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Modern and Paleoecological Perspectives on a Terrestrial-Marine Linkage in the Falkland Islands

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**MODERN AND PALEOECOLOGICAL PERSPECTIVES ON A TERRESTRIAL-
MARINE LINKAGE IN THE FALKLAND ISLANDS**

By

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A DISSERTATION

Submitted in Partial Fulfillment of the

Requirements for the Degree of

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in Ecology and Environmental Science

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By Dulcinea V. Groff

Dissertation Advisor: Dr. Jacquelyn L. Gill

An Abstract of the Dissertation Presented
in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
(in Ecology and Environmental Sciences)

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The Falkland Islands are a biodiversity hotspot in the South Atlantic Ocean, with some of the world's most important populations of seabirds and seals. The impact of climate change on these marine populations and their coastal breeding habitat in the Falklands is unknown. Coastal grasslands of *Poa flabellata* (tussac grass) form critical breeding habitat for wildlife, but have been heavily degraded by the introduction of livestock in the 17th century. This dissertation investigates the impacts of global change (climate change, grazing) on *P. flabellata* and its sensitivity to the fecal nutrient subsidies provided by marine wildlife. Chapter 1 provides the first multi-proxy reconstruction of past environmental change to understand how marine animals breeding in the Falklands responded to climate change over the past 14,000 years. At ~5,000 years ago, seabird and/or seal populations reached higher levels than the previous 9,000 years at Surf Bay, East Falkland Island. Fires were present throughout the past 14,000 years, but fire activity

was highest when marine-derived nutrient input into the coastal grasslands from seabirds and/or seals increased. The increase in marine-derived nutrients and fire coincided with an increase in grasses, as well as the onset of neoglaciation. This reconstruction suggests that the Falklands are a refuge for seabirds and/or seals during cold periods in the past, and that marine-derived nutrients are important for improving coastal grasslands. It remains unknown whether tussock grass or other grasses species responded to changes in marine-derived nutrient input in our paleoecological reconstruction. Thus, in Chapter 2, I found that phytoliths, and not pollen, of modern native grass species are useful in distinguishing tussock grass from other species, supporting future investigations of the response of tussock grasslands to global change. Chapter 3 examines the potential for *P. flabellata*, which forms extensive peat records, as a new paleoclimate proxy in the South Atlantic where other archives for paleoclimate reconstructions (i.e. tree ring records and ice cores) are absent. Through a year-long modern calibration study, I found that tussock grass tissues record inter-seasonal environmental changes in temperature and humidity, though not precipitation source. Thus, this study warrants the use of tussock grass peat records to fill in a significant gap in our knowledge of paleoclimate in the South Atlantic Ocean. Chapter 4 provides an assessment of the impact of modern and historic grazing on soils and plants in the ecologically important coastal tussock grasslands. After release from grazing, tussock grasslands recovered rapidly, and marine-derived nutrient subsidies may be critical to improve restoration efforts. Overall, this work suggests that the terrestrial-marine linkage in the Falkland Island is sensitive to both climate change and land use change.

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CHAPTER 1

A MULTI-PROXY RECONSTRUCTION OF A TERRESTRIAL-MARINE LINKAGE FROM THE FALKLAND ISLANDS

Abstract

In seabird biodiversity hotspots where conservation goals are challenged by abrupt climate change, the paleorecord offers insight into the response of seabirds to past changes. We investigated the impact of climate change on the natural range of variability in seabird populations and a terrestrial-marine linkage, with a multi-proxy paleoenvironmental reconstruction from peat cores from the Falkland Islands. An abrupt increase in the concentration of seabird-derived bioelements coincided with sea surface temperature cooling and increased ice rafted debris at the onset of neoglaciation (~5.0 ka BP). We identified increases in coastal grasslands as a response to increased nutrient input by seabirds. Increases in fire also coincided with neoglacial cooling. Furthermore, we also found that fire is a frequent component of *P. flabellata* grasslands, though whether this is due to climate or prehistoric human activity remains unknown. These results improve our understanding of how changes in the position and strength of the southwesterly winds influenced coastal *P. flabellata* grasslands and nutrient input through fluctuations in populations of marine fauna. Our results suggest that the seabirds are sensitive to warm oceanic conditions in the South Atlantic and the Falkland Islands are an important breeding refuge for seabirds during neoglacial conditions.

