocation was influenced by where the turf originated (significant interactions). In these species, when the turf was moved into the club site the phosphorus concentration increased and when the turf was moved out of the club site the phosphorus concentration also increased.

Marine derived nutrients in the terrestrial ecosystem

To identify if the increases in nutrient concentrations observed were a result of marine derived nutrients, a total of 348 samples were assessed for $\delta^{15}N$ signatures across the corelative study. Due to an error with the mass spectrometer at the time of running, ^{15}N measurements in sweet vernal grass from Hermaness were considered unreliable and were removed from analysis.

Great skua faeces and pellets had δ^{15}N signatures of 12.4 ‰ (± 0.65) and 11.0 ‰ (± 0.59), respectively, and these reflect the dominant source of marine derived nutrients (see Table 2.1). Extra and intra colony control site soils had a mean δ^{15}N signature of 1.10 ‰ (± 0.27) (Figure 2.9), which reflects the main pool of terrestrial nutrient sources to plants. In general, soils and plants from mound and club sites were enriched with ^{15}N relative to control sites. There was a significant effect of great skua use across all plant and soil samples, as well as a significant influence of the colony of origin of the samples. However, the effect of great skua use was dependent on the colony in all samples apart from sweet vernal grass (Table 2.7).

Soil samples from Fetlar and Hermaness club sites had δ^{15}N signature similar to that identified at control sites, whereas at the Noss club site the soil was enriched ^{15}N. Despite this finding, all plant species from club sites were enriched in ^{15}N relative to those from control sites. Common cotton sedge and sweet vernal grass from club sites were most enriched and had a δ^{15}N signature similar to faecal and pellet samples. Intra and extra colony control site samples for these species had a similar δ^{15}N signature to soil from the same sites. Tormentil and heather, however, were less enriched in δ^{15}N than faecal and pellet samples, and intra and extra colony control samples had a much lower δ^{15}N signature that soils from the same sites.

Table 2.7. The significance of great skua use, colony and the interaction between the two in predicting plant nutrient concentrations in the corelative study according to ANOVA. ($p > 0.1.$ = ns, $p < 0.1$ = number, $p < 0.05$ = bold,).

		Great skua use			**Colony**			**Interaction**		
	Resid. df	df	F	p	df	F	p	df	F	p
Soil	60	3	119.79	<**0.001**	2	67.69	<**0.001**	6	22.88	<**0.001**
Common cotton sedge	60	3	68.28	<**0.001**	2	7.68	<**0.01**	6	3.89	<**0.01**
Sweet vernal grass	40	3	62.90	<**0.001**	1	8.44	<**0.01**	3	0.12	ns
Tormentil	60	3	228.87	<**0.001**	2	3.80	<**0.05**	3	8.01	<**0.001**
Heather	40	3	308.18	<**0.001**	1	12.37	<**0.01**	3	3.04	<**0.05**

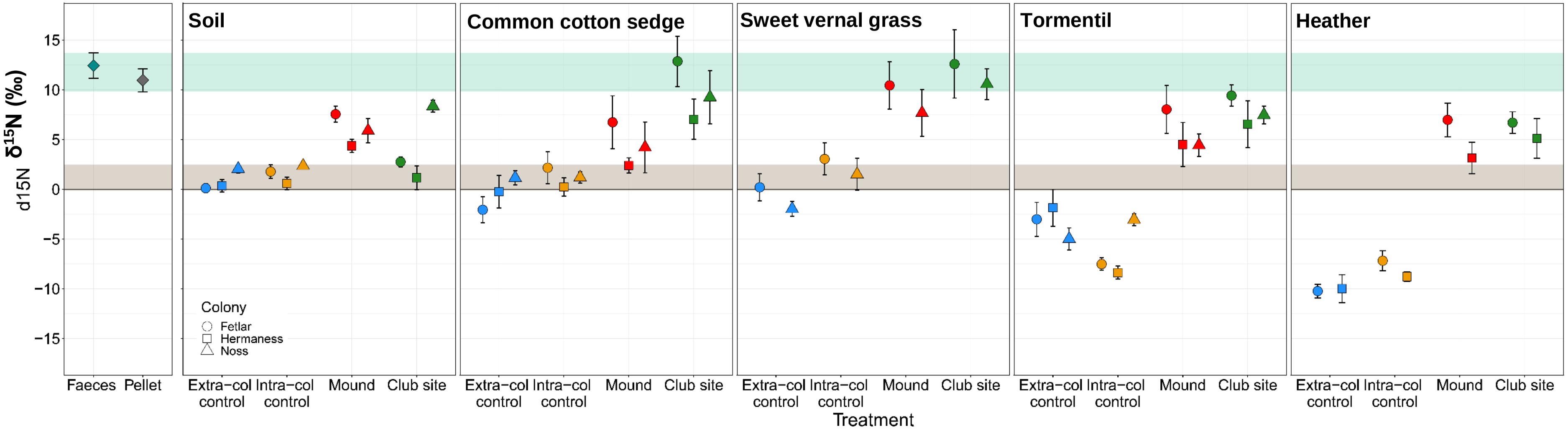


Figure 2.9 $\delta^{15}N$ signatures of great skua faeces and pellets, and the relationship between great skua use and $\delta^{15}N$ signatures in soil and plants. Each large point represents a mean $\delta^{15}N$ signature of a sample (n = 6) and the error bars are ± 95% Cis. The colour represents different great skua use (blue – extra colony control, orange – intra-colony control, red – mound and green – club) and the shape represents the colony (circle – Fetlar, square – Hermaness and triangle – Noss). The green rectangle in each graph represents the upper and lower confidence intervals of the faecal and pellet $\delta^{15}N$ signature, whereas the brown rectangle represents the upper and lower confidence intervals of control soil $\delta^{15}N$ signature. The distance of plant samples from these rectangles is an indication of the source of nitrogen for that species. For example, common cotton sedge at Fetlar club sites fall within the green rectangle indicating that the majority of nitrogen comes from a marine source, whereas, common cotton sedge from mound samples are between the two indicating that the nitrogen in partially from the marine environment.

DISCUSSION

The aim of this chapter was to quantify the amount of marine derived nutrients transported by great skuas, determine whether these are incorporated into the terrestrial ecosystem and identify the effects on the nutrient status of soil and plants. Here I show that through their faeces and pellets, great skuas deposit marine derived nitrogen and phosphorus as well as other essential plant nutrients at extremely high rates. Marine derived nutrients are assimilated by plants regardless of life history, and the nitrogen and phosphorus concentrations largely reflected great skua abundance. However, there were exceptions: when heather and sweet vernal grass were exposed to a lower abundance of great skuas using a transplant technique, leaf phosphorus concentrations increased. Changes in plant nutrient concentrations were generally reflected in nutrient concentrations in mound soils but not all club site soils. Changes in nutrient acquisition by plants can influence plant productivity and community composition, especially in ombrotrophic bogs where species are adapted to nutrient-poor conditions (Chapter 4). These changes can influence ecosystem processes as well primary consumers, or species reliant on the plant structure for shelter with cascading effects throughout the ecosystem (Chapter 3 and 5).

Nutrient inputs

The rate of marine nitrogen deposition at club sites (91.8 kg N/Ha/yr) exceeded and the rate of deposition at mound sites (34.9 kg N/Ha/yr), and is double the highest modelled rates of wet and dry atmospheric deposition in the UK at the Peak District and Lake District (35 – 45 kg N/ha/yr) (CEH, 2014). Skua-derived marine nitrogen deposition in both club and mound sites far exceeds the average background rates of deposition in Shetland (10.01 kg N/Ha/yr) (CEH, 2014). These findings clearly demonstrate the importance of marine derived nitrogen for plant nutrition in coastal, marginal ecosystems, where there are few other sources of nutrients such as emissions from industry or leaching from neighbouring agriculture (Wilson *et al.*, 2004).

Several other studies have measured or modelled seabird nutrient deposition, although few have focused on great skuas. Cross (2014) estimated that the whole great skua colony on Mingulay deposited 113-173 kgN/Ha/yr using a bioenergetic model, which equates to approximately 1.51 - 2.30 kg N/Ha/yr per breeding pair. This estimate is much less than any of the measurements from my work at mound sites, even when accounting for the large variability in the data. However, their model estimated nitrogen deposition rates for the whole breeding pairs territory, whereas the figure measured here focused on just the mounds, which is not necessarily representative of the entire territory. Furthermore, in bioenergetic models, small errors in parameters can have large effects on outputs. Cross (2014) notes that an error of just 2% in estimating great skua basal metabolic rate affected the model output by up to 12%, which would have brought the estimates in line with my measurements. Model estimates for other seabird species have also focused on nitrogen deposition at a colony scale. Macaroni penguins in South Georgia deposit an estimated 114,240 kg N/Ha/ yr, the colony of gannets on Bass Rock (150,000 pairs) are estimated to deposit 52,200 kg N/Ha/yr and the seabird colony on the Isle of May (46,000 pairs) deposit an estimated 1,420 kg N/Ha/yr (Blackall *et al.*, 2007; Riddick *et al.*, 2012). It is difficult to make direct comparisons between these studies, and with the excretion rates measured here, due to the different scales that they were measured (Colony vs club site/individual mound). However, given the areas of Bass Rock (9 ha) and the Isle of May (70 ha), this equates approximately 494,000 kg N/yr and 101,000 kg N/yr deposition, respectively, which are much higher than the estimated 22.7, 19.8 and 13.3 kg N/yr deposited by great skuas at the Fetlar, Hermaness and Noss colonies. Bancroft, Garkaklis and Roberts (2005) measured nutrient deposition at a wedge tailed shearwater colony on Rottnest Island, Australia. They measured deposition rates of 50.86 kg N, 3.61 kg P, 5.67 kg K, 3.45 kg Ca and 1.26 kg Mg per hectare per year. Again, it is difficult to make direct comparisons due to the large differences in methodologies, however, great skua faeces contained much higher relative concentrations of phosphorus and calcium, which highlights the importance of identifying species specific inputs.

The nutrient inputs varied considerably between colonies. Interestingly, breeding skuas at Fetlar had a much greater deposition rate than Hermaness or Noss. There are two potential explanations for this. First, skuas at Fetlar could have had a more accessible food resource, which would reduce commuting and foraging time and increasing the amount of time that they spent at the colony. Second, the vegetation present at Fetlar could have restricted where skuas were able to land. Heather attained the greatest height at Fetlar, less so at Hermaness and was rare at Noss and individual skuas were noted in intra-colony control sites at Noss and occasionally at Hermaness, but never at Fetlar (data not shown). Therefore, colony vegetation may influence the concentration and distribution of marine nutrients in the terrestrial ecosystem.

Changes in marine management that reduce prey abundance are likely to result in skuas spending more time away from the colony, decrease the non-breeding skua colony attendance and reduce population sizes, which will all reduce nutrient inputs (Votier, Furness, *et al.*, 2004; Bicknell *et al.*, 2013). Changes in great skua prey abundance may also lead to prey switching (Votier, Bearhop, *et al.*, 2004; Church *et al.*, 2018). Several alternative prey resources have been identified including other seabirds and rabbits. Other seabirds such as puffins will also be rich in marine nitrogen and phosphorus and therefore not stop the flow of nutrients from the sea onto the land. If rabbits increased in great skua diet however, this would reduce the flow of marine nutrients. Furthermore, rabbits are terrestrial herbivores and therefore less likely to be as rich in nitrogen and phosphorus, potentially resulting in reduced nutrient inputs (Votier, Bearhop, *et al.*, 2004).

Marine nutrients in the terrestrial ecosystem

In line with the first hypothesis, higher concentrations of total and extractable nitrogen and phosphorus were recorded in the soil at most mound and club sites. Furthermore, in line with the third hypothesis, stable isotope analysis confirmed that these nutrients were marine derived. This is consistent with a number of other studies that identified elevated marine derived nutrient concentrations in the soil in seabird colonies (Hogg and Morton, 1983; Anderson and Polis, 1999; Croll, 2005; Ellis, Fariña and Witman, 2006; Maron *et al.*, 2006; Caut *et al.*, 2012; Kolb, Palmborg and Hambäck, 2013). A notable exception to this was at Hermaness and Fetlar club sites, where ^{15}N enrichment and total nitrogen and phosphorus concentrations were similar or less than control sites. Furthermore, the change in the extractable nutrients in the manipulation experiments did not fully support the observational results. Extractable phosphorus in the soil declined when exposed to a lower great skua abundance and increased when exposed to a higher great skua abundance, as expected. However, there was no effect on ammonium and the opposite was observed for nitrate, although this is a very small change and unlikely to significantly influence plant nutrition, despite being statistically significant. This finding also contradicts other studies that found declines in nitrogen and no change in phosphorus following decreased seabird abundance (Wardle *et al.*, 2009; Kolb, Palmborg and Hambäck, 2013). However, these studies measured total nutrient levels and not extractable nutrients.

In line with hypothesis 2 and 3, all plants, regardless of life history, growing in areas of high great skua use had greater nitrogen and phosphorus concentrations and were enriched in ^{15}N indicating that marine nutrients were being assimilated in plant tissue. This is consistent with a large number of other studies that have identified marine nutrients in plants in seabird colonies as well as at higher trophic levels (Croll, 2005; Kolb, Jerling and Hambäck, 2010; Callaham Jr. *et al.*, 2012; Caut *et al.*, 2012; Cross *et al.*, 2014). All plant species that were measured at Hermaness and Fetlar club sites were also enriched in ^{15}N, despite the lack of a marine signature in the soils. This suggests that plants are accessing the marine nutrients directly and little if any nutrients are being retained in either the bulk soil or the soil microbial community, and excess nutrients are likely being leached or lost as NH_3 or N_2O. These processes have been observed in several other habitats that are subject to high levels of deposition, and losses appear to be related to pH. For example in European forests, more nitrogen was lost from sites that had low pH (Dise and Wright, 1995). Fetlar and Hermaness have a lower pH than Noss, which may in part explain the increased losses. Furthermore, the plant community at Fetlar and Hermaness was more similar to the control sites than at Noss (see Chapter 4). The greater abundance of species such as heather in Fetlar and Hermaness that retain the marine nutrients, rather than species such as Yorkshire fog (dominant at Noss) that produce more nutrient rich litter may in part explain the differences in the club sites.

The δ^{15}N signatures of the plants at high use sites varied. The two graminoids, common cotton sedge and sweet vernal grass had signatures similar to faecal and pellet samples, however, tormentil and heather were less enriched. In the control sites the graminoid species had a signature similar to the control soil, whereas the tormentil and heather signature was much lower. Differences between foliar and soil δ^{15}N signatures such as this are suggest that in control sites, in nutrient limited conditions, tormentil and heather are reliant on mycorrhizal symbionts for nitrogen acquisition (Hobbie, Macko and Shugart, 1999). In high use sites, however, the δ^{15}N signatures are more similar to the great skua faeces and pellets, especially at Fetlar. This may indicate that the increased nutrient availably caused by great skuas alters shifts nutrient acquisition pathways from mycorrhizal to simple direct assimilation through the roots, however, further work is needed to confirm this.

The manipulation experiments largely supported the correlative experiments when plants are exposed to greater levels of great skua abundance. When exposed a lower density of great skuas, leaf nitrogen declined in all species, however, phosphorus did not and increased in sweet vernal grass and heather. A number of other studies have identified elevated phosphorus but not nitrogen concentration in response to declining input. On islands where rats reduced the density of seabirds Wardle *et al.*, (2009) identified an associated decline in nitrogen cycling but not phosphorus and Kolb, Palmborg and Hambäck, (2013) identified that phosphorus remains high in abandoned sites. Furthermore, this same effect has been noted in response to livestock abandonment experiments (Marriott *et al.*, 2010). Sweet vernal grass and heather have very different growth forms and life strategies. Sweet vernal grass is a fast growing graminoid species. Therefore, the increase in phosphorus concentration in this species may be due to its predilection for rapid lateral growth in the absence of great skua disturbance. Heather, however, is slow growing and when nutrients are in excess plants will assimilate nutrients at a faster rate than they are used and store them for times of limitation (Grime *et al.*, 1997).

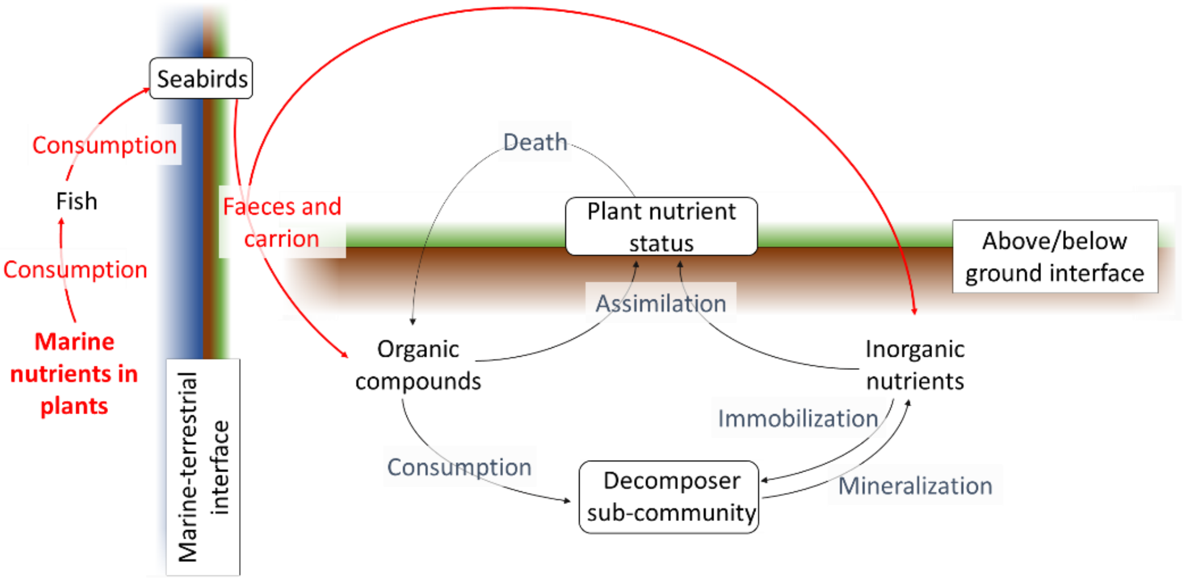
Conclusion

Great skuas facilitate the flow of nutrients from the marine ecosystem into terrestrial plants. Large quantities of essential plant nutrients are deposited into the terrestrial ecosystem by great skuas, which feeds into plant nutrition, regardless of species and life history traits and potentially causes shifts in plant nutrient acquisition pathways. Reducing great skua abundance decreases foliar nitrogen but not phosphorus concentration, suggesting declines in nitrogen but not phosphorus cycling. Soil nitrogen and phosphorus concentration did not increases at all high use sites, potentially due to local soil moisture, pH and plant community composition, but indicating that plants are rapidly assimilating the marine derived nutrients they require, and the excess is lost through surface run-off or leached through the soil. Plant nutrient status and acquisition influences several key ecosystem functions such as decomposition rates and plant community assemblage, therefore the changes identified here are likely to affect the entire terrestrial ecosystem.

Restructuring of fisheries management policy currently underway in parts of Europe is expected to cause a significant shortfall in food availability for scavenging seabirds, such as great skuas. The predicted impact wills impair their function as a mobile link species, reducing marine derived nutrient inputs into the terrestrial ecosystem. My work suggests that, as a result, foliar $\delta^{15}N$ signatures and nitrogen to phosphorus ratios in plants will decline, with potential cascading consequences for the entire ecosystem.

CHAPTER 3

MARINE RESOURCE INPUT BY GREAT SKUAS INCREASES THE RATE OF NUTRIENT CYCLING



ABSTRACT

The spatial coupling of ecosystems through flows of energy, material and organisms across ecosystem boundaries has resulted in the concept of meta-ecosystems. Species moving between ecosystems can act as biotic vectors of these items and can be essential to maintaining the meta-ecosystem. Given the increasing threat to species movement and biodiversity from anthropogenic activity such as climate changes and habitat destruction, a greater understanding of how meta-ecosystems function and the role that mobile species play can provide a better insight to how actions at a local scale can cascade into coupled ecosystems and influence whole landscapes. Throughout this thesis I use the marine-terrestrial meta-ecosystem connected by the seabird great skua as a model system to investigate this. In this chapter I address how changes in great skua abundance influences the function of below ground biota in controlling nutrient cycling. I used a fully factorial litter bag experiment to identify if elevated plant nutrients or marine derived nutrient induced changes in soil influence rates of litter decomposition. In addition, I use an in-situ bury-in-the-bag experiment in observational and manipulation studies to identify the influence of marine derived nutrient deposition on mineralization rates. I show that increased plant nutrient concentrations drive rapid initial loss mass and release of nitrogen and phosphorus from decomposing litter, but the soil has relatively little effect. In addition, increases in great skua abundance has a negligible effect on rates of mineralization. In combination with the work in Chapter 2 this suggests that rates of mineralization are not influencing plant nutrient assimilation indicating that plants are accessing nutrients through simple abiotic pathways. In addition, this suggests a decoupling of mineralization and decomposition. It is unclear if nutrients released during decomposition are lost or recycled and more work is needed to confirm this. Restructuring of fisheries management policy currently underway in parts of Europe is expected to cause a significant shortfall in food availability for scavenging seabirds, such as great skuas. The predicted impacts will impair their function as a mobile link species, reducing marine derived nutrient inputs into the terrestrial ecosystem. Given the opposing effects of leaf nitrogen and phosphorus concentrations when exposed to lower great skua abundance, such changes are likely to result in reduced nitrogen but not phosphorus cycling, with potential consequences for the entire ecosystem, specifically plant and invertebrate communities.

INTRODUCTION

A meta-ecosystem comprises multiple ecosystems connected by flows of energy, materials and organisms as one functioning unit (Loreau, Mouquet and Holt, 2003). Biotic vectors such as mobile species can greatly enhance the mobility of these items, increasing the strength of the connections between ecosystems (Bauer and Hoye, 2014). Under the meta-ecosystem conceptual framework, sink ecosystems exist in an alternative stable state, that is reliant on the connection with the source ecosystem and any disturbance in the source ecosystem is likely to also impact the recipient ecosystem (Loreau, Mouquet and Holt, 2003; Lundberg and Moberg, 2003). Given the increasing threat to species movement and biodiversity in general, a greater understanding of how meta-ecosystems function and the role that mobile species play in that functioing is essential to determine likely outcomes of how changes at a local scale can cascade into coupled ecosystems and influence whole landscapes.

Seabirds forage on marine resources and form breeding colonies in terrestrial environments, mobilising nutrients across the marine-terrestrial interface, either directly in the form of droppings and carrion or as a result of volatilization and wet and dry deposition (Ellis, 2005; Blackall *et al.*, 2007). Marine derived nutrient subsidies initiate above and below-ground trophic cascades indicative of elevated fertility (Wardle *et al.*, 2004). Above ground, increased plant nutrient concentrations and productivity and shifts in plant community dominance, have been recorded in and around seabird colonies (Mizutani and Wada, 1988; Hogg, Morton and Venn, 1989; Anderson and Polis, 1999; Croll, 2005; Ellis, Fariña and Witman, 2006; Maron *et al.*, 2006). Below ground, studies in seabird colonies have identified changes in fungal communities and a decrease in fungi-to-bacteria ratio as well as an increased in overall soil microbial biomass and activity, and high nematode, enchytraeid, rotifer and earthworm abundance relative to the non-seabird areas (Fukami *et al.*, 2006; Osono *et al.*, 2006; Towns *et al.*, 2009; Wright *et al.*, 2010; Callaham Jr. *et al.*, 2012; Durrett *et al.*, 2014). Furthermore, elevated levels of δ^{15} N have been identified at multiple trophic levels above and below ground, providing direct evidence for a role in marine derived nutrients in the terrestrial ecosystem (Croll, 2005; Kolb, Jerling and Hambäck, 2010; Callaham Jr. *et al.*, 2012; Cross *et al.*, 2014).

Above and below ground components of terrestrial ecosystems are interlinked via a number of ecosystem processes and therefore respond to environmental cues simultaneously (Putten *et al.*, 2001; Wardle *et al.*, 2002, 2004; Bardgett *et al.*, 2006). One key process is nutrient cycling. Plants acquire nutrients through the root system, which are returned below ground via leaf litter. The soil fauna, flora and microbes that comprise the decomposer community then physically and chemically breakdown the litter to simple organic compounds and inorganic nutrients. These are either released into the environment (mineralization) or retained within the decomposer community (immobilization), depending on the individuals nutritional requirements, directly influencing plant nutrient availability and acquisition (BassiriRad, 2005; Moore *et al.*, 2006).

A number of authors suggest that the above and below ground changes observed in seabird colonies are indicative of marine derived nutrient subsidies increasing the rate of terrestrial nutrient cycling (Fukami *et al.*, 2006; Wright *et al.*, 2010). Indeed, theoretically, increased nutrient availability promotes fast growing, short-lived plants, and reduces nutrient resorption efficiency, which would reduce the carbon to nutrient concentration ratio in litter, favouring bacterial- over fungal-based decomposition pathways and enhance decomposition and nutrient mineralization rates (Swift, Heal and Anderson, 1979; Bardgett *et al.*, 1999; Vesterdal, 1999; Wardle *et al.*, 2004; de Vries *et al.*, 2006; Parton *et al.*, 2007; Hobbie, 2008; Kobe, Lepczyk and Iyer, 2009). However, there is currently little empirical data supporting this in seabird colonies. Wardle et al. (2009) found that seabird predation by rats restricted the transfer of marine derived nutrients onto the land and significantly reduced nitrogen but not phosphorus cycling. Furthermore, Hawke and Vallance (2015) suggest that the carbon limitation observed in the microbial community in seabird colonies is indicative of rapid decomposition and mineralization of fresh plant litter and faeces driven priming of soil organic matter mineralization. However, neither Wright *et al.* (2010) nor Durrett *et al.* (2014) identified any significant effect of marine derived nutrients on either ammonium or nitrate mineralization rates.

In Chapter 1 I demonstrated that elevated marine derived nutrient deposition by great skuas increased plant leaf nutrient concentration and soil nutrient concentrations. The aim of this study is to determine how these changes in nutrient pools influence rates of nutrient cycling and in doing so provide a mechanistic explanation for the observed effects of seabirds on the above and below ground biota. Given that it is difficult to measure nutrient cycling directly, hypotheses were divided into two main lines of enquiry: the effect on leaf litter decomposition and nutrient loss and the effect on nutrient mineralization. First, senescing plant material was used to test the hypothesis (1) seabirds decrease the carbon to nutrient ratios by increasing the marine derived nitrogen and phosphorus in the fresh leaf litter. Subsequently, a fully factorial litter transplant experiment was established to test the hypotheses (2) changes in litter chemistry by seabirds resulted in increases in decomposition rates and nutrient loss, and (3) seabird guano could prime the decomposition of leaf litter. Finally, correlative and manipulative studies were used to test the hypothesis (4) marine nutrient deposition by seabirds increases nitrogen and phosphorus mineralization rates within the soil. In addition, given that microbial community composition, activity and function are determined by more than just nutrient availability (Berg *et al.*, 1993; Couteaux, Bottner and Berg, 1995; Aerts, 1997; Leirós *et al.*, 1999; Schmidt, Jonasson and Michelsen, 1999; Wilson *et al.*, 1999; de Vries *et al.*, 2006; Tóth *et al.*, 2017), sample locations used in the correlative study were described by edaphic conditions that vary both dependently and independently of seabirds.

METHODS

Study system

The litter transplant experiment, correlative study and manipulation experiments were established at three large great skua *Stercorarius skua* colonies in Shetland: (i) Lamb Hoga peninsula, Fetlar (Fetlar), (ii) Hermaness National Nature Reserve, Unst (Hermaness) and (iii) Isle of Noss National Nature Reserve (Noss) (see Figure 2.2). All sites comprise blanket peat bog. The vegetation communities at Fetlar and Hermaness have affinities to National Vegetation Classification (NVC) community M19 *Calluna vulgaris – Eriophorum vaginatum* blanket mire blanket mire vegetation, whereas that at Noss has a greater affinity to NVC community M17 *Trichophorum cespitosus – Eriophorum vaginatum* blanket mire and M15 *Trichophorum cespitosus – Erica tetralix* wet heath, as there is a reduced abundance of *Calluna vulgaris* largely due to historic land use (Rodwell (eds), 1991).

Great skuas form breeding colonies inland and are ground nesters. Consequently, faeces and carrion and therefore, marine derived nutrients are deposited directly into the terrestrial ecosystem. Great skua abundance across the colony is not homogeneous, but comprises a loose collection of breeding territories, each one containing the nest and at least one raised mound on which the birds stand to observe their territory. In addition, within larger colonies, there are one or more discrete areas called "club sites" where immature, non-breeding birds form large aggregations of between 10 and 200 individuals (Furness, 1987). Most of the land area of a colony away from nests, mounds and club sites is used infrequently by great skuas and is referred to here as the "intra-colony" This colony organisation of different areas of contrasting skua usage (and therefore contrasting marine nutrient input) provides an ideal system in which to test hypotheses about the great skua abundance on nutrient cycling.

The effects of marine derived nutrients on decomposition

Litter bag study design

To test whether seabirds increase the marine derived nitrogen and phosphorus in litter (hypothesis 1), senescing graminoid plant material was collected at random from a club site and an adjacent area of intra-colony control site at the North Hermaness colony (see Figure 2.1, Chapter 2). Litter was air dried, cut to approximately 2 cm strips and thoroughly mixed to produce two bulk samples of club and control litter. Litter was stored in dry, dark conditions prior to chemical analysis and use in the litter bag experiment.

To test whether changes in litter chemistry influenced decomposition and marine derived nutrient primed decomposition (hypothesis 2 and 3), a fully factorial litterbag experiment was conducted over 24 months. A total of 240 nylon mesh litter bags, measuring 4.5 cm x 4.5 cm, with a 1 mm aperture, were filled with 0.5 g of either club (120 litter bags) or control litter (120 litter bags). The size of the mesh was a trade-off between allowing the decomposition community to access the litter bags whist preventing litter loss through the holes in the bags.

Litter bags were buried vertically in the top 5 cm of soil in a block formation at both club and intra-colony control sites at Hermaness (n =12). Blocks were separated by at least 5 m, litter bags containing the same litter type were separated by approximately 30 cm and litter of different types by approximately 1m. Litter bags were incubated for 3, 6, 12, 18 and 24 months. For logistical reasons bury dates were staggered: 12, 18 and 24 month harvests were buried in July 2016 and 3 and 6 month harvests were buried at the end of May 2017 and July 2017, respectively (see Table A1 in Appendices). This strategy meant that different incubation periods would potentially be decomposing under slightly different conditions (i.e. differences soil temperature, moisture etc. in July 2016 and July 2017). However, in order to minimise this, 3 and 6 month incubations were buried at a similar time of year to the longer term incubations.

Once harvested, litter was air dried and roots and soil were removed by hand. The litter was weighed to determine mass loss and stored in dry, dark conditions prior to undertaking chemical analysis.

Sample processing and chemical analysis

Stable isotope analysis was used to determine if the nitrogen in the leaf litter was marine derived. The light nitrogen isotope (^{14}N) is preferentially used in intracellular metabolic processes and therefore the ratio of ^{14}N and ^{15}N increases at higher trophic levels. Seabirds are apex predators and nitrogen in their excreta is enriched in ^{15}N compared to terrestrial nitrogen sources (Rubenstein and Hobson, 2004). Therefore, if marine derived nutrients are causing changes in litter chemical composition, the litter from club sites should be enriched in ^{15}N compared to that at control sites.

Replicate bulk samples of club and control litter (n = 6) were analysed for the ratio of ^{14}N and ^{15}N using continuous-flow isotope ratio mass spectrometry (CF-IRMS, Costech ECS 4010 elemental analyser and Thermo Finnigan Delta Plus XP mass spectrometer) at the Life Sciences Mass Spectrometry Facility at Scottish Universities Environmental Research Centre in East Kilbride. Results are expressed in $\delta^{15}N$ (‰) deviations from the international standards.

To determine how marine nutrient deposition influenced initial litter conditions and the loss of nutrients from the litter over time, the concentration of carbon, nitrogen and phosphorus was measured in replicate bulk samples of initial litter (n = 12) and residual litter material after incubation. Prior to all chemical analysis litter was ball-milled to a fine homogenous powder. Carbon and nitrogen concentrations were quantified using an automated elemental analyser (FlashSmart, Thermo Scientific). Phosphorus concentration was determined using a nitric acid microwave digest (MARS 6, CEM) and subsequent analysis using ICP-OES (iCAP 6000, Thermo Scientific). Data are expressed as nutrient concentrations and percentage change of absolute values (concentration multiplied by dry weight of litter) from initial values for the initial litter conditions and the change in nutrient content over time, respectively.

The effects of marine derived nutrients on nitrogen and phosphorus mineralization

Study design

To test whether marine nutrient deposition by seabirds increase nitrogen and phosphorus mineralization rates (hypothesis 4) a correlative study and manipulation experiment were undertaken. The sample locations were the same as those selected in correlative study in Chapter 2. Briefly, the study used natural variation in great skua abundance across colonies to identify two high abundance treatments, club sites and mound sites, and a low abundance treatment, intra-colony control sites. At each colony, samples areas were established within a single club site in a grid formation (n = 12), at mound sites in randomly selected breeding territories within 0.5 km radius of the club site (n = 12) and at intra-colony control sites, approximately 20-30 m on a random bearing from each of the mound sites (n = 12). Furthermore, to determine if there is a colony scale effect of great skuas each colony had a paired extra-colony control site, where sampling sites were established in a grid formation separated by at least 15 m (n = 12) (see Chapter 2 for definitions and more detail of treatments and Figure 2.2 in Chapter 2 for a map of sampling areas and sites)

To empirically test the effect of marine nutrient deposition on nitrogen and phosphorus mineralization (hypothesis 4), a manipulation experiment was conducted, where turfs were exposed to higher and lower great skua abundance using reciprocal turf transplants. This experiment used the same turfs as the turf transplant experiment described in Chapter 2. Briefly, in March 2016, in a separate area of the Hermaness colony used for the correlative study, pairs of turfs in a block design (n =12) were cut from a club site and an adjacent area of intra-colony control site and placed into freely draining plastic boxes. One of the pair was reciprocally transplanted with the corresponding block in the club or intra-colony control site, while the other was placed back into the hole it was cut from (to act as a control). This established four different treatments:

1. Club site to club site (high to high great skua abundance),
2. Club site to intra-colony control site (high to low),
3. Intra colony control site to club site (low to high), and,
4. Intra-colony control site to intra-colony control site (low to low)

See Figure 2.3 in Chapter 2 for a map of the experimental set up.

In-situ buried bag experiments

The in-situ buried bag method was used to measure mineralization rates in both the correlative study and the manipulation experiment. Two duplicate soil cores (diameter = 4 cm, depth = 10 cm) were collected from each sampling location and turf. Initial concentrations of ammonium, nitrate and phosphate were determined from one of each pair of cores. The second core was placed in polythene bag to prevent plants from accessing and removing mineralized nutrients and was incubated at the sample location at a depth of approximately 5cm. Ammonium, nitrate and phosphate concentrations are measured in the buried core and the mineralization rate is the change in concentration over time. In the correlative study, soil cores were incubated for three months, between June and August 2017. In the manipulation experiment, cores were incubated in for a month each year in July 2017 and July 2018 (i.e. after turfs were exposed to increased and decreased great skua abundance for 16 and 28, respectively).

Sample processing and chemical analysis

Once the soil cores were returned to the laboratory, they were air dried, ground using a pestle and mortar and sieved to 2 mm before being stored in dry dark conditions prior to chemical analysis.

Ammonium and nitrate, and phosphate were extracted by shaking 5 g of soil in 100ml 1M KCl for 1 hour and 5g of soil in 150 ml of 2.5% Acetic acid for 2 hours, respectively. Where less soil was available the same ratio of soil to extractant was used. Nitrogen extractants were stored at -20ºC, while phosphate extractants were stored at 4ºC, prior to analysis using a SEAL AutoAnalyzer 3 constant flow analyser system (Seal Analytical, UK).

Ammonium, nitrate and phosphate concentrations in the correlative study were converted to weight per unit area using the soil bulk density. At each sample location a second core was taken using a bulk density sampler (diameter = 5.4 cm, depth = 5.9 cm). Soil was air-dried and weighed to determine dry weight per volume of soil. This conversion corrects for any influence the physical soil properties may have on resource availability and allows for the accurate comparison of samples over a large geographical area. This was not considered necessary for the manipulation experiment as it occurred within the same geographical location.

Determining soil characteristics

To determine how edaphic conditions vary dependently and independently of great skuas, soil pH, moisture, total nitrogen, total phosphorus and soil temperature were measured at each of the sample locations in the correlative study. A subsection of the soil core used to measure initial conditions in the mineralization experiment (above) was used to determine pH, moisture content, total nitrogen and total phosphorus. pH was measured using fresh subsamples in a 3:1 distilled water to soil ratio slurry suspension using a pH probe calibrated between 4 and 7 (pH210 Meter, Hanna Instruments). Moisture content was measured gravimetrically; fresh soil was weighed, dried at 105ºC for 24 hours and then re-weighed. Total nitrogen was measured on an elemental analyser (Vario EL cube, Elementar); soil was dried at 105ºC for 24 hours and ball milled to a fine homogenous powder. Total phosphorus was measured using Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES, iCAP 6000, Termo Scientific). The soil was air dried, ground using a pestle and mortar and sieved to 2 mm before being digested in concentrated nitric acid in a microwave digestion system (MARS 6, CEM). The resulting solution was diluted, and total phosphorus measured. Soil bulk density was used to express water and nutrient content in water to soil volume ratio and weight per unit area, respectively.

Soil temperature was measured at a depth of 5cm at each sample location using a moisture meter and temperature probe (HH2, Delta-T Devices) on five separate occasions evenly spread out between June and August 2017.

Statistical analysis

To test the effect of marine nutrient deposition on litter chemical composition (hypothesis 1), differences between control and club litter chemical composition (carbon, nitrogen, phosphorus, C:N, C:P and $\delta^{15}N$) were analysed with ANOVA.

The effects marine nutrient deposition on the rate of litter mass loss (hypothesis 2) was assessed using linear mixed effects models. Litter origin (two levels – club or control site), bury location (two levels – club or control site) and incubation time and their interactions were used as fixed factors and, to account for non-independence between the samples, incubation time and bury location block (n = 12) were used as random factors. Potential changes in decomposition rate over time was accounted for by applying non- linear functions (log and a single polynomial) to incubation time and the best model was selected using AIC. The effect of litter origin and bury location on the rate of mass loss was considered to be significant if the bootstrapped 95% confidence intervals of the litter origin by incubation time, bury location by incubation time interaction and litter origin by bury location by time interaction coefficients did not include a 0.

To determine the effect of litter chemistry and a marine nutrient priming effect on mass and nutrient loss (hypothesis 2 and 3), the percent change from initial conditions, and C:N and C:P ratios in the litter residue were analysed separately for each harvest using linear mixed effects models. Litter origin (two levels – club or control site), bury location (two levels – club or control site) and their interaction were included as fixed factors and bury location block as a random factor. The significance of the predictors was estimated using bootstrapped likelihood ratio tests between models, with the relevant predictor removed. If there is a significant effect of litter origin, we can conclude that the litter chemistry influences decomposition. If control litter mass and nutrient loss is significantly greater in club sites than control site, this indicates an effect of soil nutrients potentially suggesting a priming effect. A significant interaction between litter origin and bury location would suggest an effect of litter chemistry on decomposition is dependent on local soil nutrients.

The effect of marine nutrient deposition on nitrogen and phosphorus mineralization (hypothesis 4) in the correlative and manipulation experiments was assessed using linear and linear mixed effects models, respectively. In both cases, the logged concentration of the nutrient in the buried core was the response variable and the log of the initial nutrient concentration was included as an offset in the model. This model predicts how the final nutrient concentration changes in response to the predictors, given the initial concentration. In the correlative study, colony, great skua use (extra-colony control, intra-colony control, mound and club), and their interaction were used as fixed effects and the significance of the predictor was determined using ANOVA. In the manipulation experiment, data from 2017 and 2018 were analysed separately. Great skua abundance at the turf location (two levels - high or low), great skua abundance at turf origin (high or low) and their interaction were used as fixed effects, and to account for non-independence of these samples the block the turf originated from and the block the turf was moved to were used as random effects. The significance of the predictors was estimated using bootstrapped likelihood ratio tests between, with the relevant predictor removed. A graphical interpretation of the potential outcomes of this analysis is shown in Figure 3.1 (figure reproduced from Figure 2.4). No significant effect of turf origin or location indicates that great skuas do not influence mineralization (Figure 3.1a); a significant effect of turf origin only indicates that the change in great skua abundance does not influence mineralization (Figure 3.1b); a significant effect of turf location only indicates that great skua abundance is directly related to mineralization rates (Figure 3.1c); a significant effect of turf location and origin suggests that mineralization is influenced by changes in great skuas abundance, but there is a lag effect of historical abundance (Figure 3.1d); and, a significant interaction term suggests that the effect of great skuas on mineralization is dependent on the historical great skua abundance (Figure 3.1e). Marginal R^2 and conditional R^2 of each model were calculated to assess the goodness of fit.

To determine how edaphic conditions varied both dependently and independent of great skuas, a principal components analysis (PCA) was performed. For the PCA, all variables were scaled to a mean of zero and a standard deviation of 1 prior to analysis. It was not considered appropriate to use these as covariates in the main models as a lot of this variation is already accounted by the categorical predictors.

All models were checked and validated following Zuur, Ieno and Elphick (2010) and log transformed to meet assumptions of statistical models where appropriate.

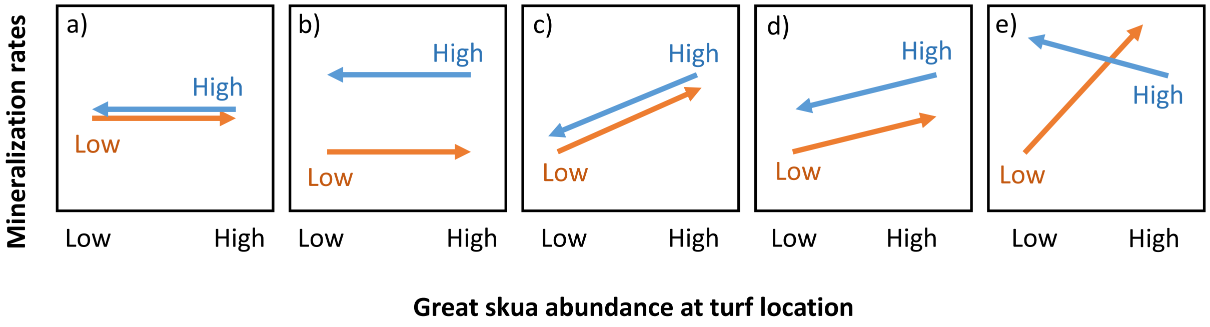


Figure 3.1 Hypothetical effects of mineralization rates in response to reciprocal turf transplants. Blue arrows represent turf that started in areas of high great skua abundance and were moved to areas of low great skua abundance, orange arrows represent turf that started in areas of low great skua abundance and moved to areas of high great skua abundance. (a) No significant effects; (b) significant effect of turf origin; (c) Significant effect of turf location; (d) Significant effect of turf location and turf origin; and, (e) Significant interaction term.

RESULTS

The effects of marine derived nutrients on decomposition

Initial litter chemical composition

Litter from club sites had approximately 55% more nitrogen and 170% more phosphorus than control sites (Table 3.1). The carbon content of litter from both sites was not significantly different and therefore, club sites had a significantly lower C: N and C: P ratios. Furthermore, club site litter was significantly enriched in $\delta^{15}N$ indicating that the increased nutrient content identified in club site litter was marine derived.

Table 3.1. Chemical properties of plant litter collected at club sites (club litter) and intra-colony control sites (control litter), used in decomposition experiments. Values are means and standard errors in brackets, significant differences are derived from ANOVA and indicated with *** p < 0.001, ** p<0.01, *p<0.5 and · < 0.1. 12 samples were analysed for each litter type, apart from isotope analysis, where n=6.

	Control litter	**Club litter**
Carbon (mg/g dwt)	452 (3.27)	453 (1.83)
Nitrogen (mg/g dwt)	8.9 (0.120)	13.9 (0.140) ***
Phosphorus (mg/g dwt)	0.447 (0.005)	1.19 (0.069) ***
C: N ratio	50.8 (0.478)	32.6 (0.301) ***
C: P ratio	1011 (12.0)	395 (26.9) ***
$\delta^{15}N$	-0.488 (0.107)	3.30 (0.112) ***

The effect of marine nutrient additions on decomposition and nutrient loss.

Decomposition rate

The decomposition rate was best modelled by a linear-log model (i.e. a log transformation of incubation time) and there was no effect of either litter chemistry or incubation site on the overall rate of mass loss (Figure 3.2). However, when the data were analysed per harvest, litter chemistry consistently significantly explained the mass of litter residue remaining (Table 3.2). As incubation time increased the variance explained by bury location increased and in the 24-month harvest both bury location and the interaction between litter origin and bury location were only marginally non-significant (p = 0.09 and p = 0.06, respectively).

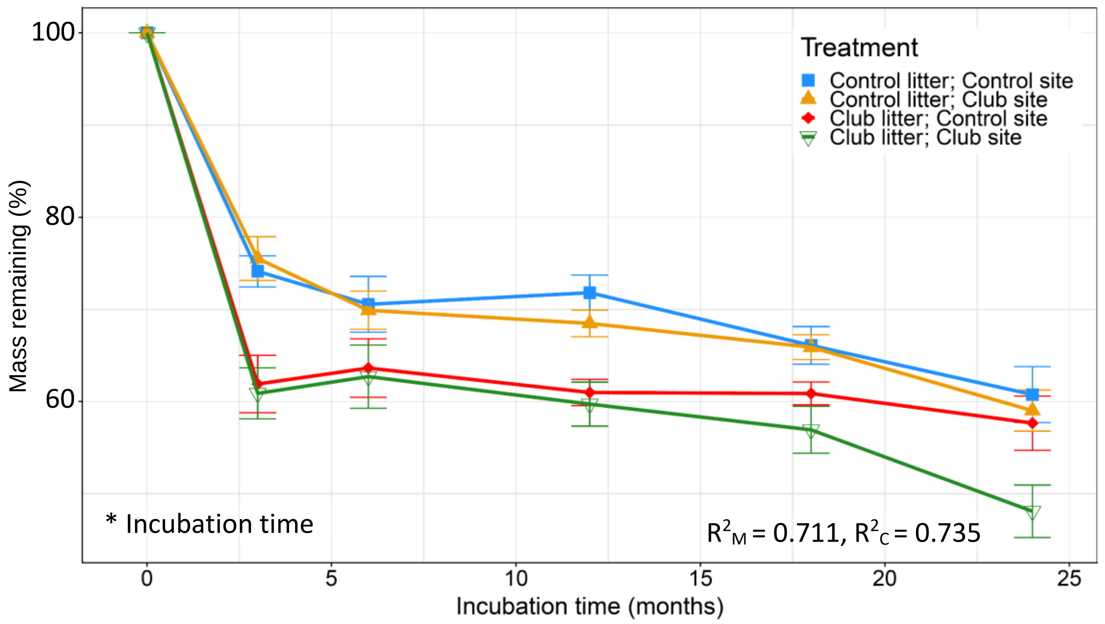


Figure 3.2. The effect of litter origin and bury location on the change in mass of litter residue remaining over time. Points represent measured means and error bars are standard errors. R^2_M and R^2_C are estimated marginal and conditional R^2 for the models.

Nutrient dynamics

In general, the loss of nitrogen and phosphorus from the litter is strongly influenced by litter origin in the first three to six months with no effect of soil conditions. However, as incubation time increases and litter chemistries converge, the bury location has a greater effect, especially with respect to phosphorus loss. Litter from club sites lost approximately 40% nitrogen and 58% phosphorus, with the majority of this lost in the first after three months of incubation (Figure 3.3 a and b). Indeed, litter origin was a significant predictor of nutrient loss at every harvest and the largest contributor to the variation in nutrient loss (Table 3.2). Litter from control sites retained more nitrogen and phosphorus than the club site during the course of the experiment (approximately 80% initial nitrogen and 85% initial phosphorus). Nitrogen was initially lost from control litter before being immobilized over the first 18 months, with significantly more immobilization at club sites at the 6-month harvest. Furthermore, phosphorus was immobilized in control litter to a greater extent at club sites than control sites (Table 3.2). Both the amount of nitrogen and phosphorus had declined in the litter residue by the final harvest.

Litter C: N and C: P ratios largely reflect changes the observed differences in nutrient release and immobilization, therefore litter origin is a significant predictor of the differences in the ratios at all harvests (Table 3.2). C: N ratio declined to a lesser extent in club site litter than control site litter over time and both litter types converge at approximately 30 after 18 months. Indeed, after 18 months of incubation, litter origin was only marginally significant and there was no effect of bury site or the interaction. C:P ratios in club litter increased and converged control litter at club sites at approximately 500.

$R^2_M = 0.711$, $R^2_C = 0.735$

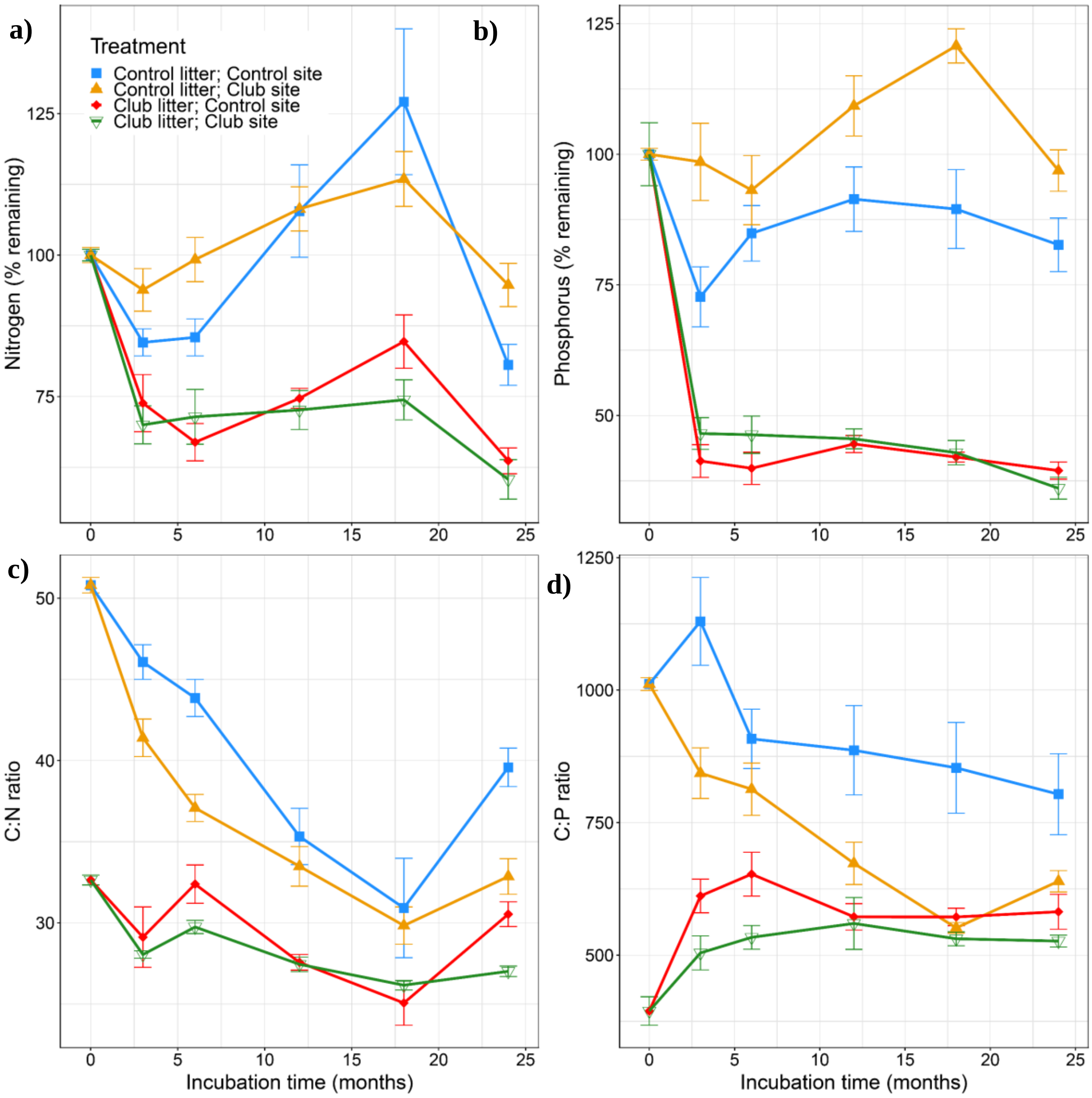


Figure 3.3 The effect of litter quality and bury location on (a) nitrogen loss, (b) phosphorus loss, (c) C: N ratio change, and (d) C: P ratio change over time. Points represent measured means and error bars are standard errors.

Table 3.2. The effect of litter quality, bury location and the interaction between the two on mass remaining, nitrogen loss, phosphorus loss, C:N and C:P different harvests (3, 6, 12 18 and 24 months). The values represent likelihood ratio test scores and level of significance (p-value codes: *** < 0.001, ** < 0.01 and * < 0.05, · < 0.1), and R^2's of the fixed (marginal) and random effects (conditional).

	Mass	**Nitrogen**	**Phosphorus**	**C:N ratio**	**C:P ratio**
Litter origin					
3	23.58 ***	19.19 ***	41.19 ***	73.03 ***	50.94 ***
6	5.66 *	27.80 ***	55.36 ***	50.38 ***	33.54 ***
12	22.88 ***	41.16 ***	65.28 ***	30.44 ***	30.10 ***
18	14.05 **	25.68 ***	70.23 ***	5.533 *	12.92 ***
24	6.73 **	36.71 ***	81.13 ***	49.97 ***	23.54 ***
Bury location					
3	0.006 (ns)	0.379 (ns)	7.482 **	7.306 **	8.801 **
6	0.076 (ns)	5.862 *	2.100 (ns)	18.59 ***	5.739 *
12	1.543 (ns)	0.010 (ns)	3.860 *	1.288 (ns)	5.521 *
18	1.141 (ns)	0.175 (ns)	10.58 **	0.307 (ns)	14.41 ***
24	3.498 ·	0.164 (ns)	1.980 (ns)	18.86 ***	4.414 *
Interaction					
3	0.247 (ns)	2.783 ·	4.882 *	2.144 (ns)	1.12 (ns)
6	0.003 (ns)	1.600 (ns)	0.089 (ns)	4.557 *	0.687 (ns)
12	0.330 (ns)	0.491 (ns)	4.260 *	0.591 (ns)	3.847 *
18	1.400 (ns)	0.654 (ns)	11.53 ***	0.151 (ns)	11.82 ***
24	2.809 ·	8.493 **	7.491 **	2.515 (ns)	1.787 (ns)
R^2_{marg} /R^2_{cond}					
3	0.39/ 0.39	0.38/ 0.38	0.64/ 0.71	0.82/ 0.82	0.69/ 0.84
6	0.11/ 0.11	0.50/ 0.50	0.67/ 0.75	0.73/ 0.73	0.54/ 0.64
12	0.40/ 0.45	0.59/ 0.63	0.79/ 0.86	0.47/ 0.49	0.46/ 0.75
18	0.28/ 0.39	0.42/ 0.42	0.83/ 0.85	0.12/ 0.12	0.52/ 0.65
24	0.22/ 0.41	0.61/ 0.71	0.85/ 0.87	0.72/ 0.82	0.39/ 0.67

The effect of marine derived nutrients on mineralization rates

The effect of great skuas on nutrient mineralization in the observational study was strongly influenced by the colony, however in general, neither nitrogen nor phosphorus mineralization rates differed markedly from zero (Figure 3.4). In general, the effect of great skua use on all forms of nitrogen mineralization was dependent on the colony. Despite some sample location variation, overall there was no nitrogen mineralization at intra and extra colony control sites, club sites and Hermaness mound sites. At the majority of these sites, ammonium mineralization accounts for the differences that occur in total nitrogen, as there was very little nitrate mineralization. However, total extractable nitrogen mineralization was greater at mound sites in Fetlar and Noss, due largely to nitrate mineralization being greater than ammonium immobilization. The effect of great skua use on phosphate mineralization was significantly dependent on the colony, although the effect size was very small.

In the manipulation experiments (Figure 3.5) origin and therefore, historic great skua use, was the only significant predictor of ammonium and nitrate mineralization in 2017 and 2018. In general, ammonium immobilization and nitrate mineralization were greater in turfs originating from the club site and increasing or decreasing great skua abundance had no effect on nitrogen mineralisation rates (Figure 3.5). By contrast, the effect on phosphate mineralization appeared to be dependent on year. Location, and therefore great skua use, was a marginally non-significant predictor in 2017 ($p < 0.1$) and a significant predictor in 2018, respectively. However, in 2017 there was less immobilization in turfs in the site with low great skua abundance, and in 2018, immobilization is greater in turfs in the site with high great skua abundance. Despite the statistical differences, nutrient mineralization did not differ markedly from zero. Furthermore, there was considerable disparity in how much variation the models explained, from just under 10% in phosphate mineralization model in 2017 to almost 50% in nitrate mineralization model in 2017 (including random effects).