Introduction

The Falkland Islands are a biodiversity hotspot, providing critical breeding habitat for seabirds, shorebirds, and marine mammals in the South Atlantic Ocean. Seabirds in the Falkland Islands are declining, and understanding their response to a rapidly changing climate is crucial to conservation efforts, yet remains unknown. Such high latitude islands are usually resource-poor, however, with many species relying on nutrients transported from the marine ecosystem by seabird guano. This terrestrial-marine linkage is a basic supporting service to a system that receives very little nutrient input otherwise (Anderson & Polis, 1999). The long history of guano deposition in terrestrial seabird habitats directly influences soil characteristics and vegetation, which in turn provides critical habitat for seabirds (Pizzaro et al., 2012; Polis & Hurd, 1996; Polis et al., 1997; Sun et al., 2013). Some of the most important seabird breeding habitats are located in high latitude islands (Woehler & Croxall, 1997), and their nutrient inputs may be essential to maintain biodiversity and ecosystem function in their habitats.

The Falkland Islands (51 °S latitude; Fig. 1.1) are centrally located within the Southern Hemisphere westerly wind belt, where the perpetually strong winds drive upwelling of the cold, nutrient-rich Southern Ocean waters (Anderson et al., 2009; Upton & Shaw, 2002). Locally, the westerlies control soil temperature and moisture balance, and exert a strong influence on the islands' treeless plant communities (Bokhorst et al., 2007). In the past 40 years, the westerly winds have been shifting south and intensified, which in turn is expected to influence the island's ecology in uncertain ways. The westerly wind belt is a key component of the global climate system and changes in its latitudinal position and strength varied over the last two glacial cycles (Denton, 2010;

Shulmeister et al., 2004). During the Holocene, however, the exact timing of when the southwesterly wind belt shifted is debated (Fletcher & Moreno, 2012; Björck et al., 2012; Kilian & Lamy, 2012), which complicates efforts to predict how the westerlies may respond in the coming century (Toggweiler & Russell, 2008). Evidence for past southwesterly wind behavior from the South Atlantic (Isla de los Estados, Tierra del Fuego, 54.4 °S) indicates that the southwesterly wind belt was displaced poleward from 12.0 to 10.0 ka BP, began to shift equatorward between 10.0 and 7.0 ka BP, and strengthened between 7.0 and 4.5 ka BP (Björck et al., 2012). Despite evidence of current warming trends in Antarctica and the Southern Ocean, however, the westerly wind belt has been trending poleward and strengthening since the 1970's (Shulmeister et al., 2004; Turner et al., 2009), which may have negative implications for the ecology of the South Atlantic.

Marine ecosystems are highly sensitive to climate change (Doney et al., 2012), which could influence terrestrial environments that rely on oceanic subsidies. In the Southern Oceans, the Antarctic circumpolar current brings nutrient-rich water via the cold Falkland current. The nutrient-rich waters make the Patagonian Shelf and Falkland Islands important feeding grounds for marine mammals and seabirds (Peterson & Whitworth, 1989). Increased water temperatures and ocean acidification influence the availability of macronutrients for primary production, and indirectly affects populations of higher-level consumers like seabirds (Barbraud et al., 2012; Weimerskirch et al., 2003) and marine mammals (Moore & Huntington, 2008). In the Southern Oceans, the biological responses of seabirds vary naturally based on climatic fluctuations with sea ice cover, atmospheric temperature (Sun et al., 2013), and changing wind patterns

(Weimerskirch et al., 2012). For terrestrial systems that rely on marine-derived nutrients, such as high latitude islands, climate impacts on ecological communities may be indirect, via the oceans (Outridge et al., 2016). Indirect effects of allochthonous nutrients include increases in 1) island primary productivity, 2) higher-level consumers, and 3) a more complex terrestrial food web (Polis & Strong, 1996). The link between the highly productive marine ecosystem to a less productive insular terrestrial ecosystem makes the Falkland Islands an ideal location to study how past global climate changes influence critical habitat of nesting seabirds and marine mammals.

Paleoenvironmental reconstructions provide useful context to understanding contemporary climate change, as they provide records of natural experiments of past shifts with similar boundary conditions to today (Jackson & Hobbs, 2009).