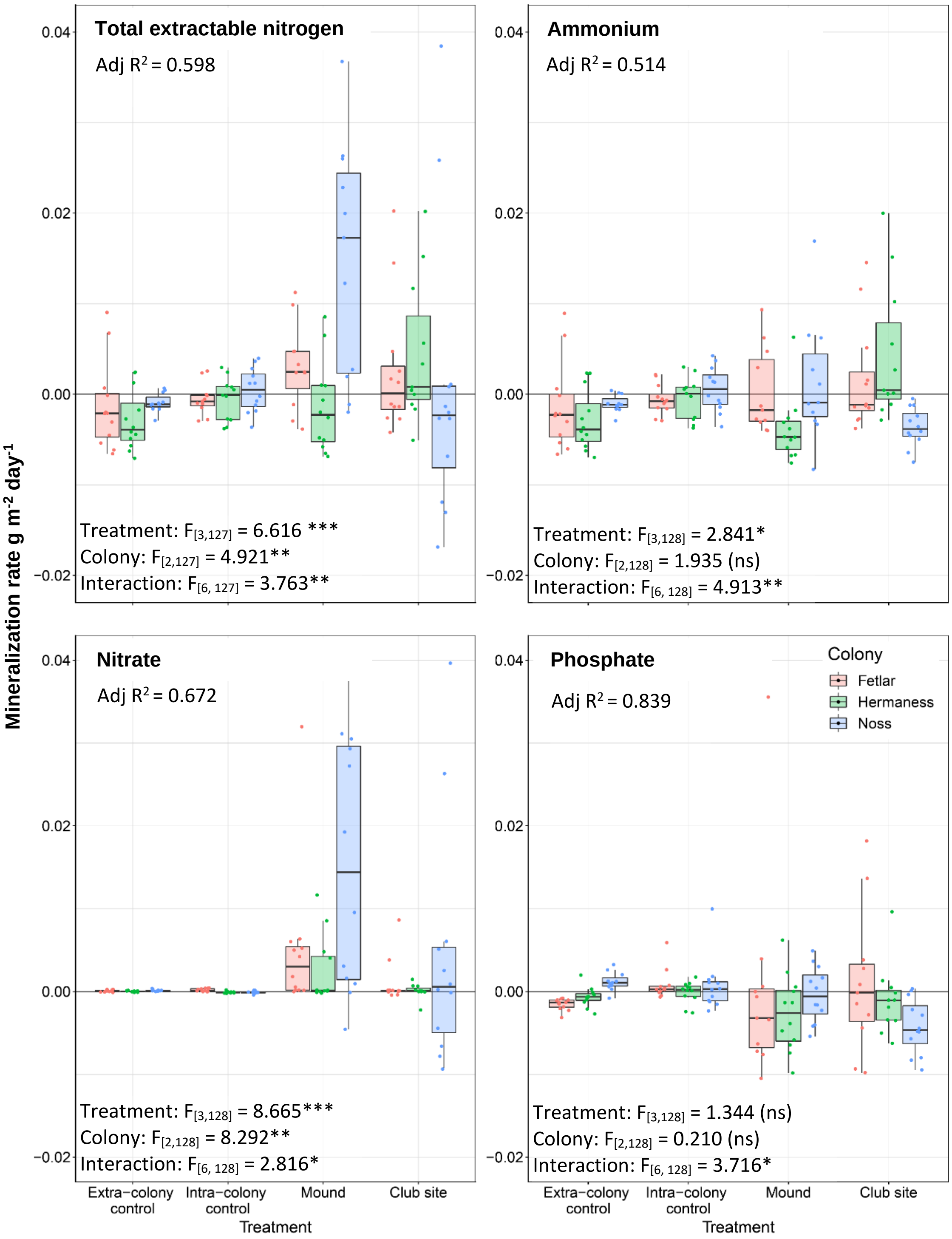


Figure 3.4 Change in nutrient mineralization rates in response to great skua use at three great skua colonies: Fetlar, Hermaness and Noss. Boxplots represents a treatment within colony (boxplot in style of Tukey) and each point represents a sample location. The black line represents no net mineralization, above this line there is net mineralization (immobilization < mineralization) and below the line is net immobilization (immobilization > mineralization). Significance of predictors are reported based on ANOVA results (p-value codes: *** < 0.001, ** < 0.01 and * < 0.05), and adjusted R^2 represents fit of the model taking account of the multiple predictors.

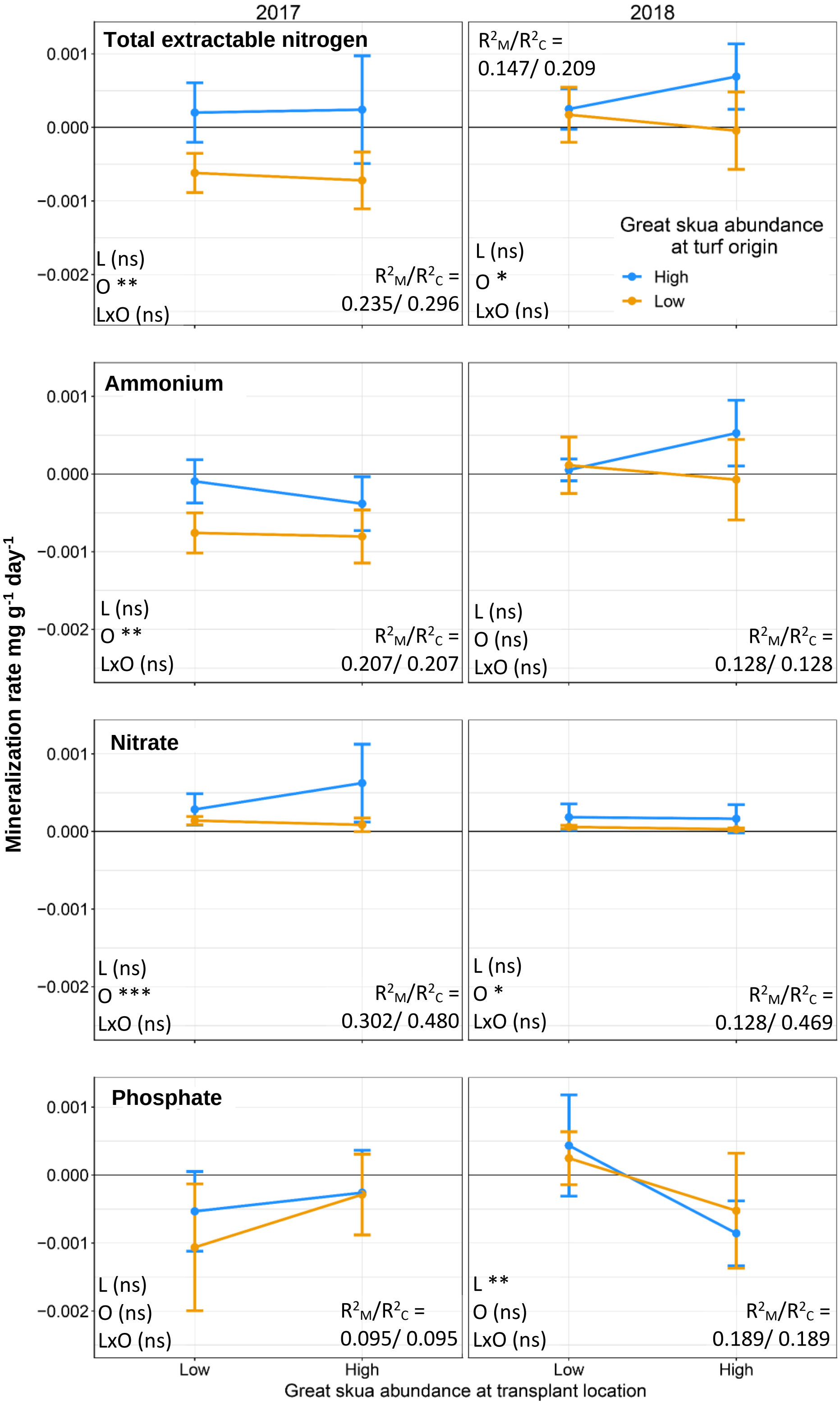


Figure 3.5 Change in mineralization rates in response to reciprocal turf transplants. Blue represents turfs that originated from areas of high great skua abundance (high to high on the right and high to low on the left), and orange represents turfs that originated from areas of low great skua abundance (Low to low on the left and Low to high on the right). Points represent sample means and error bars are 95% CI around means. The significance of turf location (L), turf origin (O) and their interaction (LxO) (p-value codes: *** < 0.001, ** < 0.01 and * < 0.05) and marginal and conditional R2's, which give an indication of model fit and effect of random predictors, are presented for each of the models in the graphs.

Variation in soil characteristics across great skua colonies

Principal components analysis showed a differentiation between great skua use sites along soil total nitrogen and phosphorus gradients and by physical properties (Figure 3.6). In general, the closer a site is to the bottom right hand corner of the plot, the drier, warmer and less acidic the soil is and the higher the total nitrogen and phosphorus concentration is.

Total nitrogen and phosphorus increased in response to elevated great skua abundance. The first principal component axis explained approximately 35% of the variation in samples and of this, approximately 82% was explained by total nitrogen and total phosphorus. In general, extra- and intra-colony control sites were characterised by lower concentrations of total nitrogen and phosphorus than mound and Club sites. One notable exception is the Hermaness club site, which occurs around a similar position to extra- and intra-colony control sites on the nutrient axes.

Samples were differentiated to a lesser extent by physical soil property gradients. The second principal component axis explained approximately 24% of the variation in sample locations and of this 93% is explained by soil moisture, pH and mean soil temperature. In general, extra- and intra-colony control sites have elevated soil moisture, lower pH and a lower average soil temperature compared to mound sites and, to a lesser degree, club sites. Furthermore, there was a degree of differentiation between the colonies, Noss was generally drier, with higher soil temperature and greater pH than Hermaness and Fetlar, especially in the intra-colony control samples. Interestingly at Noss, pH did not vary between great skua use sites (Table 3.3).

Total nitrogen and phosphorus were independent of the physical soil properties, as indicated by the almost perpendicular arrows, which suggests that the physical soil characteristics do not influence the total nutrient concentrations.

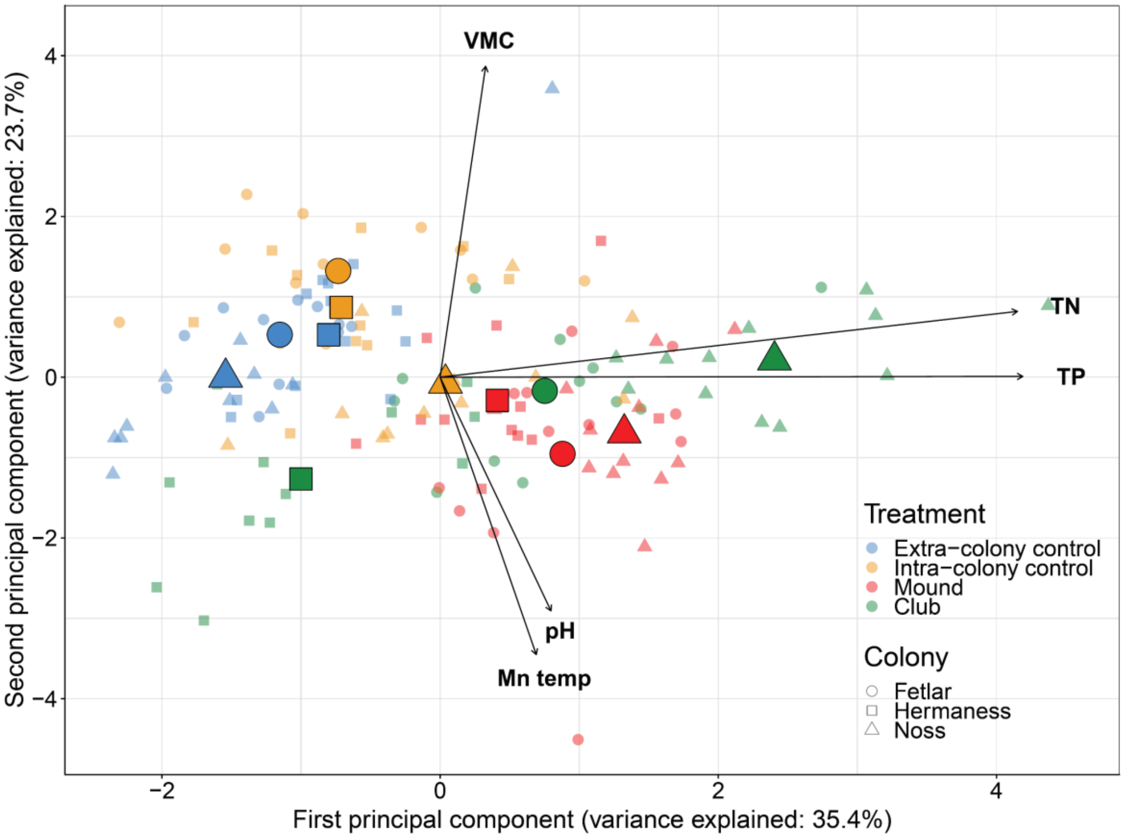


Figure 3.6 Principal components analysis biplot of edaphic conditions that influence decomposition and mineralization. Colour represents great skua (blue – extra colony control, orange – intra-colony control, red – mound and green – club) and shape represents the three separate sampling colonies (circle – Fetlar, square – Hermaness and triangle – Noss). The large points represent mean principal components and the small points represent each sample location. Arrows are pointing in the direction of increase in the soil characteristic value (VMC – Volumetric moisture content, Mn temp - Mean temperature (OC), TN – total nitrogen (g/m^2) and TP – total phosphorus (g/m^2)), the angle, and relative length of vectors to each other reflect their correlations.

Table 3.3. Summary of soil characteristics across great skua colonies. Numbers are mean and standard errors are in brackets.

	pH	**VMC (moisture)**	**Temperature (ºC)**	**Nitrogen (g/m^2)**	**Phosphorus (g/m^2)**
Extra-colony control					
Fetlar	4.23 (0.02)	0.77 (0.03)	14 (0.12)	153 (6.54)	4.45 (0.29)
Hermaness	4.43 (0.04)	0.81 (0.04)	13.7 (0.12)	170 (6.14)	4.85 (0.32)
Noss	4.22 (0.03)	0.63 (0.09)	13.9 (0.12)	118 (11.00)	5.08 (0.95)
Intra-colony control					
Fetlar	4.11 (0.04)	0.72 (0.05)	13.1 (0.18)	180 (15.00)	6.41 (0.56)
Hermaness	4.23 (0.06)	0.85 (0.04)	14.1 (0.12)	170 (10.90)	5.7 (0.37)
Noss	4.53 (0.05)	0.76 (0.05)	14 (0.2)	172 (14.10)	9.36 (0.54)
Mound					
Fetlar	4.27 (0.12)	0.61 (0.04)	15.3 (0.19)	230 (11.70)	10.4 (0.53)
Hermaness	4.27 (0.03)	0.67 (0.04)	14.7 (0.17)	212 (8.24)	9.19 (0.52)
Noss	4.5 (0.05)	0.63 (0.05)	14.4 (0.14)	248 (9.49)	11.7 (0.33)
Club					
Fetlar	4.3 (0.04)	0.72 (0.03)	14.7 (0.11)	213 (10.80)	11.1 (0.84)
Hermaness	4.42 (0.05)	0.69 (0.03)	15.4 (0.11)	124 (15.40)	5.81 (0.56)
Noss	4.46 (0.05)	0.7 (0.02)	13.8 (0.1)	260 (9.64)	18.1 (1.14)

DISCUSSION

The aim of this study is to determine how changes in nutrient pools brought about by great skuas influence rates of nutrient cycling. Here I show that plant litter from areas of high great skua use is more enriched in marine nitrogen and has elevated nitrogen and phosphorus concentrations than litter from areas of low use and it is this, rather than changes in soil nutrients or conditions, that is a key determinant of decomposition rates and nutrient loss. Furthermore, although nutrient mineralization was significantly influenced by great skua use and abundance, the differences are considered biologically insignificant.

The effect of marine nutrient deposition on decomposition

In line with the first hypothesis, the concentration of nitrogen and phosphorus in vegetative litter was greatly increased by great skuas, a finding that is consistent with other fertilization experiments (Hobbie and Vitousek, 2000; Rubenstein and Hobson, 2004; Bragazza *et al.,* 2012). The significantly elevated levels of $\delta^{15}N$ in the club litter is indicative that the nitrogen is marine derived. Greater plant nitrogen and phosphorus concentrations and $\delta^{15}N$ are widely reported in response to seabird abundance (Anderson and Polis, 1999; Croll, 2005; Ellis, Fariña and Witman, 2006; Maron *et al.*, 2006) and as resorption efficiency decreases with increased foliar nutrients, it is unsurprising the litter was so enriched (Kobe, Lepczyk and Iyer, 2009; Leonardus *et al.*, 2012).

Contrary to the first part of the second hypothesis, great skua abundance did not affect overall decomposition rates. Wright *et al.*, (2010) found that cliff nesting seabirds also did not affect decomposition rates, despite higher nutrient inputs. Whereas, Fukami *et al.*, (2006) found that decompostion rates declined with increasing seabird abundance. However, Fukami *et al.*, (2006) proposed that, whilst burrowing to form nests, the birds disturb the soil and litter and alter the microhabitat, restricting macrofauna access to litter. Disturbance of the litter layer is unlikely to occur in the great skua colonies as they are ground nesters and do not dig into the soil. Furthermore, unlike Fukami *et al.*, (2006), litter was cut into small pieces and burried in the top 5 cm of the soil, and therefore less sussecptable to changes in macrofauna activity due to the microhabitat at soil surface. When the mass remaining in the litter residue was analysed seperately for each harvest, however, mass remaining in litter residue was consistently significantly lower in club site litter, which indicates the decomposition rates of the litter from club sites was faster. These apparent discrepancies in the results may be to do with the linear models fit to the data. Although the linear-log model explained a considerable amount of the variation in the samples (~74%), plots of the model (see Figure A2 in Appendix) suggest that it does not fit the initial conditions or early harvest data very well.

In agreement with the latter part of the second hypothesis, marine derived nutrients within the leaf litter enhanced nitrogen and phosphorus release, regardless of where the litter was buried. The result is consistent with a number of other studies which identify litter chemistry as the main determinant of the rate of nutrient release (Vesterdal, 1999; Parton *et al.*, 2007; Hobbie, 2008, 2015; Papanikolaou *et al.*, 2010). Specifically, Wardle et al. (2009) found that when seabird populations declined, litter nitrogen concentrations decreased resulting in reduced nitrogen release during decomposition and highlighting the role for marine derived nutrients in nutrient cycling. Phosphorus turnover was unaffected by seabird decline, however, and the authors suggest this is due to it persisting in the soils after local colony extinctions (Holdaway et al., 1998; Wardle et al., 2009). The rapid loss of nutrients from club litter may partly be to do with how that nutrient is stored in the leaf tissue. In the club litter the rapid loss of nutrients was associated with little change or increases in C: N and C: P ratios over the first three months, whereas in the control litter, small changes in nutrient concentrations were associated with declines in C: N and C: P ratios. This suggests that in the club litter, excess nutrients in the leaf litter are stored a soluble form or are associated with decomposable cellulose, rather than in recalcitrant lignified compounds and nutrients are being lost faster than carbon is being decomposed (Couteaux, Bottner and Berg, 1995; Berg and Matzner, 1997). Furthermore, the fact that leaf litter chemistry is driving nutrient loss from litter suggests that any changes to the decomposer community composition or function within seabird colonies is mediated through the plant material, rather than due to soil conditions (e.g. Papanikolaou et al., 2010; Wright et al., 2010; Bragazza et al., 2012).

Contrary to the third hypothesis, there was no evidence of marine nutrients priming the decomposer community as there were no differences in the decomposition rates or nutrient release of the control litter buried at club or control sites. However, there may have been an effect of exogenous nutrients. In the control litter, despite the initial loss of soluble nutrients, there were increases in nitrogen and phosphorus concentrations over time. Nutrient immobilization such as this could be a result of the requirements of the decomposer community present on the litter as it changes in abundance and composition (Ponge, 1991; Herzog *et al.*, 2019) and/or the direct chemical fixation of nitrogen in litter (Berg, 1988). Whichever the mechanism, nutrient immobilization occurred significantly quicker (i.e. shorter leaching phase) and to a greater extent in club sites than in control sites where available nutrients are more abundant (Chapter 2; Staaf and Berg, 1982). Furthermore, phosphorus appears to be immobilized to a greater extent than nitrogen in the control litter buried in club site. This could be indicative of the decomposer community being more phosphorus than nitrogen limited, which has previously been noted in peat (Amador and Jones, 1993). However, this could also be a function of phosphorus rich run-off adhering to the outside of the litter, as a result of phosphorus saturation within the club site (Otero *et al.*, 2015).

The effect of marine nutrient deposition on mineralization rates

Contrary to the fourth hypothesis, increased great skua abundance did not increase nitrogen and phosphorus mineralization rates. Although there were statistically significant effects of great skua use in the correlative study, and of both location and origin in the manipulation experiments, the actual extent of mineralization rates were negligible, and therefore considered biologically insignificant. Indeed, the net nitrogen and phosphorus mineralization rates at all locations were low and roughly comparable to other studies in undisturbed peat bogs (Verhoeven, Maltby and Schmitz, 1990; Chapin *et al.*, 2003; Andersen *et al.*, 2013). Furthermore, the lack of effect of seabirds on mineralization is consistent with other seabird studies (Wright *et al.*, 2010; Durrett *et al.*, 2014). In bogs, acidic, waterlogged conditions restrict the activity of the microbial community and nutrient additions may not be able to overcome these physical limitations. However, there was a marginal increase in nitrogen mineralization rates at mound sites at the Noss and Fetlar colonies. Mound sites tended to be associated with natural hummocks and had a lower soil moisture content than other sites, increasing the soil aeration. Nitrogen mineralization has been shown to increase in peat under aerobic conditions and in drained peatlands, due to the increased oxygen availability to facilitate the oxidation of ammonium to nitrate and increased activity of nitrifying bacteria (Williams and Wheatley, 1988; Updegraff *et al.*, 1995; Bridgham, Updegraff and Pastor, 1998; Andersen *et al.*, 2013; Andersen, Chapman and Artz, 2013).

Here I found that great skuas had little effect on mineralization rates, but that nutrient concentrations in plant material (both living and senescing) is elevated in areas of high great skua abundance (See also Chapter 2). This suggests a potential decoupling of mineralization and plant nutrient assimilation and decomposition. In this system plants could be acquiring nutrients via alternative pathways. In Chapter 2, stable isotope analysis identified elevated levels of ^{15}N in plants, but not all soils suggesting that little marine derived nutrients were being stored in the bulk soil or soil microorganisms in these colonies. Rather plants could be accessing simple inorganic and organic nutrients from the faeces and carrion directly via abiotic pathways such as when fertilizer is added to crops or as in high latitude ecosystems, respectively. In high latitude ecosystems, for example, where slow decomposition and mineralization restrict the availability of inorganic nitrogen, plants from a range of taxonomic groups are capable of acquiring amino acids and short peptides directly through their roots (Näsholm *et al.*, 1998; Hill *et al.*, 2011). Although in these low nutrient environments the acquisition of some forms of organic nitrogen can be rapid, the extent to which this organic nitrogen pathway contributes to total nitrogen acquisition by plants is still unclear (Jones *et al.*, 2005). Organic nutrient acquisition by plants could also be mediated through a symbiotic association with mycorrhizal fungi (Read, 1991). Indeed, the strong negative $\delta^{15}N$ signature of heather and tormentil identified in control sites in Chapter 2 suggests that in areas of low nutrient availability plant species are acquiring nitrogen through this pathway (Chapter 2). However, previous studies in seabird colonies identified a shift from a fungi- to a bacteria-dominated decomposition pathway, suggesting a limited role for fungi in plant nutrient acquisition and simple assimilation of simple nutrients present in the seabird faeces (Fukami *et al.*, 2006; Wright *et al.*, 2010). The increase in the $\delta^{15}N$ signatures in heather and tormentil club and mound sites also support this hypothesis (Chapter 2). It is possible that in habitat such as a peat bog, the in-situ bury-in-the-bag method may not accurately reflect the full extent of nutrient mineralization. Both Wright *et al.* (2010) and Durrett *et al.* (2014) also found no effect of seabirds on mineralization using the bury-in-the-bag method. Hawke and Vallance (2015) found that marine nutrient depositon resulted in carbon limitation in the microbial community. The functioning of the microbial decomposer community is in part determined by the availability of carbon, which provides energy for metabolic process such as enzyme production, and in turn, regulates nutrient availabily. Plant root exudates represent a major source of carbon in the rhizosphere to the microbial community, especially in organic soils, such as peat, where most of the soil carbon is in recalcitrant organic compounds and inaccessable (Fontaine *et al.*, 2007; Jones, Nguyen and Finlay, 2009; Brzostek *et al.*, 2013; Dijkstra *et al.*, 2013). By isolating the soil core from the plants in the polythene bag, this carbon source is inaccessible to the soil microbial community present and their activity and therefore nutrient mineralization rates would be restricted. These explanations are not mutually exclusive and the extent to which plants obtain their nutrients through organic or inorganic pathways is species specific and situation dependent (Näsholm *et al.*, 1998; Falkengren-Grerup, Månsson and Olsson, 2000; Weigelt, Bol and Bardgett, 2005). Therefore, on an ecosystem scale, plants and leaf litter are likely to acquire marine derived nutrients in a combination of ways outlined above. However, given the inconsistancies in the results and the potential flaws in using the bury-in-the-bag the method in organic soils, more work is needed to determine the effect of marine derived nutrients on mineralization rates.

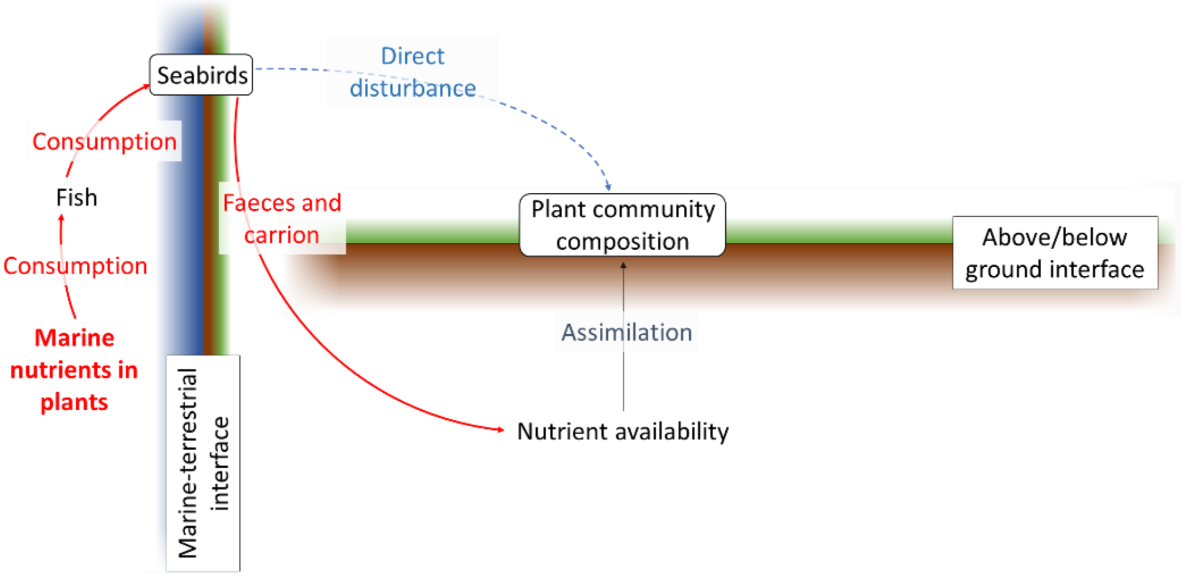
Conclusion

By transporting marine derived nutrients into the terrestrial ecosystem, great skuas elevate plant and potential alter microbial communities and function. Here I show that increased plant nutrient concentrations drive rapid initial loss mass and release of nitrogen and phosphorus from decomposing litter, but that there is relatively little effect of soil conditions. In addition, increases in great skua abundance has a negligible effect on rates of mineralization. In combination with the work in Chapter 2 this suggests that rates of mineralization are not influencing plant nutrient assimilation indicating that plants are accessing nutrients through simple abiotic pathways. In addition, this suggests a decoupling of mineralization and decomposition. It is unclear if nutrients released during decomposition are lost or recycled and more work is needed to confirm this.

Restructuring of fisheries management policy currently underway in parts of Europe is expected to cause a significant shortfall in food availability for scavenging seabirds, such as great skuas. The predicted impact wills impair their function as a mobile link species, reducing marine derived nutrient inputs into the terrestrial ecosystem. Given the opposing effects of leaf nitrogen and phosphorus concentrations when exposed to lower great skua abundance (Chapter 2), such changes are likely to result in reduced nitrogen but not phosphorus cycling, with potential consequences for the entire ecosystem, specifically plant and invertebrate communities.

CHAPTER 4

MARINE NUTRIENT INPUT AND DISTURBANCE BY GREAT SKUAS INFLUENCES PLANT COMMUNITY ASSEMBLAGE



ABSTRACT

A meta-ecosystem comprises multiple ecosystems spatially coupled by flows of energy, materials and organisms as one functioning unit. Mobile species can act as biotic vectors, greatly enhance the mobility of these items, performing an essential link in the meta-ecosystem. There is an increasing threat to global biodiversity and species movement from anthropogenic activity. Therefore, a greater understanding of how meta-ecosystems function and the role that mobile species play can provide a better insight to how changes in one ecosystem may influence coupled ecosystems across landscapes. Throughout this thesis I use the marine-terrestrial meta-ecosystem connected by the seabird great skua as a model system to investigate this. The aim of this chapter is to determine how marine nutrient depositon and disturbance influence terretrial plant community assemblege. I used a pin-drop method in an observational study to determine differences in plant community composition associated with areas of high great skua use. The same method was used in a manipulative study to empirically test the influence of great skuas on the plant community dynamics. I show that great skuas cause a rapid decline in the abundance of dwarf shrub and tall acid grassland species in favour of shorter, ruderal and graminoid species. The increased association of high use areas with ruderal species suggests that both elevated nutrients and disturbance are playing a key role in plant community dynamics. Such localised changes in plant community composition can influence both above and below ground biota and the increase in less recalcitrant graminoid species can further promote rates of decomposition and nutrient release on a community-wide scale. In addition, I demonstrate that when great skua abundance declines there is little initial change in the plant communities. This shows that there is a temporal element to ecosystem coupling and that a meta-ecosystem can stop functioning without any immediate effect on the plant community. Restructuring of fisheries management policy currently underway in parts of Europe is expected to cause a significant shortfall in food availability for scavenging seabirds, such as great skuas. The predicted impacts will impair their function as a mobile link species, reducing marine derived nutrient inputs and levels of disturbance in the terrestrial ecosystem. Although previous work suggests that this will cause changes in nutrient status of plant species, there will likely be a lag in any effects on plant community composition.