Understanding when shifts occur in the marine trophic structure of the Southern Oceans during times of similar boundary conditions in the climate will advance our knowledge of the westerly wind belt behavior during the Holocene and interaction with seabird and marine mammal population dynamics since the impacts of changing westerly wind belt on critical island habitats remains unknown. Historically, wool exports dominated the economy of the Falkland Islands, and today fishing contributes 50 to 60% of the economy (Falkland Islands Government, 2012). Following a century of sheep grazing by European settlers, overall coastal grasslands dominated by *Poa flabellata* (tussac grass) have been reduced down to 20% of their pre-European extent. These grasslands form important breeding habitat and shelter from the westerly winds for marine birds and mammals, and prevent coastal erosion, which is becoming problematic island-wide following overgrazing and sea level rise (Otley et al., 2008). Consequently, remaining

breeding sites may be at further risk due to climate change, and the sensitivity of seabirds, and the terrestrial-marine linkage they both rely on and maintain, is unknown. While the value of *P. flabellata* is recognized by Falkland Islanders and conservationists alike, efforts to restore these valuable coastal grasslands have had limited success (Falklands Conservation, 2016). Restoration ecologists have called for research on nutrient cycling and the impact of fire on *P. flabellata* regeneration (Kerr, 1997).

To test the influence of climate change on an important terrestrial-marine linkage, we conducted a paleoenvironmental reconstruction to ask: how did changes in the Southern Hemisphere westerly wind belt influence seabird and marine mammal populations and island plant communities? We hypothesize that changes in the latitudinal position or intensity of the westerly wind influenced local seabird and pinniped populations, which in turn affected *P. flabellata* grassland productivity via marine-derived nutrient subsidies. We took a multi-proxy approach to reconstruct 1) changes in the abundance of seabirds and pinnipeds in *P. flabellata* peatlands (bioelements), 2) paleovegetation (fossil pollen), and 3) fire frequency (fossil charcoal). Our results provide context for ecologists and managers about the status of seabirds, their habitats, and the sensitivity of both to global change.

Study Area

The Falkland Islands, located 500 km off the shore of South America, are an important breeding habitat for 22 species of seabirds and 4 species of pinnipeds, including the largest rookery of southern rockhopper penguins (*Eudyptes chrysocome*) in the world (White et al., 2002). Coastal habitat mainly consists of *Poa flabellata* (tussac

grass) grasslands that provide nesting habitat and shelter from the persistent westerly wind belt. The Falkland Islands lack native trees, terrestrial mammals (the only native terrestrial mammal went extinct in 1876 (Clutton-Brock 1977), amphibians, and reptiles, which is attributed in part to the harsh climate and low productivity (Otley et al, 2008). *P. flabellata* grasslands form critical habitat for invertebrate communities which function to recycle nutrients, form soils, and are a source of food for terrestrial birds (Strange, 1988). *Poa flabellata* grows on large tussock bogs, or pedestals, of dead grasses, which form extensive peatlands in the cool, moist climate (Moore, 1968). The grasses can grow as high as 3.5 m and form thick layers of peat rich in organic carbon that accumulates at rates as high as 430 to 720 g m⁻² yr⁻¹ (Smith and Clymo, 1984). *Poa flabellata* only occurs along a 250 m periphery of islands (Woods and Woods, 2006). *Poa flabellata* is endemic to the South Atlantic, and can only be found on Tierra del Fuego, South Orkney, the Falkland Islands, Gough Island, and South Georgia.

Meanwhile, the average temperature of the Southern Ocean (upper 150 m) has increased by 2.3 °C over the last 81 years; reanalysis data indicate that the intensity of the Southern Hemisphere westerly winds increased in the past 10 years (2007-2017) relative to 1949-2006 (Fig. 1.2A-B); In addition, the mean annual air temperature in Stanley, Falkland Islands in the last century increased by 0.5 °C (Lister and Jones, 2015), and is also increasing around other sub-Antarctic islands (Solomon et al., 2007; Trathan et al., 2007).

Coring sites

The cool maritime climate of the Falkland Islands (mean temperature: January 9.4 °C and July 2.2 °C) is strongly influenced by latitude, the southwesterly wind belt, and the Antarctic Circumpolar Current, the waters surrounding the Antarctic Peninsula, the Falklands Current, and the Andes of southern Patagonia (Upton and Shaw, 2002; Jones et al. 2013, 2015).