INTRODUCTION

The meta-ecosystems concept describes multiple ecosystems connected by flows of energy, materials and organisms as single functioning unit (Loreau, Mouquet and Holt, 2003). Mobile species travelling between ecosystems can act as biotic vectors greatly enhancing the motility of materials and other organisms and increasing the strength of the connections between ecosystems (Bauer and Hoye, 2014). Under the meta-ecosystem conceptual framework, sink ecosystems exist in an alternative stable state, that is reliant on the connection with the source ecosystem and any disturbance in the source ecosystem is likely to also impact the recipient ecosystem (Loreau, Mouquet and Holt, 2003; Lundberg and Moberg, 2003). There is an increasing threat to global biodiversity and species movement from anthropogenic activity such as climate change and habitat destruction (Wilcove and Wikelski, 2008; Van Gils *et al.*, 2016), therefore, a greater understanding of how meta-ecosystems function and the role that mobile species play can provide a better insight to how changes in one ecosystem may influence coupled ecosystems across landscapes.

Seabirds are highly mobile species that forage on marine resources and, during the breeding season, form nesting colonies in coastal environments. Consequently, they introduce marine derived nutrients into the terrestrial ecosystem via faeces and carrion, which increase local nutrient availability (Croll, 2005; Ellis, Fariña and Witman, 2006; Maron *et al.*, 2006; Blackall *et al.*, 2007; Callaham Jr. *et al.*, 2012; Riddick *et al.*, 2012; Zwolicki, Zmudczy and Richard, 2016; Chapter 2 and 3). In addition, species that nest inland can cause considerable disturbance in the form of trampling, burrowing and direct physical damage (Hogg and Morton, 1983; Maesako, 1999; Fukami *et al.*, 2006). Nutrient availability and disturbance are two key external factors that determine plant biomass accumulation (Grime, 1979). The extent to which plant species can compete for resources and tolerate stresses will determine their abundance within the community.

In general, plant communities associated with seabird colonies are at an early stage of succession. Compared to the surrounding habitat, fast-growing, annual species with rapid tissue turnover and low nutrient efficiency are abundant, whereas slow growing, perennial woody and shrub species are less frequent (Croll, 2005; Ellis, Fariña and Witman, 2006; Baumberger *et al.*, 2012; Zwolicki *et al.*, 2016). The role of seabirds in determining the plant community assemblage appears to be dependent on the plant species present and how seabirds interact with them. Studies have consistently identified elevated nutrient concentrations and relative abundance of ^{15}N in tissues from a broad range of plants within seabird colonies, indicating a response to marine derived nutrient inputs (Anderson and Polis, 1999; Croll, 2005; Kolb, Jerling and Hambäck, 2010; Callaham Jr. *et al.*, 2012; Zwolicki *et al.*, 2016; Chapter 2 and 3). Indeed, in the Aleutian Islands, nutrient subsidies were shown to be the dominant driver of changes to plant community composition, causing a shift from dwarf shrub dominated to graminoid dominated communities in fertilization-disturbance experiments (Croll, 2005; Maron *et al.*, 2006). Furthermore, phytomere experiments have identified toxic levels of nutrients within seabird colonies (Mulder and Keall, 2001; Ellis, Fariña and Witman, 2006; Molina-Montenegro *et al.*, 2013). However, several authors suggest that increases in species richness and plant cover at abandoned colonies and at intermediate distances from colonies is indicative of disturbance having a greater effect than nutrient subsidies (Hogg and Morton, 1983; Vidal *et al.*, 2000; Ellis, Fariña and Witman, 2006). Furthermore, on forested islands, burrowing seabird activity decreased seedling survival of some tree species but not others (Maesako, 1999). These studies demonstrate that seabirds can affect plant communities within their colonies and therefore provide an important link between the terrestrial and marine ecosystems.

Changes in the marine environment, such as fluctuating prey abundance, affect seabird behaviour, diet, population dynamics and productivity and population size, all of which can impact the magnitude of seabird influence on the terrestrial ecosystem (Furness, 1987, 2003, 2015; Klomp and Furness, 1992). Molina-Montenegro *et al.* (2013) found that tree growth in forests supporting seabird colonies increased during El Niño events and attributed this to shifts in fish distribution which caused localised decreases in seabird nest density and productivity, and therefore disturbance. Zwolicki *et al.* (2016) identified differences in plant communities around planktivorous and piscivorous seabird colonies and related their findings to differences in phosphate concentrations in the soil. Finally, in long term fixed plot monitoring, Baumberger *et al.* (2012) identified increased abundance of ruderals in the plant community in response to elevated gull nesting density but no clear response in plant communities to reduced nesting density. Despite these studies, the implications for whole plant community dynamics in response to changes in seabird populations are poorly understood. Given the dramatic changes to fisheries management that are currently underway in many parts of Europe (Regulation (EU) 2015/812 of the European Parliament and of the Council, 2015), it is crucial to gain better insight into how seabirds connect marine and terrestrial environments.

Species specific traits can be used to identify how local environmental parameters such as nutrient additions and disturbance influence community assemblage (McGill *et al.*, 2006; Díaz *et al.*, 2007; Legendre and Dray, 2008). Grimes C-S-R plant life strategy theory predicts that species-specific growth strategies can be used to determine how plant species respond to combined levels of environmental stress (such as nutrient, light, water etc. limitation) and disturbance (such as fire, trampling etc.) (Grime, 1977). Under this conceptual framework, three major life strategies are recognised: Competitor life strategy species (C) exhibit high growth rates, high leaf turnover, low seed production and high resource allocation to leaf construction to outcompete other species in absence of disturbance and stress; stress tolerant life strategy species (S) are small long lived species with slow growth rates and allocate resources to leaf maintenance and defence to thrive in nutrient, light and water limited environments; and, ruderal life strategy species (R) exhibit high growth rates and leaf turnover and allocate resources to rapid seed production to exploit areas of high disturbance and low stress (Grime, 1977). Therefore, dominant life strategies within plant communities can be used to determine the relative importance of stress and disturbance in driving community assemblage.

Here I use great skua breeding colonies in areas of blanket bog to determine how they influence plant community assemblage and dynamics and therefore, how the terrestrial plant community is coupled to marine ecosystems. Great skuas increase marine derived nutrients in a number of plant species and increase the rate at which nutrients turn over in their breeding colonies (Chapters 2 and 3), which are likely to influence plant communities. In addition, they are ground nesting and may disturb plant communities through physical trampling. A correlative study across three great skua colonies was used to test the hypotheses that (1) local plant community composition is related to differences in great skua use and specifically, (2) the abundance of dwarf shrub species is lower and graminoid species higher in areas of high great skua use. In addition, a manipulation experiment was carried out to provide empirical evidence for the influence of great skuas on plant community dynamics. It was hypothesised that (3) increases in great skua abundance would increase the proportion of graminoid species, at the expense of dwarf shrub species and (4) decreases in great skua abundance would have the opposite effect. Finally, to infer the mechanisms driving plant community dynamics Grime’s C-S-R plant strategies were used to test if (5) ruderal plant life strategies are associated with areas of high great skua use.

METHODS

Study area

The correlative experiment was established at three large great skua *Stercorarius skua* colonies on blanket bog in Shetland: (i) Lamb Hoga peninsula, Fetlar (Fetlar), (ii) Hermaness National Nature Reserve, Unst (Hermaness) and (iii) Isle of Noss National Nature Reserve (Noss) (centred at 60° 34' 39.77”N, 0° 53' 33.63”W, 60° 49' 0.15”N, 0° 53' 32.40”W and 60° 8' 22.94”N, 1° 1' 2.40”W, respectively). The manipulation experiment was undertaken at Hermaness only. The vegetation communities at Fetlar and Hermaness have affinities to National Vegetation Classification (NVC) community M19 *Calluna vulgaris – Eriophorum vaginatum* blanket mire blanket mire vegetation, whereas that at Noss has a greater affinity to NVC community M17 *Trichophorum cespitosus – E. vaginatum* blanket mire and M15 *T. cespitosus – Erica tetralix* wet heath, as there is a reduced abundance of *Calluna vulgaris* largely due to historic land use (Rodwell (eds), 1991).

Great skua abundance across the colony is not homogeneous, but comprises a loose collection of breeding territories, each one containing the nest and at least one raised mound on which the birds stand to observe their territory. In addition, within larger colonies, there are one or more discrete areas called “club sites” where immature, non-breeding birds form large aggregations of between 10 and 200 individuals (Furness, 1987). Most of the land area of a colony away from nests, mounds and club sites is used infrequently by great skuas and is referred to here as the “intra-colony”. This colony organisation of different areas of contrasting skua usage (and therefore contrasting marine nutrient input and disturbance) provides an ideal system in which to test hypotheses about the effect of great skua abundance on terrestrial plant communities.

Correlative study design

To test the hypothesis that local plant community composition is related to differences in great skua abundance and to identify species specific responses (hypotheses 1 and 2), a correlative study was established at all three great skua breeding colonies. The sample sites were the same as those selected in correlative study in Chapters 2 and 3. Briefly, the study used natural variation in great skua abundance across colonies to identify two high abundance treatments, club sites and mound sites, and a low abundance treatment, intra-colony control sites. At each colony, sample locations were established within a single club site in a grid formation (n = 12), at mound sites in randomly selected breeding territories within 0.5 km radius of the club Site (n = 12) and at intra-colony control sites, approximately 20-30 m on a random bearing from each of the mound sites (n = 12). Furthermore, to determine if there is a colony scale effect of great skuas each colony had a paired extra-colony control site, where sampling locations were established in a grid formation separated by at least 15 m (n = 12) (see chapter 3 for definitions and more detail of treatments).

Manipulation experiment design

To empirically test the influence of great skuas on the plant community and the effect of changes in great skua abundance on plant community dynamics (hypothesis 3 and 4), a manipulation experiment was conducted, where turfs were exposed to higher and lower great skua abundance using reciprocal turf transplants. This experiment used the same turfs as the turf transplant experiment described in Chapter 2. Briefly, in March 2016, in a separate area of the Hermaness colony used for the correlative study, pairs of turfs in a block design (n =12) were cut from a club site and an adjacent area of intra-colony control site and placed into freely draining plastic boxes. One of the pair was reciprocally transplanted with the corresponding block in the club or intra-colony control site, while the other was placed back into the site of origin (to act as a control). This established four different treatments, which for the purposes of this experiment were divided into the effect of increasing and decreasing great skua abundance:

- Low abundance control - turfs from intra-colony control site placed back into Intra-colony control site (i.e. transferring from low abundance sites to low abundance sites)
- Increase abundance treatment - turfs from intra-colony control site moved to club site (low to high)
- High abundance control - turfs from club sites placed back into club Site (high to high)
- Decrease abundance treatment - turfs from the club site moved to the intra-colony control site (high to low).

Vegetation sampling

The pin drop method was used to quantify the plant species abundance and community composition in both the correlative study and manipulation experiment. In the correlative study, 60 cm^2 quadrats were randomly placed within sampling locations during July 2017. A total of 16 pins were positioned evenly across the quadrat (15 cm spacing). Each vascular plant touching the pin was identified to species level (where possible) and the number of times each species touched the pin recorded. Bryophytes, liverworts and lichens were also recorded, but not identified so are not included in the analysis. The pin touches across the quadrat were summed and used as an objective measure of relative abundance.

The same method was used for the turf transplants; however, 16 pins were placed evenly in a 20 cm quadrat (5cm spacing). Quadrats were positioned in the centre of the turfs and away from any other sampling events occurring within the turfs (i.e. soil cores) to prevent confounding effect of plants colonization the edges of the turfs and non-great skua disturbance. Vegetation was sampled in early August on three occasions: in 2016, 2017 and 2019 (i.e. 5 months, 17 months and 29 months after transplantation).

Plant life strategy data

Grime's C-S-R scores were used to determine if plant life strategies mediated plant community responses (hypothesis 5). Here, life strategy codes are quantified following methodology described in Hancock (2018). Briefly, life strategy codes are based on the mean distribution of C- S- R factors within an equilateral triangle, where each corner represents a highest value for competitiveness, stress tolerance and ruderal ability and the centre of each side represents the lowest values. By drawing three axes perpendicular to the sides through the corners of the triangle, Hancock (2018), provides a numerical value (0 – 4) for each life strategy. A full list of C-S-R codes and scores is provided in Table A2 in the Appendix.

Statistical analysis

The effect of great skuas on the plant species abundance was assessed using generalized linear models (GLM) and visualised using model-based unconstrained ordination implemented through the MVAbund package and BORAL package, respectively, in R (Wang et al., 2012; Hui, 2016). The data in both the correlative study and the manipulation experiment had a strong mean-variance relationship, violating the assumptions of distance based multivariate analysis (Anderson, 2001; Warton, Wright and Wang, 2012). Using GLMs and model-based ordination allows for the specification of the data distribution to account for such relationships in the data.

Correlative study

To identify if local plant community is related to great skua use and determine species specific responses (hypotheses 1 and 2) separate GLMs were fitted to each response variable in the analysis using a common set of explanatory variables in the MVabund package. Models were then analysed together and separately to make community level and species-specific inferences about the effect of the explanatory variables. Here, the response variable comprised the number of pin touches for each plant species at each sampling location (i.e. a site by species matrix). Great skua use (extra-colony control, intra-colony control, mound and club), colony and their interactions were used as explanatory variables. Score tests (a resampling-based hypothesis test) using PIT-trap resampling were then used to make community-level (i.e. all plant species abundances at a sample location combined) and plant species-specific inferences about the effect of the explanatory variables. This test and the resampling technique was considered most appropriate for these data structures, whilst still taking into account correlations between taxa abundance (Wang *et al.*, 2012).

Manipulation experiments

To identify the role of great skuas on plant community dynamics (hypotheses 3 and 4), the same general approach was used to analyse the manipulation experiment. To determine community level response to great skua abundances, separate models were fitted for turfs exposed an increased and decreased abundance of great skuas. In each case the response variable comprised the number of pin touches for each plant species at each turf (i.e. a site by species matrix) and great skua abundance at the turf location (two levels – high and low), the time spent at that location (year that the vegetation was sampled) and block origin (12 levels) were used as explanatory variables. In addition, interactive effects between all three variables were included in the model to determine if plant species abundance changed over time in response to great skua abundance (i.e. turf location by time interaction) and to account for between block variation (i.e. block origin by turf location, block origin by time and block origin by turf location by time interactions).

However, to determine plant species specific responses to changes in great skua abundance and aid interpretation of the results, separate models were fitted for turfs exposed to an increased and decreased abundance of great skuas in different years (i.e. 6 models in total – increased and decrease abundance in 2016, 2017 and 2018). In these models, turf treatment (two levels – control and transplant) was used as the only explanatory variable. Block origin was omitted from these models as there were not sufficient degrees of freedom within the data. Data are presented in results as change in abundance, which was calculated by subtracting the abundance of a species at the control sites, high to high and low to low, from the treatment sites, high to low and low to high, respectively. In both cases, score tests using PIT-trap resampling were then used to make community-level and plant species-specific inferences about the effect of the explanatory variables.

Model based ordination

Unconstrained model-based ordination was used to visualise the plant community level response to great skua use and colony in the correlative study and to changes in great skua abundances over time in the manipulation experiment. For both data sets, pure latent variable models (LVM) were fitted to the number of pin touches for each plant species within sampling locations and turfs. Briefly, plant species abundances are regressed against two unobserved predictors (latent variables) in an GLM and Bayesian Markov chain Monte Carlo (MCMC) estimation is used to calculate model coefficients. The median coefficient estimates of both latent variables are then used to produce biplots, which are comparable to and interpreted in the same way as a Non-metric Multi-Dimensional Scaling (NMDS) ordination plot (Warton *et al.*, 2015; Hui, 2016). Standard, weakly informative prior distributions were used (as pre-set in the BORAL function in the package, see Hui, 2016).

Plant life strategies

To determine if plant life strategies mediate differences in plant communities in response to great skuas (hypothesis 5), data were reanalysed using a Correlative Response Model (CRM) implemented in the BORAL package in R (Hui, 2016). The CRM fits separate GLMs for each species abundance using a common set of explanatory variables by Bayesian MCMC estimation. To account for residual covariation between species abundances not explained by the specified explanatory variables, such as biotic interactions, two unmeasured latent variables are included in the model. Species-specific traits are incorporated into the model as random effects and the degree to which a trait is associated with the explanatory variable is reflected in the model coefficients (Warton *et al.*, 2015; Hui, 2016). Here, in all models the number of pin touches for each plant species was used as a response variable and Grimes C-S-R scores were incorporated as random effects. To determine if plant life strategies mediate the effects of great skua abundance on plant communities, separate models were fitted for different colonies in the correlative study and changes in great skua abundance within different years in the manipulation experiment, each with either great skua use or turf location included as fixed effects (i.e. 3 different models for the correlative study and 6 different models for the manipulation experiment). The association of a plant life strategy with great skua abundance was considered significant if the 95% credible intervals of the trait coefficient did not include zero (Hui, 2016).

All models were verified using Dunn-Smyth residual analysis, which identified that the negative binomial distribution was most appropriate for both data sets (Wang *et al.*, 2012; Hui, 2016).

RESULTS

Plant community composition in relation to great skua use

In the correlative study, plant community composition was significantly influenced by great skua use (score $_{[3,144]}$ = 161.1, $p < 0.05$) and colony (score $_{[2,144]}$ = 121.5, $p < 0.05$). Furthermore, the response of the plant community composition to great skua use was significantly different at different colonies (score $_{[2,144]}$ = 1518.2, $p < 0.01$). The LVM biplot (Figure 4.1) visually separated the great skua use sites into three groups. Extra- and intra-colony controls do not differ markedly from one another and occur on the top right of the ordination. This group was characterised by typical bog species such as *C. vulgaris*, *T. cespitosum*, *Empetrum nigrum* and *E. angustifolium* as well as *E. tetralix*, all of which were significantly affected by great skua use (Table 4.1). Mound sites and intra- colony control at Noss have similar species composition, with relatively little overlap with the extra colony and the other intra colony sites. These sites are characterised by species such as *Carex nigra*, *Anthoxantum odoratum*, *Luzula multiflora*, *Potentilla erecta* and *Galium saxatile,* which are significantly influenced by great skua use. Club sites form a distinct cluster in the top left of the ordination away from other great skua use sites but are generally more disperse than the other groups. These sites are characterised by a higher abundance of species such as *Juncus bufonius*, *Poa pratensis*, *Sagina procumbens*, *Holcus lanatus* and *Steleria media,* which were significantly influenced by great skua use. The distance between the site mean latent variable coefficient estimation for Fetlar and Noss club site plant communities are approximately equally different to their respective intra colony sites, whereas Hermaness club site composition is more similar to the intra-colony sites.

The abundance of *C. vulgaris*, *E. nigrum*, *A. odoratum* and *H. lanatus* were significantly influenced by the colony, as Noss supported a much lower abundance of dwarf shrubs, but a greater abundance of graminoid species such as *H. lanatus*. Furthermore, the great skua use by colony interaction had a significant influence on the abundance of *C. vulgaris* and *E. nigrum* as there was little effect of great skuas on *C. vulgaris* on Noss, but a strong negative effect on Fetlar and Hermaness.

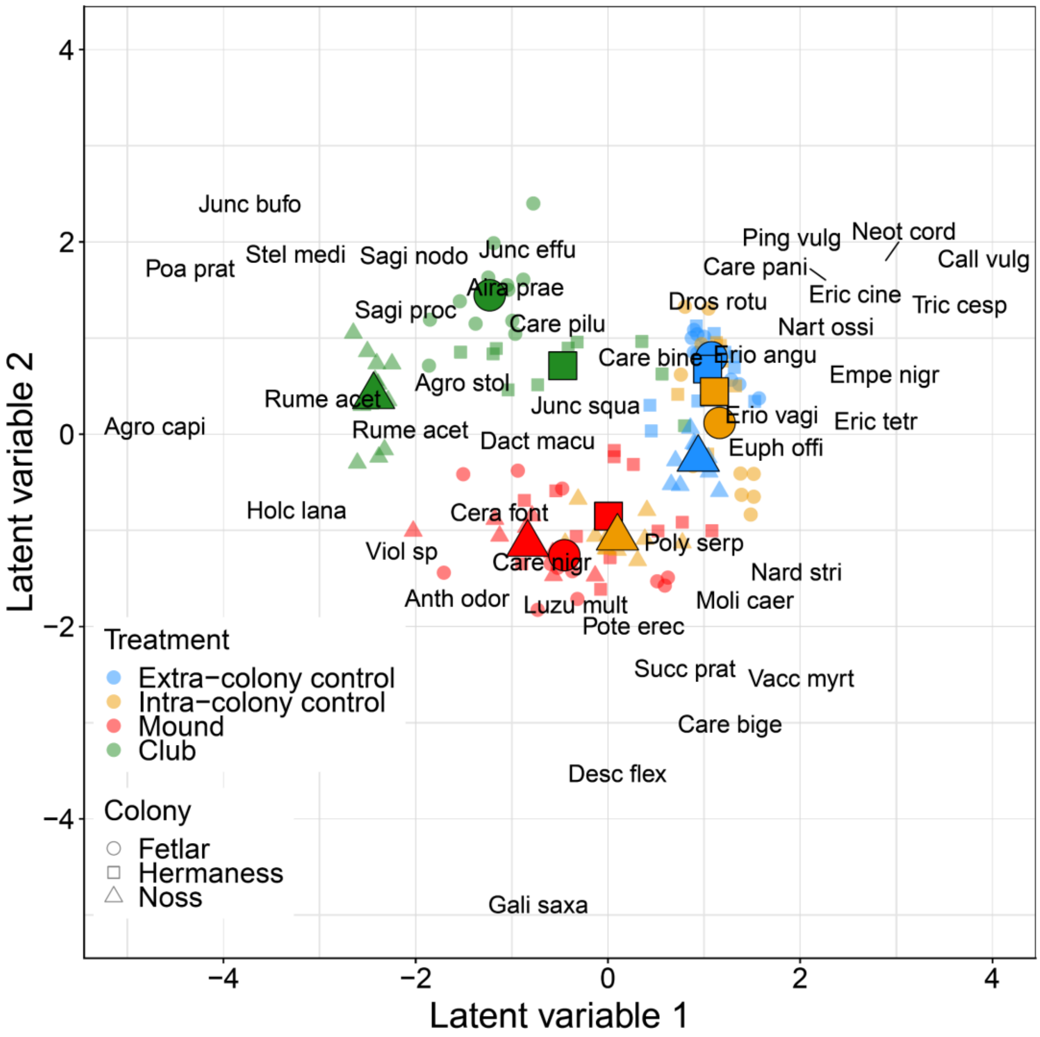


Figure 4.1. Latent variable model biplot showing the relationship between great skua use and plant community at three different great skua colonies. Colour represents the great skua use (blue – extra colony control, orange – intra-colony control, red – mound and green – club) and shape represent the three separate colonies (circle – Fetlar, square – Hermaness and triangle – Noss). The small points represent individual samples and the large points represent mean scores for great skua use sites and colony. The text represents directions of species gradients and the relative distance from the origin indicates the strength of that gradient. The first four letters of a species genus and species name represent each species (for species codes see Table A2 in Appendix). Species in the same direction and far from the origin are highly correlated e.g. *Calluna vulgaris* and *Erica cinerea*.

Table 4.1. The effect of great skua use, colony and the interaction on plant species abundance in the correlative study. The row colours relate to the groups that species associated with in the LVM (blue – extra and intra colony controls, red – mound and Noss intra colony controls, green – club sites, white – non significant effects). Significant effects are denoted by bold text, marginally non-significant effects (p>0.1) are denoted by non-bold text and non-significant effects by ns.

	Great skua use		Colony		Interaction	
Species	Score	P	Score	P	Score	P
Agrostis capillaris	3.808	ns	2.826	ns	0.001	ns
Aira praecox	3.824	ns	1.426	ns	0.338	ns
Carex bigelowii	2.083	ns	1.482	ns	0.001	ns
Carex binervis	1.579	ns	2.455	ns	1.773	ns
Carex panicea	2.370	ns	2.635	ns	2.109	ns
Carex pilulifera	3.000	ns	2.000	ns	0.001	ns
Dactylorhiza maculata	2.180	ns	1.121	ns	2.326	ns
Drosera rotundifolia	1.352	ns	0.925	ns	0.001	ns
Erica cinerea	5.634	ns	4.993	ns	3.897	ns
Eriophorum vaginatum	3.674	ns	4.555	ns	12.681	ns
Euphrasia officinalis agg.	2.490	ns	3.152	ns	0.001	ns
Juncus effusus	1.724	ns	1.182	ns	0.001	ns
Juncus squarrosus	2.378	ns	0.203	ns	4.821	ns
Narthecium ossifragum	2.565	ns	3.866	ns	2.728	ns
Pinguicula vulgaris	3.480	ns	2.459	ns	0.001	ns
Polygala serpyllifolia	2.234	ns	2.855	ns	0.001	ns
Rumex acetosa	1.741	ns	1.732	ns	0.133	ns
Rumex acetosella	5.968	ns	4.318	ns	0.001	ns
Sagina nodosa	0.608	ns	0.413	ns	0.001	ns
Succisa pratensis	1.698	ns	1.183	ns	0.001	ns
Vaccinium myrtillus	3.970	ns	1.101	ns	2.767	ns
Viola sp.	1.686	ns	4.513	ns	0.000	ns
Calluna vulgaris	24.391	**0.001**	19.884	**0.002**	36.903	**0.015**
Empetrum nigrum	8.358	**0.019**	20.581	**0.001**	19.449	0.069
Erica tetralix	14.018	**0.003**	4.046	ns	8.235	ns
Eriophorum angustifolium	32.206	**0.001**	7.613	0.086	27.930	**0.024**
Trichophorum cespitosum	19.552	**0.001**	0.512	ns	8.739	ns
Neottia cordata	9.267	**0.019**	5.463	ns	0.000	ns
Anthoxanthum odoratum	27.884	**0.001**	10.101	**0.038**	29.435	**0.024**
Carex nigra	14.930	**0.003**	15.405	**0.002**	19.124	0.069
Cerastium fontanum	20.679	**0.001**	0.966	ns	2.761	ns
Deschampsia flexuosa	14.548	**0.003**	12.656	**0.006**	11.989	0.088
Galium saxatile	19.217	**0.001**	8.154	0.069	10.432	ns
Luzula multiflora	38.545	**0.001**	9.926	**0.038**	17.473	ns
Molinia caerulea	8.152	**0.019**	5.128	ns	5.644	ns
Nardus stricta	7.390	**0.02**	4.398	ns	120.799	**0.015**
Potentilla erecta	14.291	**0.003**	30.610	**0.001**	16.263	0.069
Agrostis stolonifera	16.609	**0.002**	7.683	0.084	15.164	0.069
Holcus lanatus	7.443	**0.02**	17.033	**0.002**	9.462	ns
Juncus bufonius	11.476	**0.008**	2.492	ns	0.001	ns
Poa pratensis	8.691	**0.019**	6.830	ns	0.001	ns
Sagina procumbens	7.910	**0.019**	1.841	ns	2.896	ns
Stellaria media	23.639	**0.001**	7.107	ns	4.888	ns

The effect of great skua abundance on plant species dynamics

The LVM biplot clearly separated the plant community composition at the low and high abundance control turfs (grey and black points, respectively; Figure 4.2). The low control turfs were characterised by greater abundance of species such as *Empetrum nigrum*, *Calluna vulgaris* and *Eriophorum angustifolium*, whereas the high control turfs were characterised greater abundance of species such as *Agrostis* species and *Aria praecox*.

When turfs were transplanted to areas with higher great skua abundance, there was a significant change in the plant community composition, which shifted towards one similar to that found in the high abundance control turfs (location of the turfs represented by the orange points are between the grey and black, significant effect of great skua abundance; Table 4.2). Furthermore, whist control turfs do not change over time, the composition of the transplanted turfs became more dissimilar from the control turfs, the longer the time since transplantation (significant effect of time and marginally non-significant effect of great skua abundance by year interaction; Table 4.2). In addition, in four of the 12 turfs the plant community composition had changed to reflect that in the high use control turfs after just three years since transplantation, suggesting that the influence of great skuas is not homogenous across the high use areas (significant effect of block origin and the interaction between great skua abundance and block origin). When turfs were transplanted to areas of lower great skua abundance, there was a much smaller but significant change in the plant community composition (significant effect of great skua abundance). In addition, this varied between turfs suggesting that the resulting plant community may be influenced by the local great skua abundance prior to transplantation (blue points are fairly dispersed in the ordination and there was a significant effect of block origin and the great skua abundance by block origin interaction; Table 4.2). There was no effect of time or the interaction of great skua use by time, suggesting after the initial change in plant community composition in response to decreased great skua abundance, there is little continued change.