The site investigated in our study, Surf Bay, has underlying Devonian-Carboniferous geological structures made of orthoquartzites, sandstones, and shale (Clark et al. 1995). Surf Bay is located in the northeast of East Falkland Island and designated as a recreational open space near the town of Stanley, Falkland Islands (Fig. 1.1). There are no significant populations of seabirds or marine mammals at Surf Bay likely due to the proximity to Stanley. The dominant vegetation consists of a mix of Poaceae, including *P. flabellata*, and ericaceous shrub *Empetrum rubrum* (diddle-dee).

Methods

Peat Profiles

We excavated a 476 cm column from Surf Bay on East Falkland Island (51° 42.012' S, 57° 46.962' W) in 2016 (SUBA16), extracted as 10 to 30 cm square blocks which were wrapped in plastic wrap and aluminum foil and shipped in hard-shell coolers to the University of Maine and kept in cold storage (> 0 °C). We subsampled the peat profile at the University of Maine in 1.0 cm intervals. We used a digital line scanner for high resolution imagery of SUBA16 blocks at the LacCore National Lacustrine Core Facility.

Chronology

Grass leaf macrofossils were selected from each peat profile and submitted to the Keck Laboratory (University of California, Irvine) for ^{14}C accelerator mass spectrometry (AMS) radiocarbon dating. Radiocarbon dates were calibrated to calendar years with the Southern Hemisphere calibration curve - SHCal13 ^{14}C (Hogg et al. 2013; Table 1.1), and age-depth models were constructed using a smooth spline age-depth model in clam software (Blaauw 2010; clam v. 2.2; Fig. 1.3A).

Multi-proxy analyses

Loss on ignition

Subsamples (1 cm^3) were analyzed for loss-on-ignition (LOI) by weighing after heating in a muffle furnace at $100\text{ }^{\circ}\text{C}$ for 24 hours (dry weight), $550\text{ }^{\circ}\text{C}$ for four hours (to remove organic carbon), and $1000\text{ }^{\circ}\text{C}$ for two hours (to remove carbonates), following Heiri et al. (2001); post-LOI residue weights were also recorded to quantify the mineral fraction.

Pollen analysis

We subsampled 1 cm^3 of peat for pollen processing at 5-cm intervals for SUBA16. Fossil pollen was concentrated using modified protocols by Faegri and Iversen (1989) at the University of Maine. Each sample was processed with 10% potassium hydroxide (KOH) to remove humic acids, 10% hydrochloric acid (HCl) to remove carbonates, sieved through $250\text{ }\mu\text{m}$ mesh to remove large particles, hydrofluoric acid to remove silicates, and glacial acetic acid to dehydrate pollen grains and remove the colloidal byproducts of HF treatment. Following the removal of organics with acetolysis

(concentrated sulfuric acid and acetic anhydride), each sample was rinsed with deionized water and 95% ethanol, and dehydrated with tertiary butyl alcohol and suspended in 1000 μ l silicone oil. Samples were spiked with a 0.5 μ l solution containing known number of microspheres ($2.5 \times 10^4 \pm 8\%$ SD; LacCore) to calculate pollen concentrations (# grains/ cm^3).

Terrestrial and aquatic pollen, fern spores, algae, fungi, and were identified using a Nikon Phase microscope at 40x magnification. We counted at least 300 total pollen and spores for each subsample, except when total pollen counts per sample were very low. To estimate time and effort to encounter a new or rare pollen type for these samples, we used PolyCounter 3.1.4 by Takeshi Nakagawa to tally and create a rarefaction curve of the ratio of the number of species to total count of pollen and spores. Long-distance transported pollen (LDT) grains from South American *Nothofagus* spp., *Ephedra*, and *Podocarpus* were used as a proxy for the strength of the westerlies; these are not found on the treeless Falkland Islands (Dallimore, 1919; Macphail & Cantrill, 2006).

Charcoal analysis

Charcoal processing followed protocols modified from Whitlock and Larson (2001), using contiguous sampling 1- cm^3 sediment volumes of peat. We placed the subsamples in ~25 mL of 7% hydrogen peroxide at 50 °C for 24 hours, then wet sieved with deionized water through a 125 μ m sieve. Each sample was rinsed into a plastic petri dish, a few drops of 7% hydrogen peroxide were added, and then samples were heated in a drying oven until dry. Plates were counted under a stereoscope as concentrations (# particles/ cm^3), and then converted to charcoal accumulation rates (CHAR; # particles cm^{-1}).