Although several species responded to changes in great skua abundance, the species-specific analysis identified few significant changes (Figure 4.3). When turfs were transplanted to areas of higher great skua abundance, there was no change in the abundance of any species in 2016. However, in 2017 and 2018 there was a significant increase in *A. odoratum* abundance and a decrease in dwarf shrub species *C. vulgaris*, *E. angustifolium* and *E. nigrum* abundances. When turfs were transplanted to areas of lower great skua abundance in 2016, *A. odoratum* and *Cerastium fontanum* abundance initially significantly declined. However, no species abundances significantly differed from the controls in 2017 or 2018.

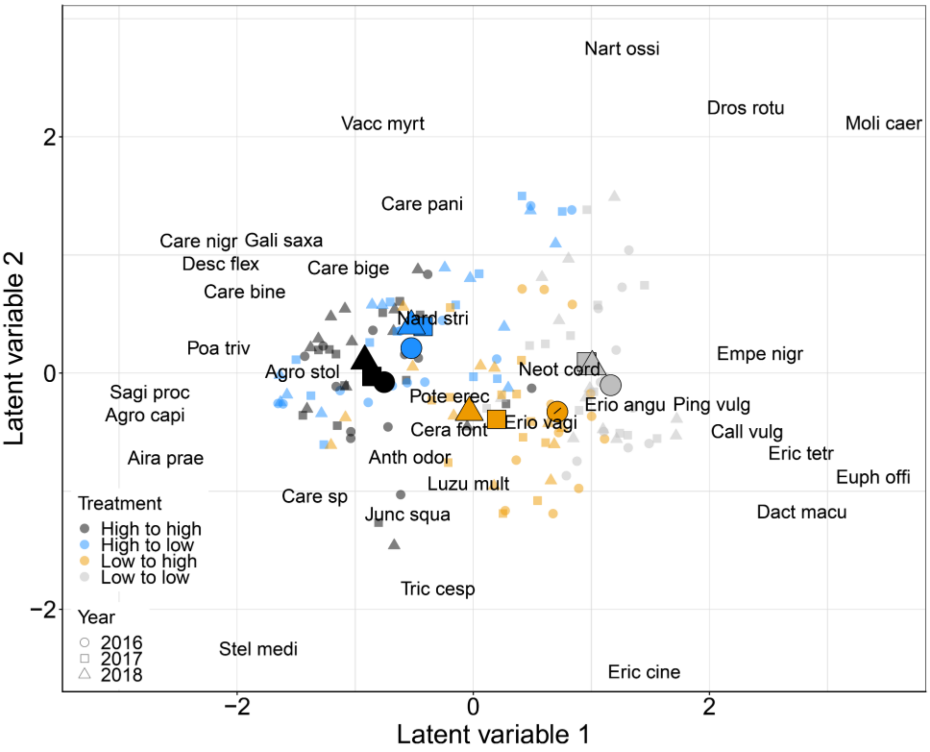


Figure 4.2. Latent variable model biplot showing the relationship between changes in great skua abundance and plant community over three years. Colour represents the change in great skua abundance: grey and black represent low and high abundance control turfs, respectively, and orange and blue represent turfs that were transplanted, low to high and high to low abundance, respectively. The shape represents the year in which the vegetation community was sampled and therefore the amount of time that the community had been at the treatment. The text represents directions of species gradients and the relative distance from the origin indicates the strength of that gradient. The first four letters of a species genus and species name represent each species (for species codes see Table A2 in the Appendix). Species in the same direction and far from the origin are highly correlated e.g. *Calluna vulgaris* (*Call vulg*) and *Erica tetralix* (*Eric tetr*)

Table 4.2 The effects of great skua abundance at the location of the turf, year of vegetation sampling and block origin on vegetation community composition in the manipulation experiments, separated into increasing and decreasing great skua abundance. Great skua abundance indicates if the turf was moved into the opposite site or was positioned back in the control site. Time represents the amount of time spent at that experimental treatment.

	Degrees of freedom	Score	P
Increase great skua abundance			
Great skua abundance	**1**	**47.01**	**0.001**
Time	**1**	**25.67**	**0.009**
Block	**11**	**321.33**	**0.001**
Great skua abundance: Time	1	28.87	0.098
Great skua abundance: Block	**11**	**274.86**	**0.011**
Time: Block origin	11	168.27	0.742
Great skua abundance: Block: Time	11	163.74	0.062
Decrease great skua abundance			
Great skua abundance	**1**	**46.99**	**0.001**
Time	1	19.98	0.109
Block	**11**	**367.64**	**0.001**
Great skua abundance: Time	1	18.02	0.546
Great skua abundance: Block	**11**	**321.70**	**0.005**
Time: Block origin	11	186.16	0.495
Great skua abundance: Block: Time	11	117.54	0.439

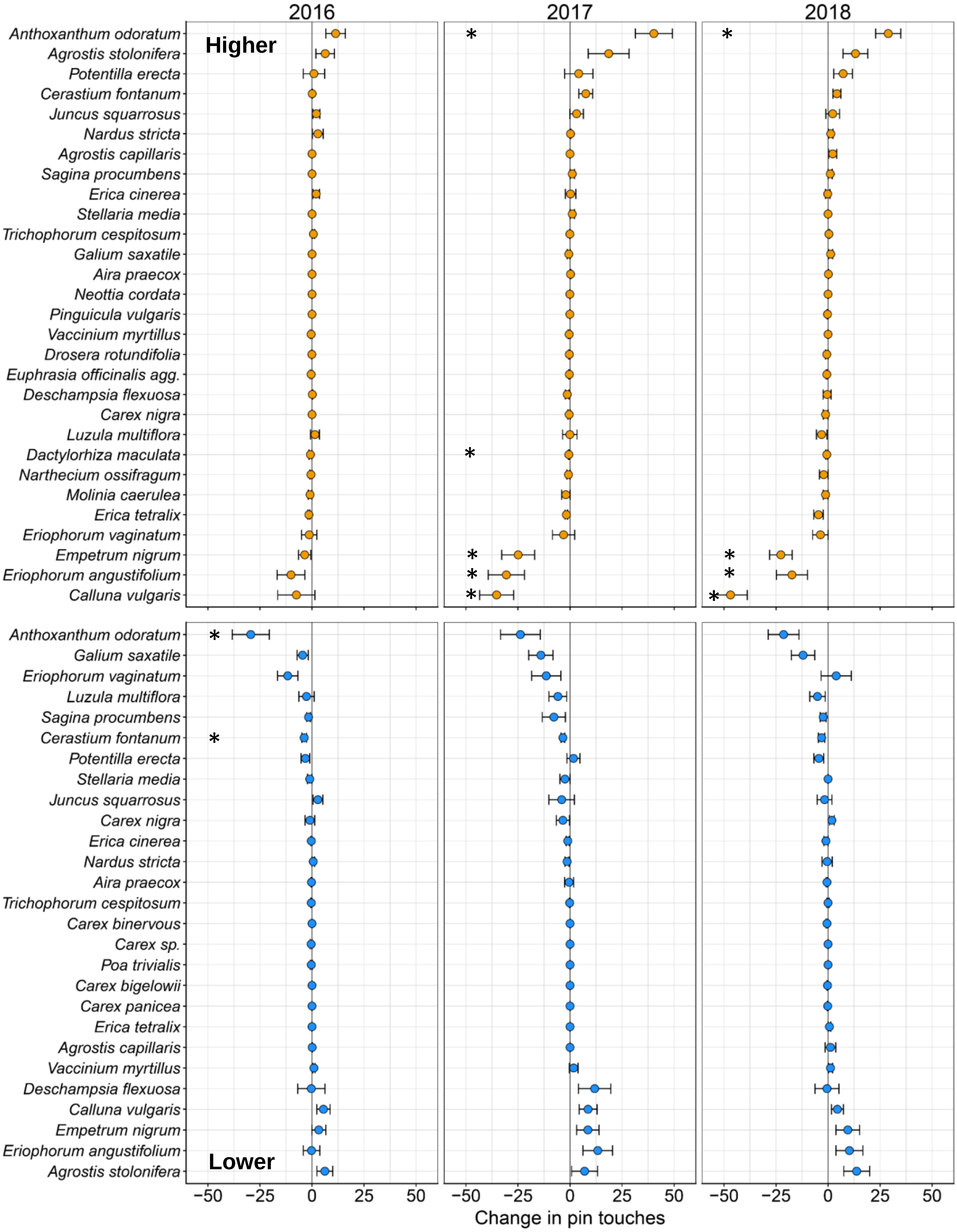


Figure 4.3. Change in plant species abundance when turfs were transplanted to areas of higher (upper row - orange) and lower (lower row - blue) great skua abundance. Change in plant species abundance was calculated by subtracting the pin touches of each species at the control sites from the transplant sites. Each column represents the year the vegetation was sampled (left to right 2016, 2017 and 2018) and therefore the length of time the community spent at the transplanted area. Each point represents the mean difference and the error bars are ± 1 standard error. The star represents species where the transplant had a significant ($p < 0.05$) effect on the abundance.

The role of plant life strategies in mediating responses to great skua abundance

In the correlative study, the association between plant species abundance and great skua abundance was related to plant life strategies (Figure 4.4). In general, there were no significant associations with competitor or stress tolerant life strategies. There was a weak positive trend for plant with competitor life strategies at intra-colony control sites. The exception to this was a significant negative association of stress tolerant life strategies at Noss Club sites, due to the dominance of species such as *H. lanatus*, *Rumex acetosa* and *Agrostis capilaris* here. Ruderal life strategies, however, were negatively associated with extra and intra colony controls, due to the dominance of species such as *C. vulgaris*, *Erica* sp. and *E. angustifolium*, and positively associated with mound and club sites and significantly so at some but not all at Fetlar and Hermaness.

In the manipulation experiment there were no significant associations between plant life strategies and treatment in either increased or decreased great skua abundance (See Figure A3 in Appendix). However, as in the correlative study, there were trends to indicate that ruderal life strategies are weekly positively associated with high great skua abundance and negatively associated with low great skua abundance.

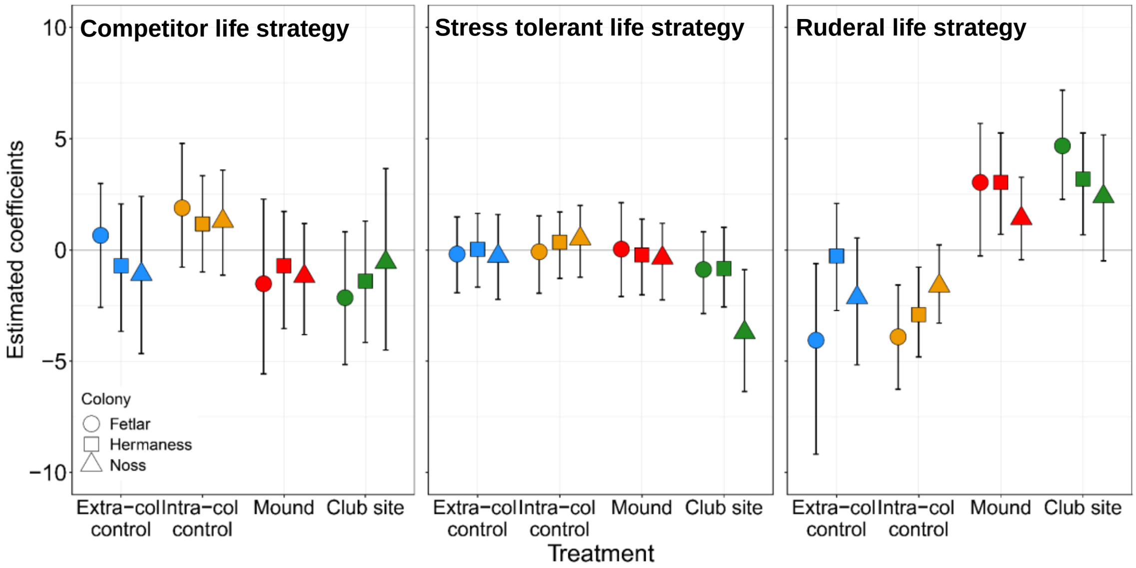


Figure 4.4. Association between great skua abundance and competitor, stress tolerant and ruderal plant life strategy. Each point represents an estimated coefficient of each of the each of the C-S-R scores as estimated by the CRM. The colour of the point represents great skua use. The error bars represent 95% credible intervals. Where the error bars do not overlap with zero there is a significant association between the life strategy and great skua use.

DISCUSSION

The aim of this study was to determine the role of great skuas in influencing plant community assemblage and dynamics, and in doing so identify how terrestrial plant communities are linked to marine ecosystems. I show that there is a lower abundance of dwarf shrubs and a higher abundance of graminoid species in areas of high great skua use, although there is significant variation between colonies. The manipulation experiments demonstrated that these changes occur rapidly when great skua abundance is increased. However, when great skua abundance declines, there is little change in the plant community composition. Finally, a positive association with ruderal species in many areas of high great skua abundance suggests that both disturbance and increased nutrient availability are driving these changes, although these were not tested directly.

The effects of great skuas on plant community composition

In accordance with hypothesis 1, local plant community composition was related to differences in great skua use and, in general, dwarf shrub species was lower in areas of high great skua use (hypothesis 2). However, the plant community composition and species-specific responses were also influenced by the colony by great skua use interaction, likely as a result of variations in local edaphic conditions such as soil moisture and acidity across the three sites (Chapter 3) and historic land use, influencing intra-colony control community composition. Plant communities at intra-colony controls and Fetlar and Hermaness intra-colony controls were dominated by species such as *C. vulgaris*, *E. nigrum* as well as other Ericaceae species, *Eriophorum* species and *T. cespitosum*. These species are well adapted to the low nutrient, wet, acidic conditions typically found in bog habitats and readily out-compete grasses in these conditions (Aerts *et al.*, 1990; Hartley and Amos, 1999). At Noss, however, the intra-colony control plant community composition was more similar to mound sites and represents a modified bog community. Noss has historically been subject to high grazing pressure which likely resulted in the reduced abundance of *C. vulgaris* and other ericoids, in favour of other bog related species such as *Eriophorum* species and *T. cespitosum*, but also more grazing tolerant species such as *M. caerula* and *N. stricta* across the island (Aerts *et al.*, 1990, Rodwell, 1991).

The plant community compositions identified at club sites were not consistent and more variable than at control or mound sites. Such variability is likely to partly be due to heterogenous use of club sites by great skuas (i.e. some areas of the club site receiving more nutrient addition/disturbance than others) as well as contrasting local edaphic conditions. Fetlar club sites supported a low abundance of dwarf shrub species, whereas species such as *Agrostis stolonifera*, *Juncus bufonicus*, *Stellaria media* and *Sagina procumbens* were common. *Agrostis* species in particular favour high nitrogen sites and are tolerant to disturbances such as grazing and trampling

(Hartley and Mitchell, 2005). Species such as *J. bufonicus, S. media* and *S. procumbens* were particularly abundant in the centre of the club site which would be subject to the highest level of great skua influence and are frequent in open communities of disturbed habitats (Rodwell, 2000). The Hermaness club site has the highest inter-site variability in plant communities (sample location points most disperse in Figure 4.1), with some sample sites overlapping with intra- and extra-colony control site species compositions. It is likely that the plant communities in a small number of the sample locations were strongly influenced by the presence of a wet hollow as the communities were dominated by *E. angustifolium*. This species can dominate areas of disturbed waterlogged peat (Rodwell, 2000); therefore, while the action of great skuas may have contributed to the decline in other typical bog plant species *E. angustifoloium* has been able to colonise and survive in the wet conditions (Rodwell, 1991). Sample locations further from the hollow, were more similar those identified at the Fetlar club site. The plant community at Noss club site had similarities to NVC MG10 *Holcus lanatus – Juncus effusus* which is characteristic of a poorly drained permanent pasture (Rodwell, 1991). Here the influence of the great skuas likely interacted with soil acidity to favour the growth of less acid tolerant species such as *Holcus lanatus*, *Agrostis stolonifera* and *Rumex acetosa* (Hill et al. 2004).

Plant communities on mounds sites had a more consistent response to great skuas: a lower abundance of typical bog species was identified in favour of a community with abundant *A. odoratum, Carex nigra, Luzula multiflora, P. erecta* and *G. saxitale,* which has affinities with NVC U5 *Nardus stricta - Galium saxatile* grasslands (Rodwell, 1993). Mounds are used by great skuas to observe their territories, and therefore tend to be higher compared to the surrounding ground, making them drier as the horizons of soil elevated away from the water table (see edaphic conditions in Chapter 3). Rodwell (1993) notes that areas of bog communities on drier peats can readily be converted into Nardetalia sward with grazing and limited fertilization. In addition, fertilization experiments in wet and dry alpine tundra communities identified differences in relative growth rates of graminoid and forb species depending on soil moisture (Bowman *et al.*, 1993).

The effects of changes in great skua abundance on plant community dynamics

The manipulation experiment provided evidence for great skuas directly affecting plant community dynamics. Increasing great skua abundance resulted in a rapid decline in dwarf shrub species and increase in graminoid cover, although only *A. odoratum* increased significantly (hypothesis 3). The speed of the change is likely a due to the low productivity of the blanket bog that great skuas breed in and highlights how productivity gradients between coupled ecosystems can influence the strength of the links (Polis, Anderson and Holt, 1997). Furthermore, the model identified a significant effect of the great skua abundance by block interaction, which adds further evidence that the heterogenous use of the club site by great skuas influences local plant community composition, not just the presence or absence of the seabirds.

Contrary to hypothesis 4, although decreasing great skua abundance did change plant community composition, this did not become more marked over time, and no consistent effect on dwarf shrub or graminoid species were identified. After local seabird colony extinction, phosphorus and to a lesser extent nitrogen remain at a high concentration within the soil (Holdaway *et al.*, 1998; Wardle *et al.*, 2009; Callaham Jr. *et al.*, 2012). Therefore, it is likely that in absence of great skua disturbance, species were able to fully utilize the nutrients to increase productivity, which could result in the small shifts in community composition observed here. Short term productivity increases have been noted in forest communities during El Nino years, when cormorant abundance and productivity declines, releasing trees from any suppressing effect of disturbance (Molina-Montenegro *et al.*, 2013). A number of authors have identified greater species richness in abandoned colonies or at intermediate distance from colonies, but these studies were not designed examine changes in plant community dynamics in response to altered seabird abundances (Hogg and Morton, 1983; Vidal *et al.*, 2000; Ellis, Fariña and Witman, 2006). Following declines in yellow-legged gulls on Mediterranean islands, Baumberger *et al.* (2012) found no clear pattern of vegetation change.

It takes a long time for plant communities to recover following a disturbance event (Bayfield, 1979; Rawes, 1983) and it is likely that our experiment was too short to identify the reversion of the vegetation community to that represented in the intra colony sites. However, this does highlight a temporal element to ecosystem coupling and a lag in species response such as this may mask declining function mobile species as a link between ecosystems and entire meta-ecosystems.

Areas of high great skua influence are associated with ruderal species

In accordance with hypothesis 5, plant life strategies mediate plant community response to great skuas to some extent. Despite differences in species composition, great skua use had a positive association with ruderal life strategies and, at Noss a negative association with stress tolerant life strategies. Increases in ruderal life strategies and traits have also been identified in gull colonies in the Mediterranean and in North America (Vidal *et al.*, 1998; Ellis, Fariña and Witman, 2006; Baumberger *et al.*, 2012). Gulls have a similar nesting habit to great skuas and therefore likely influence the vegetation composition in the same way. Ruderal life strategies are associated with high growth rates, high rates of leaf turnover and resource allocation to seed production, which allows them to outcompete other species in low stress, disturbed environments (Grime, 2001). This implies that the plant community is responding to both great skua disturbance and marine nutrient subsidies. Croll (2005) found that fertilization alone was enough to decrease dwarf shrub cover and shift plant communities to those observed within seabird colonies. However, when fertilization was applied in combination with disturbance, designed to replicated burrowing seabirds, graminoid cover reduced. Several studies in blanket bog and heather moorland have identified a positive effect on dwarf shrub biomass in response to fertilization (Hartley and Mitchell, 2005; Bubier, Moore and Bledzki, 2007; Juutinen, Bubier and Moore, 2010). Hartley and Mitchell (2005) found that *C. vulgaris* decreased in abundance only when fertilization was applied in combination with grazing, but in these circumstances the rate of fertilization determined the species of grass that replaced it. Unlike burrowing seabirds, great skuas trample and physically attack the plant tissue, often ripping off fresh growth, rather than digging into the soil and turning over turf, and therefore the distrubance to the vegetation community is likely to be similar to that caused by grazing livestock.

The manipulation experiments, however, did not identify significant association with ruderal species with any of the turf treatments. This could be because physical disturbance to plants could decrease their abundance within the community but may not disturb the ground sufficiently to allow species with ruderal life strategies to increase in abundance in the short term (i.e. 3 growing seasons). However, there was significant variation on the effect of great skuas across the club site (see above). During the 2018 vegetation surveys, transplants in the centre of the club site (represented by orange triangles in the bottom left of Figure 4.2), which are subject to greater trampling supported a high abundance of *S. media* which has a high ruderal score.

In this study, I use C-S-R plant life strategy theory to infer information about the mechanisms driving plant community change. In a review, Wilson and Lee (2000) highlight that there several assumptions underlying this theory that are difficult to demonstrate empirically. Additionally, it has been argued that the theory oversimplifies reality, particularly for species that are attributed extreme C, S or R life strategies. For example, *E. angustifolium* was identified in the control sites at all colonies and also readily occupy disturbed waterlogged peat such as at the Hermaness club site but is given a ruderal score of zero (Rodwell, 1991; Hancock, 2018). Therefore, more work is needed to conclusively determine the relative importance of disturbance and marine nutrient subsidies in this system.

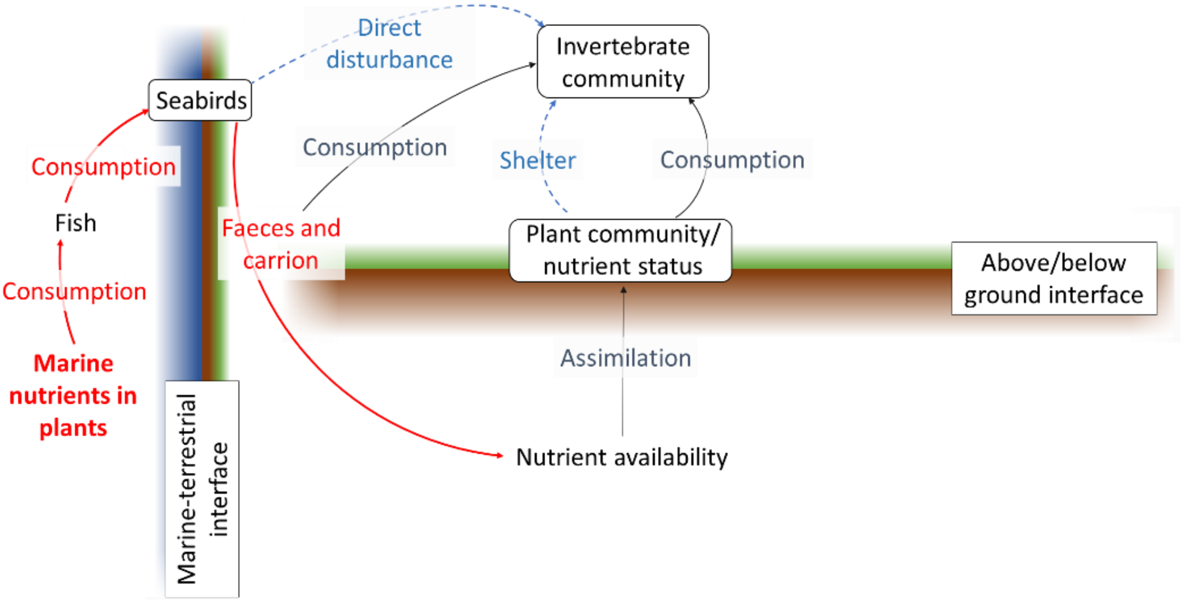
Conclusion

Here I show that great skuas cause a rapid decline in the abundance of dwarf shrub and tall acid grassland species in favour of shorter, ruderal and graminoid species. The increased association of high use areas with ruderal species suggests that both elevated nutrients and disturbance are playing a key role in plant community dynamics. Such localised changes in plant community composition can influence both above and below ground biota (Wardle *et al.*, 2004) and the increase in less recalcitrant graminoid species can further promote rates of decomposition and nutrient release on a community-wide scale (See Chapter 3). In addition, I demonstrate that when great skua abundance declines there is little initial change in the plant communities. This shows that there is a temporal element to ecosystem coupling. A lag in species response such as this may mask declining function mobile species as a link between ecosystems and entire meta-ecosystems, which would be important to understand if the meta-ecosystem supported rare habitats or species of conservation of concern.

The proposed changes in fisheries management currently underway in the EU include a ban on discarding unwanted parts of the catch. This is represents the loss of a major food resource for scavenging species such as great skuas and is predicted to decrease colony attendance and potentially population size (Bearhop *et al.*, 2001; Votier, Furness, *et al.*, 2004; Bicknell *et al.*, 2013). My works shows that this is likely to influence the plant communities, but that changes will occur slowly.

CHAPTER 5

GREAT SKUAS INFLUENCE THE TERRESTRIAL INVERTEBRATE COMMUNITY ASSEMBLAGE



ABSTRACT

Mobile species can act as biotic vectors, transporting energy, material and organisms, across ecosystem boundaries. As a result, ecosystems can become spatially coupled into meta-ecosystems. Given the increasing pressures of anthropogenic activity on global biodiversity and species movement, a greater understanding of how mobile species influence the functioning of the meta-ecosystem will provide a better insight to how changes in one ecosystem may influence coupled ecosystems across landscapes. Throughout this thesis I use the marine-terrestrial meta-ecosystem connected by the seabird great skua as a model system to investigate this. The aim of this chapter is to determine how changes in environmental conditions induced by great skuas influence above ground invertebrate communities. I used pitfall trapping in an observational study to idetnify differences in invertebrate community composition associated with areas of high great skua use. Invertebrate communities were assessed on two levels: all individuals were identified to order to assess general changes to the entire community and ground beetles were identifeid to species level. I demonstrate that in areas of elevated great skua abundance invertebrate communities are characterised by a greater abundance of detritivorous orders specifically collembola, a greater abundance of small predatory ground beetles and a lower abundance of predatory orders such as spiders and large immobile ground beetle relative to areas of low great skua abundance. Using the ground beetle community, I demonstrate that the decline in large bodies predators is in part mediated through decreases in vegetation structure associated with the changes plant communities and the physical disturbance caused by great skuas. However, the relative importance of these in controlling ground beetle abundance appears to partly be mediated through species mobility. This may also release top down pressure on other species, such as smaller collembola predators, which may explain their elevated abundance. Furthermore, I show that great skuas influence on ground beetle community composition is much lower at small mound sites compared to larger club sites, despite similar influences on plant community composition at these sites. This result highlights the importance of considering the scale of influence of the mobile species when examining how coupled ecosystems may respond to changes in source ecosystem. Restructuring of fisheries management policy currently underway in parts of Europe is expected to cause a significant shortfall in food availability for scavenging seabirds, such as great skuas. The predicted impacts will impair their function as a mobile link species, reducing marine derived nutrient inputs and plant nutrients, as well as carrion and direct disturbance. In response, it is predicted that detritivorous orders will decline and large bodied predatory species will increase. However, vegetation communities have been shown to respond slowly to changes in great skua abundance therefore, species such as spiders and some carabids which are reliant on high vegetation structural complexity may take longer to recolonise areas. Future work should

focus how changes in the ecosystem connectivity influences the invertebrate community dynamics.

INTRODUCTION

Mobile species can connect ecosystems by acting as biotic vectors, transporting energy, material and organisms across ecosystem boundaries. This movement can exert a significant influence on resident communities, ecosystem processes and trophic interactions, especially where there are large dissimilarities between ecosystems in the quantity of the transported item (Polis, Anderson and Holt, 1997; Banks-Leite and Ewers, 2009; Bauer and Hoye, 2014). This has given rise to the meta-ecosystem theory, whereby two or more coupled ecosystems function as single unit. Under this conceptual framework, any disturbance in the source ecosystem is likely flow through the mobile link species and influence the source ecosystem (Loreau, Mouquet and Holt, 2003). Given the increasing pressures of anthropogenic activity on global biodiversity and species movement, a greater understanding of how mobile species influence the functioning of the meta-ecosystem will provide a better insight to how changes in one ecosystem may influence coupled ecosystems across landscapes.

In coastal environments, seabirds couple the marine and terrestrial ecosystems. During the breeding season, seabirds form nesting colonies in terrestrial environments whilst continuing to forage on marine resources, thereby mobilising nutrients across marine-terrestrial ecosystem boundaries in the form of faeces and carrion (Blackall *et al.*, 2007; Riddick *et al.*, 2012). Evidence of marine derived nutrients have been identified in soils and in species at multiple trophic levels, including terrestrial invertebrates, within and around seabird colonies (Croll, 2005; Kolb, Jerling and Hambäck, 2010; Callaham Jr. *et al.*, 2012; Caut *et al.*, 2012; Cross *et al.*, 2014). Furthermore, where colonies are formed inland, seabirds can cause significant amounts of disturbance to vegetation through trampling and burrowing (Hogg and Morton, 1983; Maesako, 1999; Fukami *et al.*, 2006). Marine nutrient subsidies and disturbance can independently and interactively cause increases in local nutrient availability, plant productivity and plant nutrient content, alter plant community composition and structure, change the quantity and decomposability of plant litter and increase rates of nutrient cycling (Mizutani and Wada, 1988; Hogg, Morton and Venn, 1989; Anderson and Polis, 1999; Croll, 2005; Ellis, Fariña and Witman, 2006; Fukami *et al.*, 2006; Maron *et al.*, 2006; Wardle *et al.*, 2012).