2 yr⁻¹) using CharAnalysis v. 1.1 for Windows OS (Higuera et al., 2009; Higuera et al., 2011).

CharAnalysis was used to calculate the low-frequency background component, CHAR_{BACK}, using a robust 500 year Lowess smoothing window (Higuera et al., 2009). High-frequency peaks above background, CHAR_{PEAK}, were identified significant fire events in the time series (Clark et al., 1996). The calculated signal-to-noise index (SNI) of >5.365 (Kelly et al., 2011) indicates that the records are suitable for peak analysis testing. CHAR_{PEAK} values were calculated using the residuals of the difference between CHAR_{interpolated}-CHAR_{BACK} (Whitlock and Larson, 2002; Higuera et al., 2007). Threshold values were selected to separate fire peaks from background noise using a 99th percentile Gaussian mixture model for CHAR_{PEAK} identification. The fire return interval analysis in CharAnalysis (Higuera et al., 2009; Higuera et al., 2011) identified the number of years between significant fire events (FRI; # years between fires) and fire frequencies (# fires per 1000 years) were calculated using a 1000-yr mean and 95% CI.

Geochemical analysis - bioelements

To reconstruct seabird populations, we analyzed 48 peat samples from SUBA16 for bioelements associated with guano (Outridge et al., 2016; Huang et al., 2009; Sun et al., 2000; Sun et al., 2013; Michelluti et al., 2010; Roberts et al., 2017). Bulk samples were dried at 100 °C for 12 hours and pulverized using an agate mortar and pestle. Approximately 0.5 g of dried, homogenized sediment was digested using a nitric acid-only microwave digestion (Maine Soil Testing Services, University of Maine) and analyzed with ICP-MS (Sawyer Water Research Laboratory, University of Maine) using internal standards and blanks (International Soil-Analytical Exchange: ISE921 7-31-

2000, Riverclay-91, Netherlands) for concentration (ppm) of Al, As, Ba, Be, Cd, Co, Cr, Cu, Fe, Mn, P, Pb, Se, Ti, U, V, and Zn. The bioelements (As, Cd, Cu, P, Se, and Zn) were normalized by aluminum (Al) and are represented as the ratio of the bioelement to Al. Aluminum was presumed to be an indicator of terrigenous or aeolian input based on a Principal Components Analysis of all elements to detect assemblages of bioelements and other elements corresponding to local lithology.

Numerical Analyses

Hierarchical R-mode cluster analyses were conducted with the R package ‘Pvclust’. Downcore cluster-zonation was undertaken on fossil pollen percentage data and square-root transformed and standardized (mean-1 σ) geochemical data using the R packages *vegan* and *rioja*. The CONISS broken stick cluster analysis was used to determine the significant number of zones and plotted using R (R Core team 2013).

Results

Peat profiles, chronology, and loss-on-ignition

The basal calibrated radiocarbon date for SUBA16 was 14,125 calibrated years before present at 472.5 cm. The age model for SUBA16 showed linear sedimentation throughout the profile (Fig. 1.3A), with accumulation rates of 29.95 years per cm. Loss-on-ignition for % organic values were highly variable in SUBA16, and ranged from 5.62% to 98.24% (Fig. 1.3B). For SUBA16, the organic fraction of the peat sediments gradually increased from <10% to between 14.0 ka BP to 13.0 ka BP. The organic fraction remained > 80% until ~0.30 ka BP, except for two large peaks of the inorganic fraction at 7.68 ka BP (~31%) and 0.31 to 0.21 ka BP (between ~70-80%).

Paleovegetation at Surf Bay, Falkland Islands (SUBA16)

The paleovegetation reconstruction at Surf Bay revealed alternating grassland to *Empetrum*-heathland and fern transitions, with occasional dominance of Asteraceae taxa. The CONISS broken stick model indicated there are seven significant zonations in the paleovegetation reconstruction of SUBA16 (Fig. 1.4). Each zone is characterized below and in Table 1.2.

Zone 1: In basal pollen Zone 1 (14.0–11.2 ka BP), grass pollen dominates (>80%), and Asteraceae taxa were present at low % abundances (Fig. 1.4). Long distance transported pollen were present up to 1%. *Colobanthus* abruptly declined at 11.7 ka BP. Asteraceae were present in low abundances. The herbaceous pollen, composed primarily of *Gunnera magellanica* and *Colobanthus*, were present at low (<5%) pollen abundances. Overall pollen concentration during Zone 1 is low (Fig. 1.5M).

Zone 2: An abrupt decline in Poaceae pollen abundances from >80% to <30% marks the transition to Zone 2 (11.2–10.7 ka BP); this decline coincides with an increase in abundance of the shrub *Empetrum* (>60%). Long distance pollen and herbaceous pollen are present at low abundances. Poaceae pollen concentrations (grains/cm³) declined during this interval (Fig. 1.5M). Pollen Zone 2 is interpreted as a clear transition from a grass dominated peatland to shrub heathland.

Zone 3: Zone 3 (10.7–9.9 ka BP) is marked by an abrupt increase in fern spores (>60%), primarily composed of *Blechnum penna-marina* and *Blechnum magellanicum*. Two large peaks in fern spores coincide with a decline in *Empetrum* pollen (<15%). Poaceae pollen abundances remain relatively low (~40%). The transition from Zone 2 to Zone 3 is interpreted to indicate a change from dry heathland, dominated by *Empetrum*, to coastal vegetation dominated by ferns (wet).

Zone 4: Poaceae dominated in Zone 4 (9.9–7.0 ka BP) with pollen abundances >80%, coinciding with a sharp decline in fern spore abundance (<10%). *Empetrum* pollen abundances were as low as <2%. Asteraceae pollen were present at low abundances (<10%). Long distance transported pollen % abundance increased to >5% by 7.0 ka BP and their pollen concentrations reached the highest levels at 7.5 ka BP (Fig. 1.5G). Unknown 45 pollen were high at abundances reaching ~30% (Fig. 1.4).

Zone 5: In Zone 5 (7.0–5.7 ka BP), Poaceae pollen abundances declined to ~ 60% and remained dominant. Asteraceae pollen abundances reached ~20%, and total pollen concentrations are low among all taxa except for Asteraceae pollen types (Fig. 1.5H). Herbaceous pollen types reached abundances of >10%. Fern spores were present at low abundance ~10%. Unknown 45 pollen abundances sharply increased to >50% followed by an abrupt decline to <5% (Fig. 1.4). The transition from Zone 4 to Zone 5 is marked by the highest pollen abundances of long distance transported pollen and interpreted as a

time of increased wind, coinciding with very low total pollen accumulation rates (low productivity).

Zone 6: Zone 6 (5.7–4.5 ka BP) is marked by a decline in Poaceae pollen abundances (~40%), coinciding with high abundance of Asteraceae pollen (>30%). Ferns spores reached moderate abundance up to 20%. Herbaceous pollen abundances increased to >10%. *Colobanthus* disappeared after 5.0 ka BP (Fig. 1.6F). The transition from Zone 5 to Zone 6 is characterized by increased pollen of heathland shrub *Empetrum* (>40%).

Zone 7: Zone 7 (4.5–0.041 ka BP) is dominated by Poaceae pollen abundances >80% and two sharp declines (~40%) at 3.3 ka BP and 0.351 ka BP, coinciding with two sharp peaks in fern spore abundances reaching ~50% and ~60%, respectively (Fig. 1.4). Herbaceous pollen abundances peaked at 3.7 ka BP, and remained in low abundances until pollen abundances peaked at 0.454 ka BP (Fig. 1.6F). The transition from Zone 6 to Zone 7 is marked by abrupt declines in Asteraceae and *Empetrum*.

Bioelements

Principal components analysis (PCA) of ICP-MS elements distinguished between seabird-related bioelements and local lithologies found in SUBA16 (Fig. 1.7). SUBA16 bioelement concentrations were low during Zone 1 (except arsenic), and remained low until Zone 6, except arsenic had initially high concentrations that declined (Fig. 1.5).

During Zone 7, bioelemental concentrations gradually increased beginning ~5.0 ka BP until present. Increased bioelement concentrations coincide with both increased Poaceae concentrations (Fig. 1.5L) and total pollen concentrations until 1.8 ka BP (Fig. 1.5M)). At 1.8 ka BP, there is a transition in the assemblage of bioelements from higher concentrations of As, Cu, Cd, and Zn to increased levels of P and Se from 1.8 ka BP reaching highest concentrations at ~1.0 ka BP (Fig. 1.5).