Basal ecosystem resources, such as these, can influence the distribution and interactions of invertebrate species by changing the relative importance of top-down and bottom-up controls of food web dynamics and structural heterogeneity of habitats. In some cases, there is evidence of bottom-up trophic cascades in invertebrate communities. Elevated plant productivity, plant nutrient content and plant species diversity has been shown to increase invertebrate herbivore diversity, and abundance. In addition, increased plant litter and allochthonous carrion has been shown to result in greater detritivore abundance. These changes in primary consumer communities can then, in turn, influence predator and parasitoid communities (Siemann *et al.*, 1998; Knops *et al.*, 1999; Hawes *et al.*, 2003; Wimp *et al.*, 2010; Hoekman *et al.*, 2011). However, changes in plant diversity and productivity are often associated with changes in habitat structure. A meta-analysis found that prey and parasitoid species are vulnerable to decreases in structural complexity in their habitats, irrespective of prey abundance (Langellotto and Denno, 2004). Therefore, changes in plant community composition can also alleviate top-down pressures on primary consumers. In addition to trophic guilds, changes in vegetation structure have been shown to influence the diversity of whole taxonomic groups. For example, carabid beetle diversity declines with decreased vegetation structure and increased disturbance, as larger carabid species are more prone to predation in open habitats (Blake *et al.*, 1996; Brose, 2003; Rainio and Niemelä, 2003).

Studies carried out within seabird colonies to date demonstrate that the response of different trophic and taxonomic invertebrate guilds are not consistent. In the Gulf of California and the Stockholm archipelago, elevated terrestrial detrivorous and scavenger invertebrate species abundances were identified in seabird colonies due to increases in carrion, plant productivity and nutrient run-off into adjacent freshwater habitats (Sanchez-Pinero and Polis, 2000; Kolb, Jerling and Hambäck, 2010; Kolb *et al.*, 2012). However, the corresponding response of predators varies between location and is dependent on taxonomic guild and plant cover. On arid islands in the Gulf of California, where seabirds inputs increase plant cover, the elevated prey resource promoted spider abundance (Polis and Hurd, 1995; Wait, Aubrey and Anderson, 2005). In the Stockholm archipelago, however, where high nesting density inhibits plant growth, coleopteran predators increases, but there was no corresponding increases in web building spider abundance and the abundance of Lycosid (wolf) spider declined within seabird colonies (Kolb, Jerling and Hambäck, 2010; Kolb *et al.*, 2012). Other studies that focused on broad taxonomic groups such as order also identified contrasting results. Towns *et al.* (2009) found that when rat invasions reduced seabird densities, the abundance of Gastropods, Ampioda, Collembola, Psocoptera, Coleoptera, Lepidoptera, Hymenoptera, Chilipoda orders also declined. In contrast, Kolb *et al.* (2012), found little change in most invertebrate order abundances to variation in nesting seabird density. Finally, Bassett *et al.* (2014) found that different seabird species differentially affected invertebrate abundance across order, coleopteran trophic guild and coleopteran species.

The reported inconsistencies of the effect of seabirds on invertebrate communities make broad generalizations on how the changes in the marine ecosystem may influence terrestrial invertebrates difficult. Most of these studies only identified specimens to a taxonomic resolution necessary to detect a change in the community (taxonomic sufficiency) (Ellis, 1985). Whilst community descriptions based on higher taxonomic levels, such as order, can be similar to that of more precise taxonomic analysis, there is a loss of information associated with species-specific factors such as life history traits or behaviours (Pik, Oliver and Beattie, 1999; Terlizzi *et al.*, 2003). An alternative approach to taxonomic sufficiency is to use indicator species or groups (Carignan and Villard, 2002). By determining how this subset of the community and individual species within it respond to environmental stimuli we can infer potential mechanisms driving the whole community. Carabid beetles have been recommended as bio-indicator species as they are specious, easy to capture and identify, species are well defined, they are sensitive to several different environmental factors, exist across a wide range of habitats and include a broad spectrum of functional groups (Rainio and Niemelä, 2003). Therefore, here we focus on abundance and species of carabids for testing impacts of the bottom-up effects of marine-derived nutrients onto land.

Here I use the marine-terrestrial meta-ecosystem connected by great skuas, ground nesting seabirds of the NE Atlantic, as a model system to determine how mobile species can influence terrestrial invertebrate community composition. In chapters 2 and 3, I demonstrated that great skuas influenced plant community composition by increasing soil nutrient concentrations and causing considerable physical disturbance. Here, I take a correlative cross-section approach across areas of contrasting skua usage in three great skua colonies to test the hypotheses that (1) the broad invertebrate order abundance (number of individuals in an order) and community assemblage is related to differences in great skua use within the colony. Specifically, it was anticipated that in areas of high great skua influence invertebrate orders that supported many detritivorous species would have a higher abundance and visual predatory species spiders would have a lower abundance. In addition, ground beetles were used to get a higher resolution data set to test the hypothesis that (2) carabid beetle species abundance and communities are influenced by great skua abundance. I was predicted that these would follow a similar trend to order scale, and large bodied predators would have a lower abundance in areas of high great skua influence. Furthermore, in order to identify environmental mechanisms explaining carabid species abundance I test the hypothesis that (3) carabid species abundances are specifically influenced by great skua density, soil nutrient concentration and great skua induced changes in vegetation structure, where great skua density is being used as a proxy for the level of direct disturbance.

METHODS

Study area

The study was established at three large great skua colonies in the Shetland Island archipelago, Scotland: Lamb Hoga peninsula, Fetlar (Fetlar), Hermaness National Nature Reserve, Unst (Hermaness) and Isle of Noss National Nature Reserve (Noss) (See Figure 2.2). All sites comprise blanket peat bog. The vegetation communities at Fetlar and Hermaness have affinities to National Vegetation Classification (NVC) community M19 *Calluna vulgaris – Eriophorum vaginatum* blanket mire blanket mire vegetation, whereas that at Noss has a greater affinity to NVC community M17 *Trichophorum cespitosus – Eriophorum vaginatum* blanket mire and M15 *Trichophorum cespitosus – Erica tetralix* wet heath, as there is a reduced abundance of *Calluna vulgaris* largely due to historic land use (Rodwell (eds), 1991).

Great skuas form breeding colonies inland and are ground nesters. Consequently, faeces and carrion, and therefore, marine derived nutrients are deposited directly into the terrestrial ecosystem and there can be a considerable amount of direct disturbance of the vegetation in areas of high skua usage. Great skua abundance across the colony is not homogeneous, but comprises a loose collection of breeding territories, each one containing the nest and at least one raised mound on which the birds stand to observe their territory. In addition, within larger colonies, there are one or more discrete areas called “club sites” where immature, non-breeding birds form large aggregations of between 10 and 200 individuals (Furness, 1987). Most of the land area of a colony away from nests, mounds and club sites is used infrequently by great skuas and is referred to here as the “intra-colony”. This colony organisation of different areas of contrasting skua usage (and therefore contrasting marine nutrient input and disturbance) provides an ideal system in which to test hypotheses about the effects of different levels of marine nutrient input on terrestrial invertebrate communities.

Correlative study design

Sampling locations were the same as those selected in the correlative study in Chapter 2 to test the effect of great skuas on soil and plant nutrient status. Briefly, I used the natural variation in great skua abundance at each colony to establish two great skua high use treatments (club sites and mound sites) and used the intra-colony areas to establish control sites due to the very low great skua use (intra-colony control sites). At each colony, within a single club site, 9 m^2 sampling locations were established in a grid formation (n = 12 per colony); sampling locations were established on whole mound sites in randomly selected breeding territories within 0.5 km radius of the club site (n = 12 per colony); and, 9 m^2 sampling locations were established at intra-colony control sites, approximately 20-30 m on a random bearing from each of the mound sites (n = 12 per colony). Furthermore, to determine if there is a colony scale effect of great skuas each colony had a paired extra-colony control site, where 9 m^2 sampling locations were established in a grid formation separated by at least 15 m (n = 12) (see Chapter 2 for definitions and more detail of treatments).

Invertebrate sampling

Invertebrate sampling was carried out using pit-fall trapping. Traps comprised plastic cups (127 mm depth x 96 mm diameter) buried flush with the soil surface and partially filled a 50% propylene glycol antifreeze solution (diluted with water). Traps were protected from rainwater and excessive external interference by a clear lid (140mm diameter) held 15mm from the ground by two U shaped pegs. Traps were established in June 2017 and were left open for a period of 4 weeks and emptied at two-week intervals. The trap contents were stored in 70% ethanol, before all individuals were identified to order, all coleoptera were identified to family and all carabids to species. The exception to this was *Pterosichus rhaeticus/nigrita*, which can be reliably separated only using genetic analysis (Luff, 2007).

In a preliminary study, flooding of traps and interference by great skuas was an issue. In order to overcome this, two traps were set at least 1 m apart within each sampling location. One trap from each site was selected randomly (unless it was the only one still intact) for sample processing.

Summary community descriptions

Several summary descriptors and indices were calculated to provide an overview of the carabid community and the effect of great skua use. These comprised the proportion of the total Coleopteran individuals that were carabids, the total number of individual carabids recorded (abundance), carabid species richness and Simpson's Diversity Index (D) and Simpson's measure of evenness the carabid community (Magurran, 2003).

Environmental data

Environmental parameters (skua density, soil total and extractable N and P, soil bulk density, vegetation height) were used to identify the mechanism by which great skuas influence carabid community (hypothesis 3).

Great skua use was measured using vantage point spot counts of individual skuas within each sampling location. Counts were undertaken at each sampling location between 08:00 and 10:00 on 14 days evenly spaced between 9th June and 23rd August 2017. The counts were converted into densities to account for the variation in the size of mound sites.

Total and extractable soil nitrogen and phosphorus concentrations were measured in a single soil core taken from taken at each sample location within 2m of the pitfall traps. A second core was taken to measure bulk density and convert concentrations to gram per m^2 to account for different physical properties of the soil at different colonies (See chapter 2 for more detail of sample processing).

Ground vegetation height was measured at each sampling location within 2m of the pitfall traps using a pin drop method. A total of 16 pins were positioned evenly across a $60cm^2$ quadrat (15cm spacing). At each pin the distance between the soil or litter layer and the highest plant touching each pin was measured. The mean vegetation height from the 16 pins at each sampling location was used for statistical analysis.

Prior to statistical analysis, multicollinearity was assessed using Pearson correlation coefficients and the correlation between variables was considered acceptable if the coefficient was less than 0.6 (Inoue, Stoeckl and Geist, 2017). Total and extractable soil nitrogen and phosphorus were correlated. Therefore, a Principle Components Analysis of these four variables was undertaken and the first principle component (PC1) was used as a compound measure of soil nutrients. This axis explained approximately 70% of the variation in sampling sites, with each nutrient contributing approximately equally to the axis loadings (see Figure A4 and Table A5 in Appendix). No other correlations between explanatory variables were identified.

Statistical analysis

The effect of great skuas on terrestrial invertebrate order and carabid species abundance (hypothesis 1 and 2) was assessed using generalized linear models (GLM) and visualised using model-based unconstrained ordination implemented through the MVAbund package and BORAL package, respectively, in R (Wang *et al.*, 2012; Hui, 2016). Both data sets had a strong mean-variance relationship, violating the assumptions of distance based multivariate analysis (Anderson, 2001; Warton, Wright and Wang, 2012). Using GLMs and model-based ordination allows for the specification of the data distribution to account for such relationships in the data.

In the MVabund package, separate GLMs were fitted to each response variable in the analysis using a common set of explanatory variables. Here, the response variables comprised the number of individuals in each invertebrate order (hypothesis 1) and the number of individuals in each carabid species (hypothesis 2) at each sampling location (i.e. a site by order/species matrix). In both models, great skua use (extra-colony control, intra-colony control, mound and club), colony and their interactions were used as explanatory variables. Score tests (a resampling-based hypothesis test) using PIT-trap resampling were then used to initially make community-level (i.e. all taxa abundances at a sample location combined) and, subsequently, taxon-specific inferences about how the explanatory variables influenced the invertebrate order and carabid species abundances. This test and the resampling technique was considered most appropriate for these data structures, whilst still taking into account correlations between taxa abundance (Wang *et al.*, 2012).

Unconstrained model-based ordination was used to visualise the community level response to great skua use and colony. For both data sets, pure latent variable models (LVM) were fit to the number of individuals in each invertebrate order (hypothesis 1) and the number of individuals in each carabid species (hypothesis 2) within sampling locations. Briefly, taxon abundances (order/carabid species) are regressed against two unobserved predictors (latent variables) in an GLM and Bayesian Markov chain Monte Carlo (MCMC) estimation is used to calculate model coefficients. The median coefficient estimates of both latent variables are then used to produce biplots, which are comparable to and interpreted in the same way as a Non-metric Multi-Dimensional Scaling (NMDS) ordination plot (Warton *et al.*, 2015; Hui, 2016). Standard, weakly informative prior distributions were used (as pre-set in the BORAL function in the package, see Hui, 2016).

To identify environmental mechanisms that explain carabid species abundance response to great skuas (hypothesis 3), data were reanalysed using a Correlative Response Model (CRM) implemented in the BORAL package in R (Hui, 2016). The CRM fits separate GLMs for each species abundance using a common set of explanatory variables by Bayesian MCMC estimation. To account for residual covariation between species abundances not explained by the specified explanatory variables two unmeasured latent variables are included in the model (Warton *et al.*, 2015; Hui, 2016). Here, the number of individuals in each carabid species was used as a response variable and great skua density (individual sampling location counts), soil nutrient concentration and vegetation height were used as continuous explanatory variables. Mound sites were removed from this analysis because small scale changes in environmental conditions (i.e. areas less than 3m radius) are not likely to influence carabid community composition (Cole *et al.*, 2010) and mound sites tend to be under 3m wide (see Results and Discussion). For each carabid species, median explanatory coefficient estimates were extracted from the model and the association of the variable with the species abundance was considered significant if the 95% credible intervals did not include a zero. In addition, variance decomposition was used to quantify the amount of variation in carabid species abundance explained by the predictors and the amount of residual variation explained by the latent variables.

All models were verified using Dunn-Smyth residual analysis, which identified that the negative binomial distribution was most appropriate for both data sets (Wang *et al.*, 2012; Hui, 2016).

RESULTS

The effect of great skuas on invertebrate orders

A total of 47,878 individual specimens were identified to order level across all great skua use sites and colonies, comprising 18 different orders. The multivariate GLM analysis showed that the invertebrate order community was significantly influenced by great skua use (score $_{[3,144]}$ = 269.74, $p < 0.002$) and colony (score $_{[2,144]}$ = 144.68, $p < 0.001$). Furthermore, the interaction between great skua use and colony was significant (score $_{[6,144]}$ = 274.19, $p < 0.01$) indicating that the effect of great skua use on the invertebrate order community composition differed between different colonies.

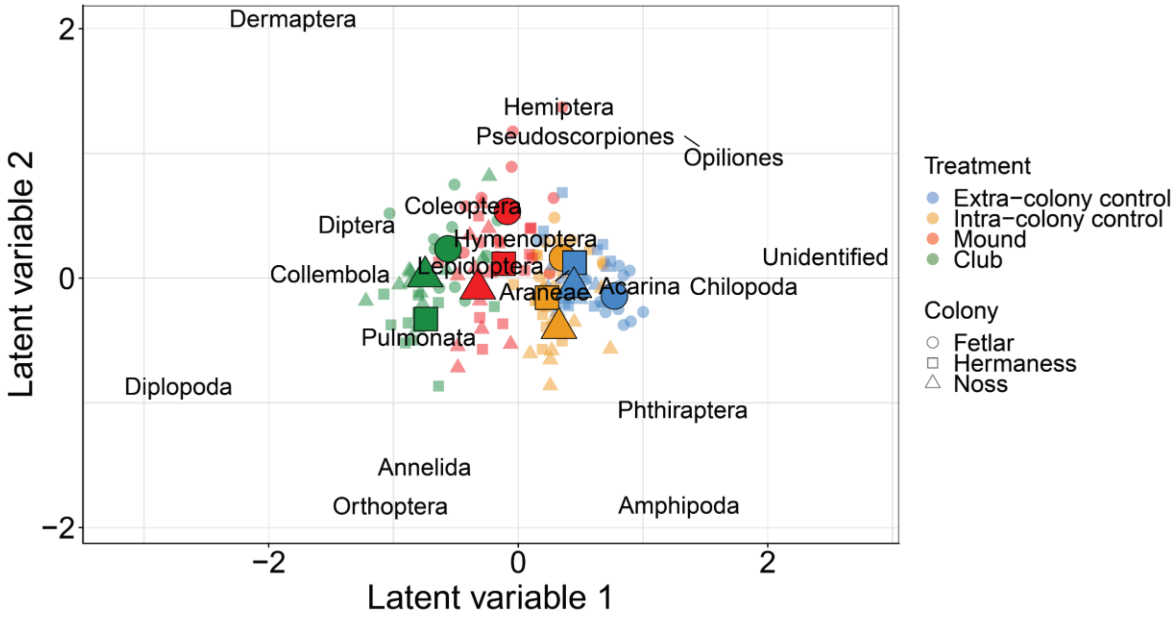


Figure 5.1. Latent variable model biplots of sites and invertebrate order. The colour represents the great skua use (blue – extra colony control, orange – intra-colony control, red – mound and green – club) and shape represents colony (circle – Fetlar, square – Hermaness and triangle – Noss). The small points represent each sampling location and the large represent great skua use and colony means. The text represents directions of order gradients and the relative distance from the origin indicates the strength of that gradient. Orders in the same direction and far from the origin are highly correlated e.g. Pseudoscorpiones and Opiliones.

For 11 of 22 invertebrate orders, abundance (i.e. number of individuals) was significantly influenced by great skua use. In addition, the first latent variable in the LVM separated the sample location order community composition by great skua use (Figure 5.1). Club and mound sites were characterised by higher abundances of Diptera, Collembola and Coleoptera than intra- and extra-colony control sites, whereas intra- and extra-colony control sites supported greater abundances of Araneae and Chilopoda. A total of 11 out of 22 invertebrate orders differed significantly between colonies. Nearly all the orders that were influenced by great skua use were also affected by the colony (see Table 5.1). In addition, there was a significant effect of the interaction between great skua use and colony on the abundance of 8 out of 22 orders, indicating that was the effect of great skua use was dependent on the colony at which they occurred. The significant interaction was reflected in the LVM biplot (Fig. 5.1), where sampling locations were separated by colony along the second latent variable axis but the relative differences in the order community composition at great skua use sites (i.e. club, mound etc.) are not consistent across colonies.

Table 5.1. The effect of great skua use, colony and great skua use by colony interaction on invertebrate order abundance. The significance of the predictor is calculated using ANOVA on 999 bootstrap resampling iterations. Significant effects are denoted by bold text, marginally non-significant effects (p>0.1) are denoted by non-bold text and non-significant effects by ns.

	Great skua use		Colony		Interaction	
Invertebrate order	Score	P	Score	P	Score	P
Acarina	35.812	**0.001**	40.182	**0.001**	35.710	**0.011**
Amphipoda	3.000	ns	2.000	ns	0.001	ns
Annelida	5.116	ns	14.329	**0.025**	4.903	ns
Araneae	21.338	**0.001**	16.307	**0.012**	49.549	**0.004**
Chilopoda	3.000	ns	2.000	ns	0.001	ns
Coleoptera	58.979	**0.001**	36.740	**0.001**	45.933	**0.004**
Collembola	80.735	**0.001**	14.985	**0.02**	34.314	**0.012**
Dermaptera	20.149	**0.001**	12.520	**0.029**	5.6572	ns
Diplopoda	5.001	ns	6.228	0.071	0.001	ns
Diptera	62.714	**0.001**	36.539	**0.001**	39.243	**0.005**
Hemiptera	61.329	**0.001**	8.763	0.071	28.065	**0.022**
Hymenoptera	17.978	**0.001**	33.518	**0.001**	23.287	**0.03**
Lepidoptera	19.457	**0.001**	12.371	**0.029**	3.7699	ns
Opiliones	16.130	**0.003**	17.321	**0.009**	49.683	**0.004**
Orthoptera	1.724	ns	1.1821	ns	0.001	ns
Phthiraptera	4.197	ns	9.528	ns	0.000	ns
Pseudoscorpiones	3	ns	2.000	ns	0.001	ns
Pulmonata	42.410	**0.001**	11.301	**0.044**	5.709	ns
Unidentified	6	ns	4.000	0.086	0.001	ns

The effect of great skuas on carabid community

A total of 5324 of the invertebrate specimens were identified as Coleoptera, comprising 14 families. Carabids were the most abundant family identified, accounting for just under half of all Coleoptera (2465 specimens). The proportion of individuals that were carabids and carabid abundance differed between great skua use (Table 5.2). Carabids across all colonies comprised 24 different species. At individual sampling locations carabid species richness was fairly low although species richness and diversity were slightly higher at mound sites compared to other great skua use sites within each colony (Table 5.2).

Table 5.2 Mean (±SE) carabid community descriptive indices. % Coleopteran carabid represents the proportion of all coleoptera individuals identified as carabids. Abundance represents the number of carabid individuals. Species richness is the number of carabid species. Simpson's D is Simpson's diversity index of carabid species and Simpson's E is Simpsons measure of evenness.

	% Coleopteran carabids	Abundance	Species richness	Simpson's D	Simpson's E
Extra-colony Control					
Fetlar	73.56 (6.52)	4.00 (0.90)	2.17 (0.44)	0.56 (0.09)	0.45 (0.12)
Hermaness	45.55 (8.04)	3.92 (0.97)	3.92 (0.93)	0.53 (0.12)	0.15 (0.05)
Noss	54.05 (4.36)	7.42 (0.90)	3.42 (0.40)	0.68 (0.04)	0.42 (0.07)
Intra-colony control					
Fetlar	79.16 (3.28)	27.08 (5.13)	4.83 (0.52)	0.55 (0.06)	0.33 (0.05)
Hermaness	60.49 (7.02)	3.58 (0.57)	2.67 (0.43)	0.56 (0.09)	0.49 (0.16)
Noss	51.58 (4.22)	14.42 (2.09)	5.92 (0.67)	0.72 (0.07)	0.20 (0.03)
Mound					
Fetlar	43.52 (4.25)	21.42 (2.39)	6.08 (0.45)	0.66 (0.04)	0.28 (0.04)
Hermaness	46.09 (6.56)	6.42 (0.73)	4.42 (0.42)	0.73 (0.02)	0.37 (0.06)
Noss	29.71 (3.56)	21.42 (3.71)	7.42 (0.60)	0.76 (0.02)	0.20 (0.03)
Club					
Fetlar	54.55 (3.57)	54.00 (5.93)	5.58 (0.42)	0.52 (0.03)	0.39 (0.04)
Hermaness	63.82 (5.57)	17.92 (2.68)	3.92 (0.38)	0.58 (0.06)	0.38 (0.06)
Noss	31.06 (5.57)	23.83 (2.76)	5.42 (0.48)	0.65 (0.03)	0.34 (0.05)

Carabid community composition was significantly influenced by great skua use (score $_{[3,144]}$ = 36.13, $p < 0.05$) and colony (score $_{[2,144]}$ = 29.90, $p < 0.001$). Furthermore, a significant skua use by colony interaction suggests that the effect of great skua use on the carabid community was significantly different at different colonies (score $_{[6,144]}$ = 16.36, $p < 0.01$).

The abundance of 13 out of 24 carabid species were significantly influenced by great skua use (Table 5.3). The LVM biplot (Figure 5.2) indicates that difference in carabid community at club sites largely accounts for this, as intra- and extra-colony control sites and mound sites at each colony occur at similar locations in the ordination. Club sites supported a higher abundance of *Loricera pilicornis*, *Pterostichus rhaeticus*/*nigrita*, *Pterostichus strenuus* and *Pterostichus diligens*, whereas, *Pterostichus adstrictus*, *Calathus melanocephalus*, *Carabus problematicus*, *Pterosticus nigra* and *Trechus obtusus* were more common at mound and control sites. In addition, that 7 out of 24 species differed significantly between colonies. The first latent variable in the LVM biplot separated carabid species abundance at sampling locations consistently by colony, with Noss sites occurring right side of the ordination, Hermaness in the centre and Fetlar on the left (Figure 5.2) Therefore, species such as *Harpalus latus*, *Pterostichus strenuus* and *Dyschirius globosus* have significant association with Noss, *Pterostrichus adstrictus* with Hermaness, *Pterostichus niger* with both Hermaness and Fetlar and *Agonum fuligninosum* with Fetlar. In addition, *Pterostichus strenuus* and *Pterostichus diligens* abundance were significantly influenced by the interaction between great skua use and colony. Furthermore, there was a marginally non-significant effect of the interaction on the abundance of 5 carabid species, indicating that the effect of skua use on these species varied with colony.

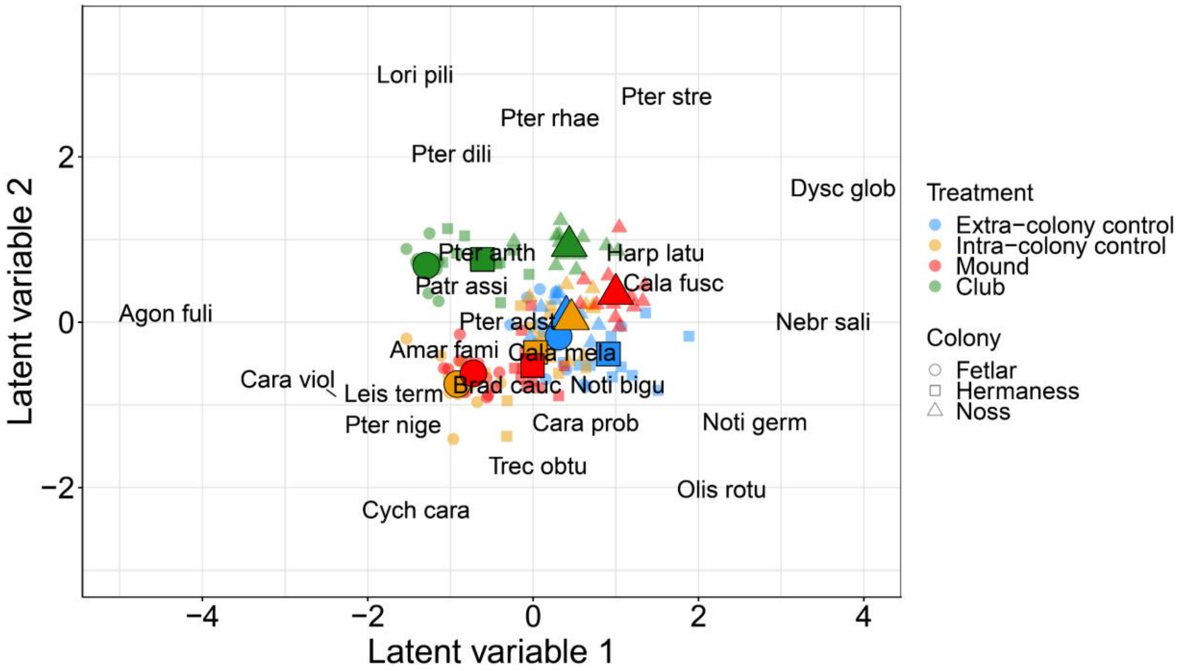


Figure 5.2. Latent variable model biplots of sites and carabid species. The colour represents the great skua use (blue – extra-colony control, orange – intra-colony control, red – mound and green – club) and shape represent the three separate colonies (circle – Fetlar, square – Hermaness and triangle – Noss). The small points represent each sample and the large represent great skua use site and colony means. The text represents directions of species gradients and the relative distance from the origin indicates the strength of that gradient. The first four letters of a species genus and species name represent each species (for species codes see Table 5.3). Species in the same direction and far from the origin are highly correlated e.g. *Loricera.pilicornis* and *Pterostichus.diligens*.

Table 5.3. The effect of great skua use, colony and the interaction on invertebrate order abundance. The significance of the predictor is calculated using ANOVA on 999 bootstrap resampling iterations. Significant effects are denoted by bold text, marginally non-significant effects (p>0.1) are denoted by non-bold text and non-significant effects by ns.

		Great skua use		Colony		Interaction	
Carabid species	LVM code	Score	P	Score	P	Score	P
Agonum fuliginosum	Agon fuli	495.95	**0.001**	1233.44	**0.001**	7.62	ns
Amara familiaris	Amar fami	3.00	ns	2.00	ns	0.00	ns
Bradycellus caucasicus	Brad cauc	3.00	ns	2.00	ns	0.00	ns
Calathus fuscipes	Cala fusc	10.46	ns	7.82	ns	6.81	ns
Calathus melanocephalus	Cala mela	39.52	**0.014**	13.03	ns	28.53	0.07
Carabus problematicus	Cara prob	28.60	**0.025**	1.81	ns	14.51	ns
Carabus violaceus	Cara viol	6.00	ns	4.00	ns	0.00	ns
Cychrus caraboides	Cych cara	3.00	ns	2.00	ns	0.00	ns
Dyschirius globosus	Dysc glob	30.71	**0.025**	29.46	**0.018**	32.72	0.07
Harpalus latus	Hara latu	37.51	**0.017**	53.20	**0.001**	35.91	0.063
Leistus terminatus	Leis term	3.00	ns	2.00	ns	0.00	ns
Loricera pilicornis	Lori pili	697.06	**0.001**	8.69	ns	32.96	ns
Nebria salina	Nebr Sali	6.09	ns	6.73	ns	11.00	ns
Notiophilus biguttatus	Noti bigu	3.00	ns	2.00	ns	0.00	ns
Notiophilus germinyi	Noti germ	15.00	0.095	9.39	ns	13.00	ns
Olisthopus rotundatus	Olis rotu	12.00	ns	3.50	ns	0.00	ns
Patrobus assimilis	Patr assi	27.62	**0.025**	4.04	ns	25.63	0.07
Pterostichus adstrictus	Pter adst	25.67	**0.025**	26.36	**0.018**	36.92	0.051
Pterostichus anthracinus	Pter anth	2.00	ns	1.00	ns	2.00	ns
Pterostichus diligens	Pter dili	96.99	**0.001**	7.84	ns	52.58	**0.043**
Pterostichus niger	Pter nig	118.95	**0.001**	87.41	**0.001**	9.81	ns
Pterostichus rhaeticus/nigrita	Pter rhae	102.13	**0.001**	190.63	**0.001**	10.12	ns
Pterostichus strenuus	Pter stre	81.39	**0.001**	242.32	**0.001**	68.81	**0.043**
Trechus obtusus	Trec obtu	18.59	**0.043**	12.48	ns	8.76	ns

Environmental mechanisms explaining carabid species abundance

The Correlative response model identified 10 out of 24 carabid species that have significant associations with the measured environmental factors that were deemed to be influenced by great skuas (combined soil nutrient index, ground vegetation height and great skua density) (Figure 5.3). *Pterostichus strenuus*, *P. rhaeticus/nigrita* and *C problematicus* had significant positive associations with soil nutrients. *P. adstrictus*, *C. fuscipes*, *Trechus obtusus* and *C. problematicus* had significant negative associations with great skua density. Finally, *P niger* and *P. assimilis* had a positive association with vegetation height, whereas, *P. diligens* and *L. pilicornis* had a negative association with vegetation height.

The amount of variation in species abundance explained by the measured environmental factors differed considerably (Figure 5.3). For example, approximately 97%, 85% and 70 % of the variation in *C. problematicus*, *T. obtusus* and *C. fuscipes* abundance was explained by soil nutrients, great skua density and vegetation height. Conversely, only 25% and 22% of the variation in *P. assimilis* and *P niger* abundance was explained by these environmental parameters (See the bottom left hand panel of Figure 5.3). In each case, the remaining 3%, 15%, 30%, 75% and 78% respectively of the variation is explained by the Latent Variable 1 and Latent Variable 2, which may account for correlations with unmeasured abiotic variables such as pH, soil carbon or moisture, or biotic interactions between species.

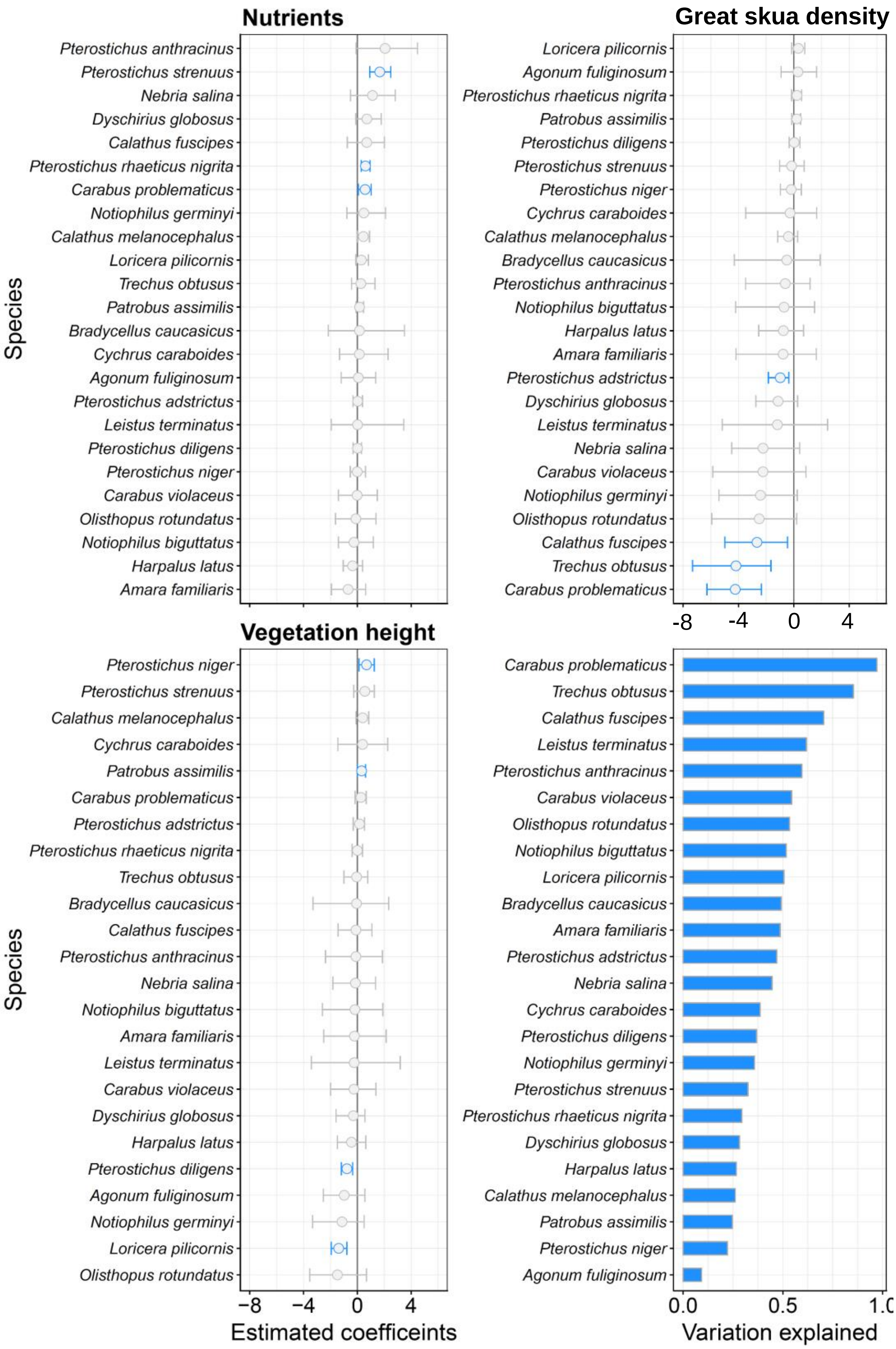


Figure 5.3. The effect of soil nutrients, great skua density and vegetation height on carabid species abundance. The first three graphs (nutrients, great skua density and Vegetation height) display the median parameter estimates and 95% credible intervals for each carabid species. The effect of the predictor on species abundance is considered significant if the credible intervals do not include a zero and are shown here in blue. Positive values mean that species abundance increases with that environmental parameter while negative values mean that species abundance decreases with that environmental parameter. The bar chart shows the proportion of variation in the species abundances explained by all the predictors

DISCUSSION

The aim of this study was to determine how mobile species can influence terrestrial invertebrate community composition using the marine-terrestrial meta-ecosystem connected by great skuasas a model system. By transporting marine derived nutrients and causing significant disturbance, great skuas elevate nutrient status of soils and plants and nutrient cycling and alter plant communities and structural complexity. Here, I show in areas of elevated great skua influence invertebrate communities are characterised by a greater abundance of detritivorous orders specifically collembola, a greater abundance of small predatory ground beetles and a lower abundance of predatory orders and such as spiders and large immobile ground beetles relative to areas of low great skua abundance. In addition, I demonstrate the relative role of direct great skua disturbance, vegetation structure and soil nutrients in determining the ground beetle community assemblage. Furthermore, I show that great skuas influence on ground beetle community composition is much lower at small mound sites compared to larger club sites, despite similar influences on plant community composition at these sites.

Great skua influence over invertebrate orders

In support of hypothesis 1, I found that the broad invertebrate order abundance and community assemblage is related to differences in great skua use. The abundance of individuals within several key orders were driving the changes in the communities such as higher abundances of Collembola, Dermaptera, Diptera, Pulmonata and Coleoptera and reduced abundances of Arenaea and Opliones at high use great skua sites. Collembola, Dermaptera, Diptera and Pulmonata all contain detritivorous species and increases in detritivores has been identified in other seabird colonies (Fukami *et al.*, 2006; Towns *et al.*, 2009; Kolb, Jerling and Hambäck, 2010; Zmudczyńska *et al.*, 2012). Collembolan and Dipteran abundances have been shown to increase in response to artificially elevated food resource in other studies (Chen and Wise, 1999; Oelbermann, Langel and Scheu, 2008) and it is likely that great skuas are providing direct and indirect food subsidies for detritivores. Firstly, great skuas deposit a considerable amount of nutrient rich carrion into the terrestrial ecosystem which would provide a direct food subsidy (Chapter 2). Secondly, plant communities within seabird colonies tend to be dominated by species that have high rates of leaf turn over and litter with elevated concentrations of marine nutrient (Baumberger *et al.*, 2012; Wardle *et al.*, 2012; Chapters 3 and 4), which, is likely to provide an indirect high-quality food source for detritivorous taxa. Finally, high quality plant litter entering the soil food web in seabird colonies promote overall microbial biomass (Fukami *et al.*, 2006; Wright *et al.*, 2010). Soil microflora is a key food source for several collembola species, therefore, this would provide an additional food source subsidised by marine nutrient inputs.

Predator abundance such as Arenaea and Opliones were lower in areas of higher great skua use, despite increases in potential detrivorous prey taxa such as collembola. A number of studies in open habitats such as grasslands, including on seabird islands, have noted concurrent increases in spider and other predator abundances with other trophic guilds following nutrient and detritus subsidies (Polis and Hurd, 1995; Chen and Wise, 1999; Fountain *et al.*, 2008; Oelbermann, Langel and Scheu, 2008). However, as well as providing nutrient subsidies, great skua and other seabirds decrease the cover of dwarf shrubs through nutrient deposition and direct disturbance such as trampling and pulling (Chapter 4; Maron *et al.*, 2006; Kolb, Jerling and Hambäck, 2010). This reduces the structural complexity of the habitat which restrict prey capture rates for spiders and decrease refuge from predation themselves (Langellotto and Denno, 2004). This has also been observed in cormorant colonies, where minimal plant growth, due to very high nutrient levels, inhibited spider abundance, even though the spider's main prey (aquatic diptera) were more abundant due to the elevated nutrients (Kolb, Jerling and Hambäck, 2010). With respect to the wider community and food web dynamics, the negative effect of great skuas on spiders is likely to have benefited prey species abundance. Therefore, detritiverous taxa abundance is not only promoted by bottom-up food subsidies but also alleviation of top-down predation pressure.

The interpretation of great skua induced changes on invertebrate community at the order level is limited as a number of functional traits, such as trophic guilds, require a finer scale identification. For example, Coleopteran abundance is significantly elevated at high great skua use sites, however, this is difficult to interpret as the order includes a broad range of species-specific trophic guilds and functional groups.

Great skua influence on carabid species

My results mainly support the second hypothesis that carabid beetle species abundance and communities are influenced by great skua use. In general, the number of individual carabid beetles was higher at sites with greater great skua abundance in conjunction with slightly higher species richness and lower species diversity and evenness. However, the species composition of the carabid communities at the two high use sites - mound and club sites - were different from each other; mound carabid communities displayed considerable overlap with those at intra and extra-colony control sites, whereas club sites did not. Both club and mound sites have a more open vegetation structure than intra or extra-colony control sites due to the decrease in dwarf shrubs and increase in graminoid plant species (Chapter 4). Vegetation structure has been shown to have a strong influence on carabid communities, with large bodied species such as *Carabus problematicus* and *Pterostichus nigra* actively avoiding areas of open habitat and high disturbance, where they are more vulnerable to predation (Brose, 2003). A possible explanation for the observed is differences in carabid communities is the size of the great skua site areas. Cole *et al.* (2010) found that fine spatial scale changes in environmental conditions (under 3m radius) did not strongly influence carabid community composition. The size of mound sites varied with colony, but all were less than 3m across and are therefore likely too small to influence local carabid community composition or individual species abundance. Club sites, however, ranges between 200 and 250m^2 (Chapter 2) and therefore, represent a large area of unsuitable habitat that is actively avoided by certain carabid species. This result highlights the importance of considering the scale of influence of the mobile species when examining how coupled ecosystems may respond to changes in source ecosystem.

The carabid community at club sites were dominated by *Loricera pilicornis*, *Pterostichus strenuus* and *Pterostichus diligens*. These species likely benefited bottom-up increases in food availability and alleviation of top-down predation pressure. These three species are small bodied collembola predators (Ribera *et al.*, 2009; Pakeman, 2011; Luff, 2007) and increase in collembola abundance at club sites likely provide an abundant food source. Furthermore, large bodied species such as *Carabus problematicus* and *Pterostichus nigra* had a much lower abundance at club sites. Both will depredate the smaller bodied *L. pilicornis*, *P. strenuus* and *P. diligens*, therefore, their reduced abundance in the community will reduce top-down pressure (Forsythe, 1982; Wallin and Ekbom, 1994).

The effect of great skuas on carabid community was fairly consistent across colonies, suggesting that species abundance responds to common changes in environmental conditions, such as changes in vegetation structure, rather than colony specific ones, such as plant species or soil nutrient concentration (Chapters 4 and 2). However, the abundance of several species varied between colonies. For example, *Agonum fuligninosum*m and *Dyschirius globosus* and *Harpalus latus* are more abundant at Fetlar and Noss, respectively, and rare elsewhere. Furthermore, *Pterostihus diligens* was more abundant at Hermaness and Fetlar club sites, whereas *P. strenuus* is more abundant at Noss club sites (both had a significant interaction term in the model). Both species belong to the subgenus *Arguto* and are collembola predators and are likely to be fulfilling the same functional roles within the ecosystem at different colonies (Ribera *et al.*, 2009; Pakeman, 2011; Luff, 2007). The major difference between these two species is their habitat preferences. *P. strenuus* is significantly associated with improved neutral grassland, whereas *P. diligens* is associated more with moorland and acid grassland (Luff, 2007; Chetcuti, Kunin and Bullock, 2019). This is consistent with variation in soil conditions and plant community composition at the club sites of the three colonies. The club site at Noss is more like a neutral grassland and has a higher pH (4.46 ± 0.048) than either the Hermaness or Fetlar club sites. Noss is also dominated by the perennial grass Yorkshire Fog (*Holcus lanatus)* and has higher soil nutrient content. In contrast, Hermaness and Fetlar club sites, comprise acid grassland/blanket bog plant communities over deep peat (see Chapter 2, 3 and 4).

Environmental mechanisms explaining carabid species abundance

My results mainly supported the third hypothesis as several carabid species abundances were influenced by soil nutrient concentration, great skua density and changes in vegetation structure. The abundance of *Pterostichus strenuus, Pterostichus rhaeticus/nigrita* and *Carabus problematicus* are positively associated with high nutrient sites; increasing great skua density has a negative effect on *Pterostichus adstrictus*, *Calthus fuscipes*, *C. problematicus* and *Trechus obtusus* abundance; and, taller vegetation promotes *Pterostichus niger* and *Patrobus assimilis* abundance, whilst *Pterostichus diligens* and *Loricera pilicornis* abundance is associated with shorter vegetation.

Here great skua density is used as a proxy for the levels of great skua disturbance such as trampling and vegetation height as a measurement of habitat structural complexity. Several studies identified that disturbed, early successional habitats favour carabid communities dominated by smaller, highly mobile, short-lived species, whereas less disturbed habitats with greater structural complexity support a greater abundance of larger, longer-lived more sessile species (Niemela and Kotze, 2002; Small, Sadler and Telfer, 2002; Brose, 2003; Kotze and O’Hara, 2003; Rainio and Niemelä, 2003; Neumann *et al.*, 2016). *Carabus problematicus Pteristichus niger*, *Pterostichus adstrictus*, and *Calthus fuscipes* are all medium to large species, with mean body lengths of 21.9 mm (± 1.27), 18.3 mm (± 1.06), 10.9 mm (± 0.51) and 11.5 mm (±0.57), respectively. However, *Trechus obtusus* is very small, with a mean body length of 3.41mm (± 0.19) (body sizes from unpublished data). All four species negatively influenced by great skua disturbance are apterous or brachypterous; their hind wings are absent or reduced, which makes them flightless, poor dispersers (Ribera *et al.*, 2009; Pakeman, 2011; Luff, 2007). Whereas *P. niger* has macropterous hind wings, and is capable of flight (Luff, 2007). Therefore, whilst disturbance and vegetation structural complexity both reduce large bodied species, great skua disturbance appears to be acting specifically to reduce the abundance of species with poor mobility. This is consistent with a number of other studies that found that physical disturbance such as trampling by humans and livestock reduced species with traits associated with poor dispersal ability across several taxa (Bell, Wheater and Cullen, 2001; Niemela and Kotze, 2002; Pedley and Dolman, 2014). The precise mechanism for this is unclear, but it could be that mobile species are able to evade short term disturbances and are therefore still present in these areas when the vegetation is of a suitable height. Future work focussing on how great skua abundance influences beetle life history traits may help to identify the mechanisms that determines community assemblage.

The amount of variation in species abundance explained by soil nutrients, great skua density and vegetation height (predictor variables) was not consistent between species. For example, the predictors in model explained 97%, 85% and 70% of the variation in abundance for *Carabus problematicus, Techus obtusus* and *Calthus fuscipes,* respectively, but only 25% and 22% of the variation in *Patrobus assimilis* and *Pterosticus niger* abundance. Two latent variables were included in these models, which are designed to account for additional covariance in the species abundance, for example un-measured predictor variables and/or species-species abundance correlation (i.e. accounting for predator-prey or symbiotic interactions) (Warton *et al.*, 2015; Hui, 2016). My results suggest that whist disturbance is a very important factor in regulating *Carabus problematicus*, *Techus obtusus* and *Calthus fuscipes* abundance, decreased vegetation height is only part of the reason for reductions in *Patrobus assimilis* and *Pterosticus niger* abundance. A further explanation for the reduced abundance of these species could be specifically due to changes in vegetation composition and habitat. *Patrobus assimilus* in particular is known to have a strong association with bog habitats and moorland (Luff, 2007,Chetcuti, Kunin and Bullock, 2019). Further work exploring plant species community composition and plant traits as well as key bog characteristics such as soil moisture influenced by great skuas may provide clearer picture of important factors regulating these species' abundance (e.g. Pakeman and Stockan, 2014; Spake *et al.*, 2016).

Increased great skua density and decreased vegetation structure may also increase the risk of direct predation by great skuas, especially of large bodied beetles. Brose (2003) found that large carabid species preferentially occupy areas of dense vegetation to avoid predation. Beetle elytra have been identified in great skua pellets (Gilbert. L, unpublished data) and although this is not common, large beetles may be taken opportunistically by great skuas.

Several species were positively influenced by shorter vegetation sward created by great skuas. *Loricera pilicornis* abundance was positively associated with short vegetation, as was *Notiophilus germinyi* although this association was not significant. Both these species are fast runners with long thin legs and such species have been identified associated with open habitats in other studies (Small, Sadler and Telfer, 2002).

This demonstrates the relative importance of different great skua effects on the terrestrial ecosystem in regulating ground beetle species abundance and in part how great skuas influence the ground beetle community assemblage.

Conclusions

This work shows that the effects of great skuas are both direct, through disturbance and nutrient addition, but also meditated through their effects on the plant nutrient content, community and structure. This in turn influences the invertebrate food web structure by altering the relative importance of bottom up resource availability and top-down predation controls on community assemblage. Similar effects of great skuas were observed at the order and carabid species levels. In general, elevated great skua density resulted in increases in smaller, more mobile species able to exploit food subsidies, high nutrient conditions and increased prey availability mostly in the absence of large invertebrate predators, which were potentially excluded from club sites by reduced vegetation complexity and direct great skua disturbance. Interestingly, great skuas had a lower influence on ground beetle community composition at small mound sites compared to larger club sites, despite similar levels of nutrient deposition and disturbance as well as on plant community composition at these sites. This result highlights the importance of considering the scale of influence of the mobile species when examining how coupled ecosystems may respond to changes in source ecosystem.

Restructuring of fisheries management policy currently underway in parts of Europe is expected to cause a significant shortfall in food availability for scavenging seabirds, such as great skuas (Bicknell *et al.*, 2013). The predicted impacts will impair their function as a mobile link species, reducing marine derived nutrient inputs, including carrion, and direct disturbance. In Chapters 2, 3 and 4 I showed that this will result in decreased nitrogen but not phosphorus cycling and vegetation community composition will change slowly. Therefore, it is predicted that detritivorous orders will decline and large bodied predatory species, affected by direct disturbance will increase. However, species such as spiders and some carabids which are reliant on high vegetation structural complexity may take longer to recolonise areas. Future work should focus how changes in the ecosystem connectivity influences the invertebrate community dynamics.

CHAPTER 6

GENERAL DISCUSSION

Summary of Results

The meta-ecosystem concept describes spatial coupling of ecosystems through flows of energy material and organisms across ecosystem boundaries. Mobile species can act as biotic vectors to facilitate the movement of these items between ecosystems and can be essential to maintaining the meta-ecosystem. Global changes from habitat destruction and invasive species to anthropogenic climate change as well as over exploitation of resources are posing increasing threats to biodiversity. As well as reducing population sizes and influencing species phenology (Van Gils *et al.*, 2016), these actions can also directly threaten movement of populations and individuals between ecosystems (Wilcove and Wikelski, 2008) and therefore the functions of meta-ecosystems. Here I use the marine-terrestrial meta-ecosystem linked by the seabird great skua as a model system to determine how mobile species influence the functioning of the meta-ecosystem. This work therefore provides a better insight to how changes in one ecosystem may influence coupled ecosystems across landscapes.

Throughout this thesis I used a combination of observational and manipulation studies to identify how great skuas are influencing the function of the terrestrial ecosystem and therefore determine their role in the meta-ecosystem. Observational studies were used to provide evidence to support or reject hypotheses on a large scale. The manipulation studies however, allowed me to expose mesocosms to increased and decreased great skua abundance and manipulate the level of association with the marine ecosystem. These therefore provide empirical evidence of how the functioning of the terrestrial ecosystem changes in response to marine ecosystem change and how the mobile species function within the meta-ecosystem.

In Chapter 2 I showed that great skuas facilitate the flow of nutrients from the marine ecosystem into terrestrial plants. Large quantities of essential plant nutrients are deposited into the terrestrial ecosystem by great skuas, in some areas up to 9 times more nitrogen than background deposition rates. Stable isotope analysis demonstrated that the marine derived nutrient deposition feeds into plant nutrition, regardless of species and life history traits. Exposing plant communities to a lower abundance of great skuas caused a decline in leaf nitrogen concentration across all species, but phosphorus concentration did not change and increased in some species. Greater marine derived nutrient deposition did not result in elevated soil nitrogen and phosphorus concentrations at all sampling locations, indicating that plants are rapidly assimilating the marine derived nutrients they require, and the excess is lost through surface run-off or leached through the soil.

In Chapter 3 I demonstrated that increased plant nutrient concentrations drive rapid initial loss mass and release of nitrogen and phosphorus from decomposing litter, but the soil has relatively little effect. In addition, increases in great skua abundance has a negligible effect on rates of mineralization. In combination with the work in Chapter 2 this suggests that rates of mineralization are not influencing plant nutrient assimilation indicating that plants are accessing nutrients through simple abiotic pathways. In addition, this suggests a decoupling of mineralization and decomposition, but it is unclear if nutrients released during decomposition are lost or recycled.

In Chapter 4 I showed that great skuas cause a rapid decline in the abundance of dwarf shrub and tall acid grassland species in favour of shorter, ruderal and graminoid species. The increased association of high use areas with ruderal species suggests that both elevated nutrients and disturbance play a key role in plant community dynamics. In addition, I demonstrated that when great skua abundance declines there is little initial change in the plant communities. This suggests that there is a temporal element to ecosystem coupling and that a meta-ecosystem can stop functioning without any immediate effect on the plant community.

In Chapter 5 I demonstrated that in areas of elevated great skua abundance invertebrate communities are characterised by a greater abundance of detritivorous orders specifically collembola, a greater abundance of small predatory ground beetles and a lower abundance of predatory orders such as spiders and large immobile ground beetle relative to areas of low great skua abundance. Using the ground beetle community, I showed that a decline in vegetation structural complexity and increased direct disturbance by great skuas both reduce large bodied species abundance but great skua disturbance appeared to be acting specifically to reduce the abundance of species with poor mobility and that low vegetation height favoured fast running species. In addition, the reduction in large bodied predators is likely to release top down pressure on other species, such as smaller, faster collembola predators, which may explain their elevated abundance. Furthermore, I show that great skuas influence on ground beetle community composition is much lower at small mound sites compared to larger club sites, despite similar influences on plant community composition at these sites.

Marine ecosystem link increases the fertility of the terrestrial ecosystem

The main role great skuas have in the marine-terrestrial meta-ecosystem is to transport marine derived nutrients. Under normal conditions, blanket bog is considered an infertile system, dominated by slow growing acid loving species such as ericoid dwarf shrub. In infertile ecosystems such as this, most net primary productivity is returned to the soil as recalcitrant plant litter (Wardle *et al.*, 2004). As a result, nutrient cycles are slow, nutrients are conserved, and plant nutrition is dependent on interactions with ericoid mycorrhizal fungi. My results suggest that the addition of large quantities of marine derived nutrients by great skuas support function analogous to high fertility system, characterised by rapid, leaky nutrient cycles, with fast growing ruderal plant species assimilating plant nutrients through simple pathways resulting in high tissue nutrient concentrations (Figure 6.1).

Allochthonous, marine derived, nutrient deposition appears to decouple above- and belowground communities and functioning. The function of the soil biota was not influenced by marine derived nutrient deposition: Mineralization was unaffected by great skua abundance and the rate of decomposition and nutrient release from litter was largely determined by the litter quality rather than where the litter was buried (i.e. decomposition of high quality litter was the same at high and low great skua abundance sites). Plant tissue nutrient concentrations, however, were significantly higher in areas of high great skua influence and plant community dominance shifted from dwarf shrub to ruderal graminoid species, which are typical of fertile ecosystems (Wardle *et al.*, 2004). This suggests a decoupling of the soil biota functioning and above ground community composition and that plants are assimilating available nutrients in faeces and carrion via a direct abiotic pathway. This has previously been shown in seabird colonies on islands in New Zealand where sterilization treatments of soil from within and outside of seabird colonies had no influence on plant growth (Wardle et al., 2012).

Stable isotope analysis of heather and tormentil tissues also indicate that marine derived nutrient deposition causes a change in plant nutrient acquisition pathways from symbiotic relationship with ericoid mycorrhizae to direct assimilation through the root system. Nitrogen application has been shown to decrease the soil fungi to bacteria ratio (de Vries *et al.*, 2006) and, whilst changes in the plant community are likely to contribute at a community scale (Cornelissen *et al.*, 2001), the breakdown of this symbiotic relationship in these species specifically may provide a mechanistic explanation to the decreases in fungal biomass observed in other seabird colonies (e.g. Wright *et al.*, 2010). Furthermore, in agricultural systems decreases in the fungi to bacteria ratio is associated with increased nutrient leaching (Wardle *et al.*, 2004; de Vries *et al.*, 2006). At two of three club sites, plant N and P and $\delta^{15}N$ concentrations were elevated whilst soil concentrations were not suggesting that the nutrients not assimilated into plant tissue is lost through surface run-off and/or leached through the soil. This is analogous to fertile ecosystems which are characterised by soil food webs where bacteria-based energy channel, macrofauna and earthworms regulate rapid, leaky nutrient cycling (Wardle *et al.*, 2004). Future work should explore the how marine derived nutrients influence plant-mycorrhizae fungi relationship to determine if plants are switching their nutrient acquisition pathways and how this influences the loss of nutrients from the system and soil biota communities in this system in general.

The changes in plant community composition from ericoid dwarf shrub to ruderal, graminoid species are typical of fertile systems and can further promote rates of nutrient cycling and local fertility. *Calluna vulgaris* and other dwarf shrubs grow slowly, retain nutrients and allocate resources to leaf maintenance and defence (Grime, 1977). As a result, these species produce low amounts of recalcitrant litter that promoting infertile conditions and the requirement of ericoid mycorrhizae-plant symbiotic relationships (Wardle *et al.*, 2004). Ruderal graminoid species, however, have high leaf turnover and leaf nutrient concentrations and therefore produce high quality litter that rapidly release nutrients during decomposition (Grime, 1977; Wardle *et al.*, 2004). Therefore, as great skuas promote an increase the cover of graminoid and ruderal species in association with increases in plant nutrient content they will likely further increase in nutrient cycling on a community scale. Future work that that incorporated different plant species in decomposition experiments would clarify the effect of the marine ecosystem on community wide ecosystem functioning such as decomposition.