Charcoal analysis

From 14.0 ka BP to 10.7 ka BP, charcoal accumulation rates (CHAR) were low (<10 particles/cm³), suggesting low-intensity fires and/or low landscape fuel loads for paleovegetation Zones 1 and 2 (Fig. 1.6A). Between 10.7 and 9.9 ka BP, CHAR were slightly higher than previously. Higher CHAR (~50 particles /cm³) occurred between 8.5 ka BP and 6 ka BP.

Between 6.0 ka BP and 5.0 ka BP, CHAR were low (<10 particles/cm³). After 5.0 ka BP, CHAR was elevated above previous, with 15 peaks above 50 particles/cm³. An increasing trend in CHAR_{BACK} between 8.0 to 6.7 ka BP and between 3.0 and 2.0 ka BP indicates that the amount of biomass burned increased. Fluctuations in background CHAR reflect changes in fire frequency and fuel loads available. Poaceae pollen concentrations (Fig. 1.5L) increased during both intervals (8.0–6.7 ka BP and 3.0 –2.0 ka BP) of increased CHAR_{BACK} (Fig. 1.6A). The SNI was generally above the threshold of 3, with a mean of 5.365. The mean fire return interval for SUBA16 was 268 years per fire (mFRI range of

230-305 years per fire) using a 1,000 year mean (Fig. 1.8A-B), and the fire frequency, number of fires per 1,000 years ranged between 2 and 5 fires per 1,000 years (Fig. 1.8C).

Discussion

Our work provides the first paleoecological reconstruction of a linkage between terrestrial and marine ecosystems in the Falkland Islands. Seabirds at Surf Bay in the Falkland Islands were sensitive to abrupt changes in oceanic conditions, in part driven by the westerly winds and cooling sea surface temperatures. Seabirds increased nutrient inputs into the coastal grasslands that make up their breeding habitat beginning at ~5.0 ka BP (Fig. 1.9F-K), at the onset of neoglaciation. Before the increase in seabirds ~5.0 ka BP, seabirds were either in much lower abundances or not present at Surf Bay, as indicated by a lack of seabird-derived bioelements (Fig. 1.9F-K).

The seabird increase at the onset of neoglaciation coincided with an abrupt increase in sea ice cover around Antarctica, when ice expanded north to 53 °S in the South Atlantic (Hodell et al., 2001). Expanding Antarctic sea ice may have increased oceanic productivity by providing a substrate for primary producers (Arrigo & Thomas, 2004), which would in turn have increased prey distribution and abundance (Ainley et al., 2005; Barbraud et al., 2012; Hoegh-Guldberg & Bruno, 2010; Weimerkirsch et al., 2003). Sea ice margins are areas of high biological productivity and important for Southern Ocean productivity (Eicken, 1992; Smith, & Nelson, 1986). For example, krill, an important source of food for seabirds and marine mammals, are known to have high densities along sea ice margins (Brierley et al., 2002; Nicol, 2006), and observed to be

negatively correlated with sea surface temperatures in South Georgia (Whitehouse et al., 2008). Alternatively, as sea ice expanded, seabirds could have been displaced from southerly sites, i.e. summer feeding grounds (Ainley et al. 2017), instead of increased oceanic productivity. Or, a combination of increased sea ice and intense westerly winds in the past may have benefited flying seabirds by reducing energy expenditure when foraging (Weimerskirch et al., 2012). Coinciding with declining sea ice at 2.0 ka BP, seabird-derived bioelements transitioned from an assemblage of As, Cd, Cu, and Zn to an assemblage represented by Se and P. We hypothesize that these two assemblages of bioelements represent a community shift either in seabird species and/or pinniped species, which remains to be determined. This transition in bioelements at ~1.7 ka BP (Fig. 1.9F-K) occurred after a ~2 °C warming of February SSTs at 53 °S in the South Atlantic Ocean (Hodell et al., 2001) and enhanced westerly winds over Tierra del Fuego at 1.75 ka BP (Björck et al., 2012). The increase in seabirds at both 5.0 ka BP and 2.0 ka BP in the Falklands also coincide with well-known colony abandonment (Emslie et al., 2007) and redistribution of seabirds in Antarctica (Baroni & Orombelli, 1994; Emslie et al., 2014; Sun et al., 2013; Sun et al., 2000) because of unfavorable climate and oceanic conditions. We hypothesize that these abandonments and redistributions could have led to reorganization and migration of seabirds in search of breeding habitat and subsequent increases in seabirds in the Falkland Islands.