In addition to influencing decomposition changes in plant community coupled with increases in plant tissue nutrient content likely benefits detritivorous invertebrate species, especially in the absence of large herbivores. Typically, in fertile systems, a high proportion of the net primary productivity is consumed by herbivores and returned to the soil as labile faecal matter, which maintains graminoid dominated plant communities with high nutrient status (Wardle *et al.,* 2004). Sheep are the only large herbivore at these sites and herd sizes are kept low to prevent over grazing of the blanket bog vegetation (Swaile, J. Pers. Comm). Given that no congregations of sheep were identified in areas of high great skua abundance, sheep are not enriched in δ^{15}N (Cross *et al.*, 2014) and there was no colony wide increases in δ^{15}N (as would be expected if sheep were further transporting marine derived nutrients throughout the loose colony), it is likely that there was no substantial increase in herbivory as a result of marine derived nutrient deposition. Instead, great skuas are providing a constant supply of plant nutrients to maintain the plant communities, but an unusually large proportion of the nutrient rich plant material is likely to re-enter the soil as nutrient rich litter and provide high quality food for detritivores species, promoting their abundance. This in turn cascades through the food chain and promotes small predatory beetles, especially in the absence of large predators caused by increased disturbance and decreased vegetation structural complexity.

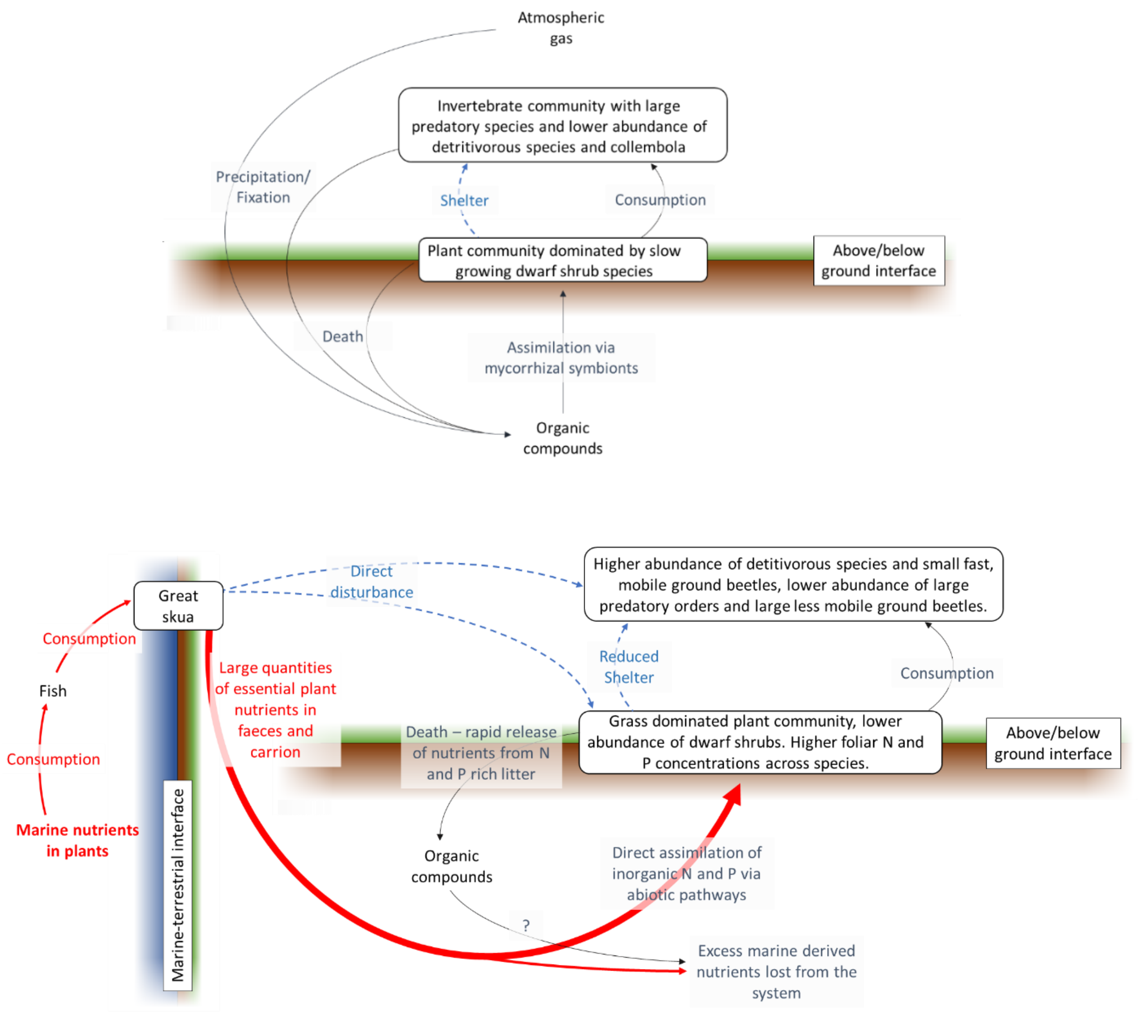


Figure 6.1. Summary of effects of great skuas within the terrestrial ecosystem. The top figure shows nutrient cycling, plant communities and invertebrate communities in terrestrial ecosystem that is not influenced by the marine ecosystem. The bottom figure demonstrates the roles that great skuas play in the functioning of the terrestrial ecosystem. The precipitation/fixation of atmospheric gasses and recycling of nutrients from dead invertebrates has been removed from this figure for simplicity.

The scale in meta-ecosystems

The overall effect of great skuas within the landscape is small. Great skuas did not have a significant colony level influence on any of the aspects of the terrestrial ecosystem measured here (i.e. intra- and extra-colony control sites were regularly the same). Therefore, the actual size of the area affected by great skuas is relatively small in comparison to the size of the colony. For example, Hermaness supports approximately 980 breeding pairs of great skuas and the average size of mound sites were 5.05m^2. When combined with the club sites at Hermaness, this equates to approximately 0.65 Ha influenced by great skuas or 0.07% of the entire reserve. However, this does mean that within great skua colonies there are small areas of habitat that are linked to the marine ecosystem within a wider landscape that is not. At a landscape scale, great skuas will therefore increase habitat heterogeneity. Low levels of elevated habitat heterogeneity has been shown to increase gamma diversity, taxonomic functional diversity with the landscape, ecosystem productivity and increasing ecosystem resilience (by creating islands of fertility) (Bonachela *et al.*, 2015; Leung, 2015).

The size of the ecosystem affected by the mobile link species appears to be an important consideration in the functioning of the meta-ecosystem. Here although at mound sites increases in soil and plant tissues nutrient concentrations and changes plant community were identified there was little effect on the ground beetle community composition. This is line with other studies that found that fine spatial scale changes in environmental conditions do not strongly influence ground beetle community composition (Cole *et al.* 2010) but rather represent small areas of unsuitable habitat that are not actively avoided. This suggests that where the size of the area effected by the flows of material is small, there is likely to be more influence of the surrounding landscape that are not coupled to other ecosystems. There is potential that this additional spatial element will be influenced by the mobility and home range size of the species in the surrounding landscape (Polis, Anderson and Holt, 1997; Loreau, Mouquet and Holt, 2003).

Temporal coupling of ecosystems

By artificially manipulating the great skua abundance, the turf transplants provide empirical evidence of how the functioning of the terrestrial ecosystem changes in response to marine ecosystem change. Furthermore, it allowed me to identify how change in great skua abundance would influence the terrestrial ecosystem over time.

When turfs were exposed to higher great skua abundance, the plant community responded quickly. There was rapid decline in the cover of dwarf shrubs in favour of graminoid species and, after three growing seasons, four of the 12 plant communities had converged with those at the high abundance control sites. There was also a corresponding increase in plant nitrogen and phosphorus concentrations in all plant species studied. In contrast, when turfs were exposed to a lower great skua abundance, there was only a very small initial response of the plant community composition, but this did not continue to change over time. In addition, although nitrogen concentrations declined in all plant species’ tissue, foliar phosphorus concentrations either did not decline or increased as in *Calluna vulgaris* and *Anthoxanthum odoratum*. This result was not surprising, given that plant species are known to respond quickly to disturbance events and take a long time to recover (Bayfield, 1979; Rawes, 1983). Furthermore, elevated levels of soil and plant phosphorus have been recorded at temporarily and permanently abandoned seabird colonies (Holdaway *et al.*, 1998; Molina-Montenegro *et al.*, 2013; Kolb *et al.*, 2015), where predation has reduced breeding populations (Wardle *et al.*, 2012) and in abandoned sheep pasture (Marriott et al., 2010). This demonstrates that ecosystems can be coupled temporal as well as spatially.

Temporal coupling of ecosystems where there is a lag in species and/or community response, such as this, means that the functional link between the two ecosystems can decline or disappear without any immediate impact on the sink ecosystem. This would of particular concern if the the meta-ecosystem supported rare or endangered habitats or species and demonstrates the importance of understanding the functioning of meta-ecosystem and the role of mobile species in that.

Terrestrial implications of marine ecosystem management

In commercial fisheries around Shetland, great skuas have formerly been the dominant scavenging seabird found around fishing vessels, and discarded white fish contribute a significant part of their diet (Reeves and Furness, 2002; Votier, Furness, et al., 2004; Church et al., 2018). In the past 40 years, the superabundance of discards in the marine ecosystem resulted in population growth, reduced foraging trip duration and increased numbers of non-breeding adults attending summer breeding colonies (Furness and Hislop, 1981; Furness, 1987; Caldow and Furness, 2000; Bearhop *et al.*, 2001; Furness, 2003). This would have resulted in increases in marine derived nutrient deposition and direct disturbance in the terrestrial breeding colonies. I have shown this would have resulted in rapid localised changes across the ecosystem: declines in dwarf shrub species in favour of graminoid and ruderal species; increases in plant tissue nutrient concentrations and changes in plant nutrient assimilation; and, declines in larger immobile invertebrate predator species and increases in detrivorous species.

The adoption of the Landing Obligation by EU member state fisheries, which will ban the practice of discarding by 2019, will represent a large short fall in great skua food availability. This is predicted to increase the duration of foraging trips, change colony demographic, whereby recruitment into the breeding population increases causing rapid declines in the non-breeding population, and potentially increase mortality and reduce productivity which will eventually cause a decrease population sizes (Klomp and Furness, 1992; Votier, Bearhop, *et al.*, 2004; Bicknell *et al.*, 2013). All these changes to great skua behaviour and population will weaken the link to the marine ecosystem and therefore decrease the marine derived nutrient deposition and direct disturbance by great skuas in the terrestrial ecosystem. My results suggest that plants are accessing nutrients directly from faeces and carrion, therefore this will result in a reduced the availability of inorganic nutrients in the soil. The plant community composition is will be slow to respond to this, and grass and ruderal species will remain dominant. Nitrogen concentration in plant tissues will decline but phosphorus concentrations will remain elevated and even increase in some species. I demonstrated that litter nutrient concentration largely controlled nutrient release during decomposition. This in combination with the sustained phosphorus plant tissue concentration, suggests that phosphorus cycling in the terrestrial ecosystem will remain high, whereas nitrogen cycling will decline. Furthermore, because of the decline in inorganic nutrient availability species such as tormential and heather may revert to utilising mycorrhizal symbionts to assimilate nutrients. Above ground it is predicted that the abundance of invertebrate species that were strongly influenced by direct disturbance, such as *Carabus problematicus*, will likely increase. However, those that are more influenced by vegetation structure and have strong association with bog habitats, such as spiders and *Patrobus assimilis*, will take longer to recolonise as the plant community composition recovers.

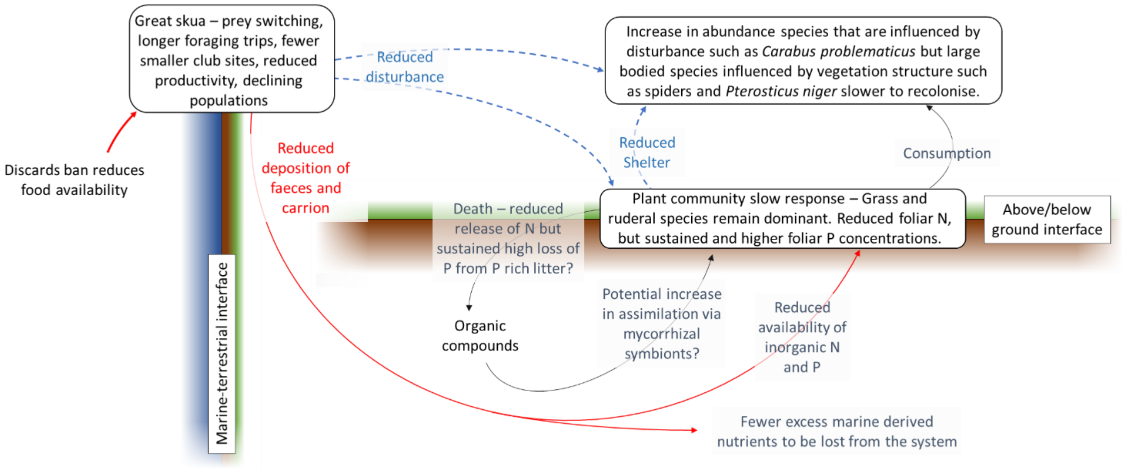


Figure 6.2. Summary of the potential changes within the terrestrial ecosystem as a result of marine resource management strategy to ban the practice of discarding unwanted parts of the catch. The precipitation/fixation of atmospheric gasses and recycling of nutrients from dead invertebrates has been removed from this figure for simplicity.

Great skuas are opportunistic predators, therefore the decline in one prey source (discarded fish) may result in some individuals seeking alternative food source (Votier, Furness, *et al.*, 2004; Church *et al.*, 2018). In other colonies around the UK, where fisheries discards are less available other seabird species such as Atlantic puffin *Fratercula arctica* (Linnaeus, 1758) or storm petrels *Hydrobates pelagicus* (Linnaeus, 1758) make up a significant proportion of great skuas diet (Phillips, Thompson and Hamer, 1999; Gilbert, L., unpublished data). A switch to preying on seabirds in Shetland colonies will maintain the link to the marine ecosystem but may alter the relative amounts of nutrients entering the terrestrial ecosystem. Rabbits are also abundant in most great skua colonies in Shetland and are regularly found in great skua pellets (Church *et al.*, 2018; Gilbert, L. unpublished data). Rabbits are terrestrial herbivores and therefore likely to have different nutritional value to fish or seabirds and as a result alter the relative nutrient concentrations in faeces. Furthermore, if they contributed more to great skuas diet the link with the marine ecosystem will be reduced. In Spitzbergen, differences in seabirds diet gave rise to different plant communities (Zwolicki *et al.*, 2016), therefore further work could focus on how prey switching may influence the terrestrial ecosystem.

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APPENDICES AND SUPPLEMENTARY MATERIAL

Table A1 Summary of litter bag set up and incubation times.

Incubation time (months)	Bury Date	Harvest date	Club site (n)		Intra-colony control site (n)	
			High litter quality	Low litter quality	High litter quality	Low litter quality
0	-	-	12	12	-	-
3	31/05/17	28/08/17	12	12	12	12
6	11/07/17	11/01/18	12	12	12	12
12	11/07/16	11/07/17	12	12	12	12
18	11/07/16	11/01/18	12	12	12	12
24	11/07/16	11/07/18	12	12	12	12

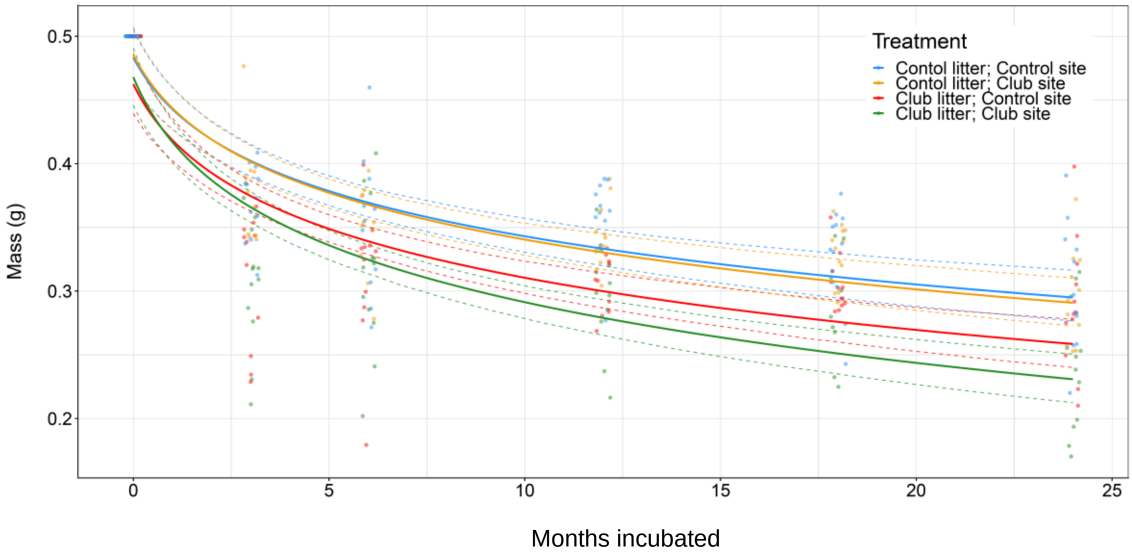

Figure A2 The effect of litter origin and bury location on the change in mass of litter residue remaining over time. Points represent measured means, the solid lines represent the prediction from the log-linear model and the dotted lines represent 95% confidence intervals.

Table A3 Plant species codes and CSR scores. The column CSR refers to the categories established by Grime and the scores are those used in this analysis.

Species	**Latent variable code**	**CSR code (Grime, 2007 & 1979)**	**CSR scores (Hancock, 2018)**		
			Competitive	**Ruderal**	**Stress tolerant**
Agrostis capillaris	*Agro capi*	CSR	1.33	1.33	1.33
Agrostis stolonifera	*Agro stol*	CR	2	2	0
Aira praecox	*Aira prae*	RS	0	2	2
Anthoxanthum odoratum	*Anth odor*	SR/CSR	0.6	1.7	1.7
Calluna vulgaris	*Call vulg*	S/SC	1	0	3
Carex bigelowii	*Care bige*	No data	NA	NA	NA
Carex binervis	*Care bine*	S	0	0	4
Carex nigra	*Care nigr*	S/SC	1	0	3
Carex panicea	*Care pani*	S/CSR	0.675	0.675	2.65
Carex pilulifera	*Care pilu*	S	0	0	4
Carex sp.	*Care* sp.	No data	NA	NA	NA
Cerastium fontanum	*Cera font*	R/CSR	0.675	2.65	0.675
Dactylorhiza maculata	*Dact macu*	SR	0	2	2
Deschampsia flexuosa	*Desc flex*	S/SC	1	0	3
Drosera rotundifolia	*Dros rotu*	SR	0	2	2
Empetrum nigrum	*Empe nigr*	CS	2	0	2
Erica cinerea	*Eric cine*	S/SC	1	0	3
Erica tetralix	*Eric tetr*	S/SC	1	0	3
Eriophorum angustifolium	*Erio angu*	S/SC	1	0	3
Eriophorum vaginatum	*Erio vagi*	S/SC	1	0	3
Euphrasia officinalis agg.	*Euph offi*	SR	0	2	2
Galium saxatile	*Gali saxa*	S/CSR	0.675	0.675	2.65
Holcus lanatus	*Holc lana*	CSR	1.33	1.33	1.33
Juncus bufonius	*Junc bufo*	R/SR	0	3	1
Juncus effusus	*Junc effu*	C/SC	3	0	1
Juncus squarrosus	*Junc squa*	S/CSR	0.675	0.675	2.65
Luzula multiflora	*Luzu mult*	S/CSR	0.675	0.675	2.65
Molinia caerulea	*Moli caer*	SC	2	0	2
Nardus stricta	*Nard stri*	S/SC	1	0	3
Narthecium ossifragum	*Nart ossi*	S/CSR	0.675	0.675	2.65
Neottia cordata	*Neot cord*	No data	NA	NA	NA
Pinguicula vulgaris	*Ping vulg*	SR	0	2	2
Poa pratensis	*Poa prat*	CSR	1.33	1.33	1.33
Poa trivialis	*Poa triv*	R/CSR	0.675	2.65	0.675
Polygala serpyllifolia	*Polyg serp*	S/CSR	0.675	0.675	2.65
Potentilla erecta	*Pote erec*	S/CSR	0.675	0.675	2.65
Rumex acetosella	*Rume acet*	SR/CSR	0.6	1.7	1.7
Rumex acetosa	*Rume acet*	CSR	1.33	1.33	1.333
Sagina nodosa	*Sagi nodo*	S/SR	0	1	3
Sagina procumbens	*Sagi procs*	R/CSR	0.675	2.65	0.675

Species	Latent variable code	CSR code (Grime, 2007 & 1979)	CSR scores (Hancock, 2018)		
			Competitive	Ruderal	Stress tolerant
Stellaria media	*Stel medi*	R	0	4	0
Succisa pratensis	*Succ prat*	S/CSR	0.675	0.675	2.65
Trichophorum cespitosum	*Trich cesp*	S/SC	1	0	3
Vaccinium myrtillus	*Vacc myrt*	SC	2	0	2
Viola sp.	*Viol* sp.	No data	NA	NA	NA

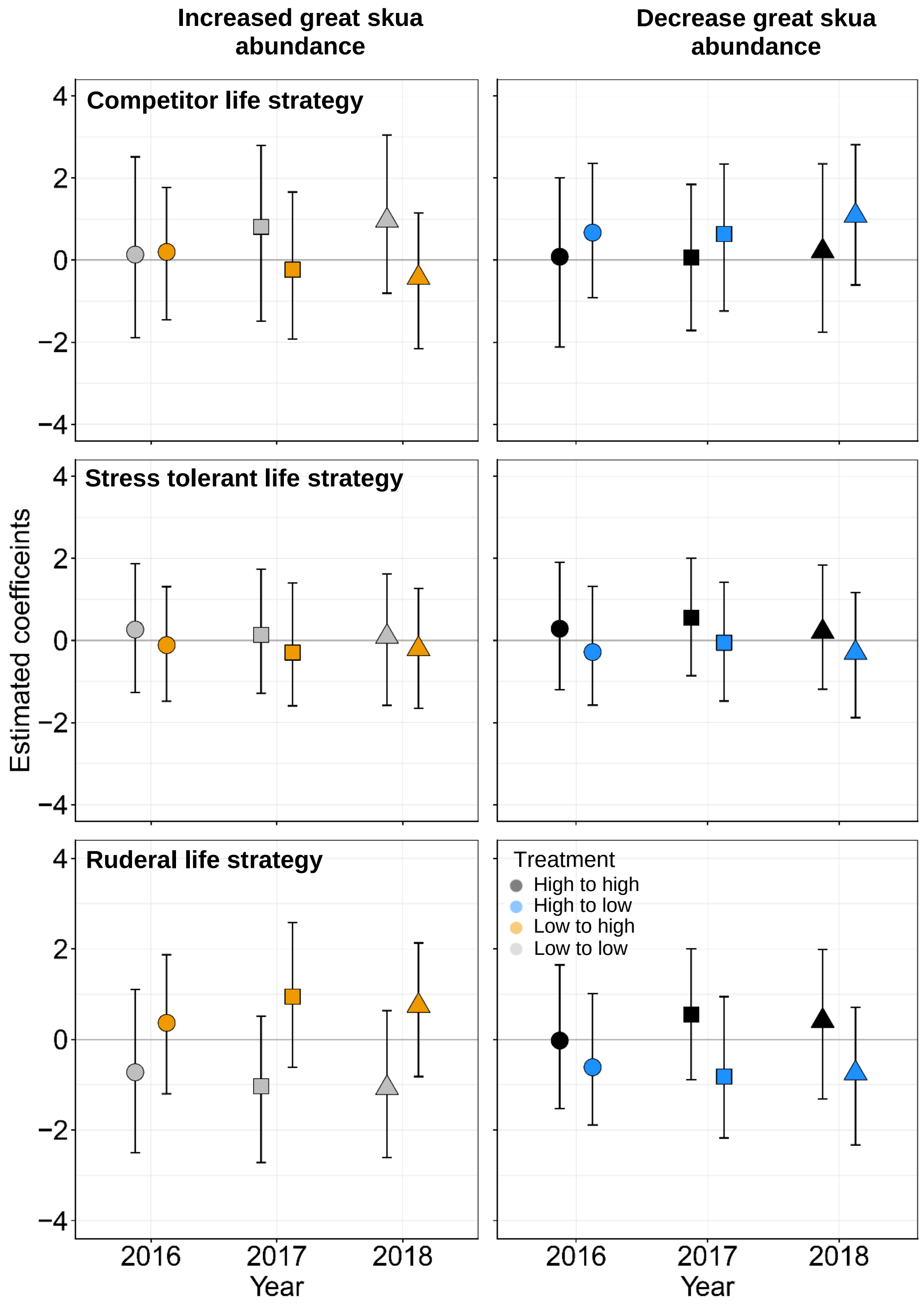

Figure A4 Association between increased (panels in the left row) and decreased (panels in the right row) great skua abundance and plant life strategy scores for competitor, stress tolerant and ruderal species in the manipulation experiment. Each point represents an estimated coefficient of each of the each of the C-S-R scores as estimated by the CRM. The colour of the point represents great skua use: grey and black represent control turfs (low to low and high to high, respectively), orange and blue represent transplanted turfs (low to high and high to low, respectively). The error bars represent 95% credible intervals. Where the error bars do not overlap with zero there is a significant association between the life strategy and turf transplant treatment.

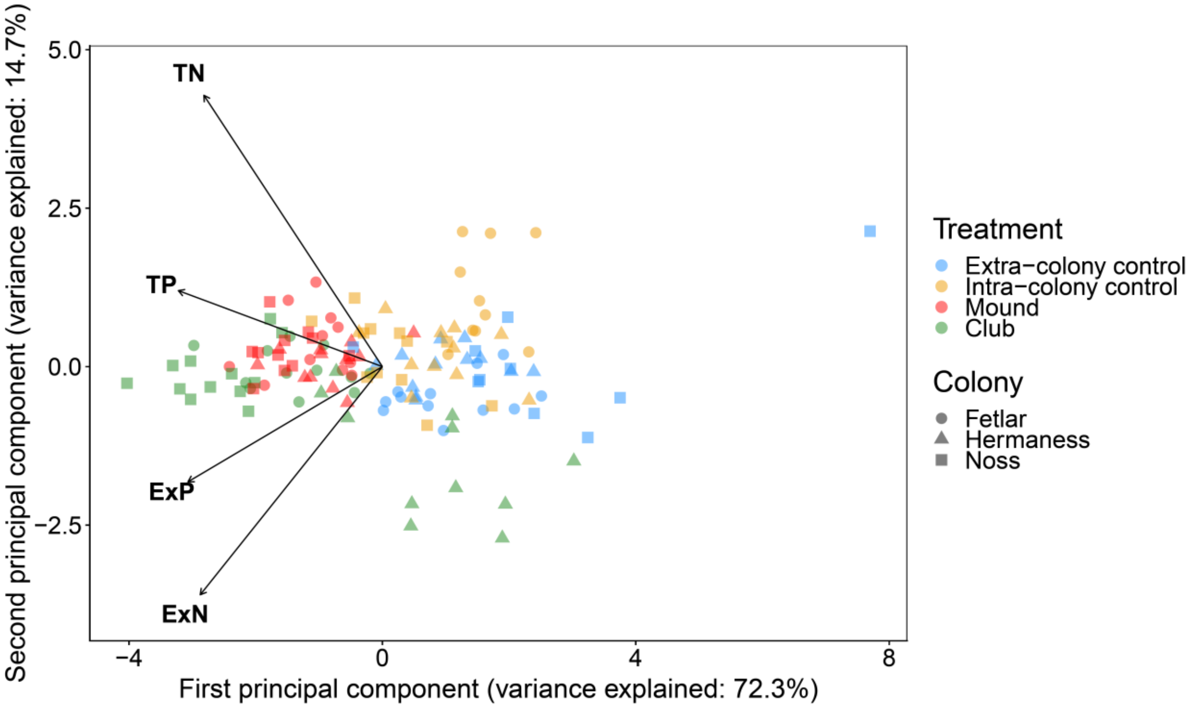

Figure A5 Principal components analysis of soil nutrients. The points represent individual sampling locations, The colour represents the great skua use (blue – extra colony control, orange – intra-colony control, red – mound and green – club) and shape represent the three separate colonies (circle – Fetlar, square – Hermaness and triangle – Noss). The text and arrows represent directions of nutrient gradients (TN – total nitrogen, TP – total phosphorus, ExP – extractable phosphorus and ExN – extractable nitrogen) and the relative distance from the origin indicates the strength of that gradient.

Table A6 Variance explained of the first two principal components in the principal component analysis of the soil nutrient concentrations

	PC1	**PC2**
Total variation explained	72.34	14.73
Variation explained by variables		
Total nitrogen	23.51	39.29
Total Phosphorus	26.88	11.01
Extractable nitrogen	24.00	33.03
Extractable Phosphorus	25.62	16.68