As seabirds increased ~5.0 ka BP, grasses gradually increased until the transition in bioelements at ~1.7 ka BP and then began to decline, as confirmed by increased pollen concentrations (# grains/cm³; Fig. 1.9L). We hypothesize that the transition in assemblages of seabird-derived bioelements and decline of grasses indicates a shift in the

animal community in response to warming February SSTs (Hodell et al., 2001).

However, nutrient additions alone may not explain the increase in grasses (McAdam et al., 1990) and precipitation amount must be considered in future studies. Around the same time, but further west of the Falkland Islands, higher precipitation and less evapotranspiration on South Georgia ~ 2.2 to 2.0 ka BP led to the formation of wet ombrogenous mesotrophic bogs (Van Der Putten et al., 2012).

Prior to seabird influence, coastal grassland and heathland plant communities shifted in response to changes in temperature and/or hydrologic conditions, driven by the fluctuating position and/or intensity of the westerly wind belt. By 14.0 ka BP, our record indicates that grasses dominated the coastal peatlands, with low pollen concentrations of herbs and Asteraceae; this was followed by a period of dominance by *Empetrum* shrubs by 11.5 ka BP, and ferns by 11.0 ka BP (Fig. 1.5I-J). This shift coincided with a decrease in wind as the westerly wind belt shifted poleward to a position south of 55 °S (Isla de los Estados; Björck et al., 2012; Fig. 1.5C). Modern *Empetrum* shrubs and ferns, primarily *Blechnum penna-marina* and *Blechnum magellanicum*, are found in drier coastal habitats and well-drained slopes of hills and mountains in the Falkland Islands. Thus, we characterize the shift from grassland to *Empetrum* and ferns as a transition from wet to dry conditions. The dry interval ended at 10.0 ka BP when the winds began to intensify (Fig. 1.6) and February SSTs were warmest (10.0-5.5 ka BP) in the early Holocene. Although tussac grass forms nearly single-species dominant grasslands, and important wildlife habitat along the coasts of the Falkland Islands, we still do not know whether this increase in grass pollen concentration can be attributed solely to tussac grass. It is plausible that other grasses like *Cortaderia pilosa*, *Hierochloë redolens*, and *Poa*

alopecurus also contribute to the total grass pollen; thus, we cannot determine if tussac grass responded to climate prior to seabird influence. Because the pollen of many grasses are not identifiable to species, an analysis of grass phytoliths could be revealing to further our understanding of the ecological interaction between seabirds and tussac grass. Recent work on phytoliths of native grasses in the Falkland Islands (Chapter 4) supports their capacity to decipher pre-seabird grasslands shifts (Groff 2018, *unpublished*).

Our record of exotic pollen (transported long-distance from mainland South America; primarily *Nothofagus*) indicated that either the westerly winds gradually intensified, or the core of the westerly wind belt centered over the Falkland Islands from 10.0 ka BP until 7.0 ka BP (Fig. 1.6). This intensification of the westerlies found in our record is similar to a pollen-based wetness index from southern South America (Björck et al., 2012). However, we cannot rule out that our record of long distance transported pollen abundance may also track the gradual expansion of *Nothofagus* in South America in the early Holocene; *Nothofagus* concentrations are highest in our pollen record at the same time as they reach peak concentrations at sites of a similar latitude in South America (Kilian & Lamy, 2012). Regardless, it is extremely unlikely that *Nothofagus* would have been transported to the Falkland Islands in the absence of the westerlies.

The fire history of the grassland at our study site likely responded to both wind and changing moisture conditions. During the wind intensification and increasing wetness at ~7.0 ka BP, fires increased above background charcoal accumulation rates (Fig. 1.6A-B), and grasses dominated the study site and provided sufficient fuel. After 7.0 ka BP, fires declined during a period of drying, which may be the result of reduced fuel loads (Vannière et al., 2011). Fuel loads in grasslands often increase with moisture,

resulting in increased biomass burning (Grimm et al., 2011). If LOI 550 C can be considered a proxy for plant productivity, we found no evidence for decreasing plant productivity (Fig. 1.3B) between 7.0 and 5.0 ka BP and cannot attribute the decreased fire activity to diminished plant productivity and fuel loads (Fig. 1.9), as indicated by low total pollen concentrations (Fig. 1.5M). Our vegetation reconstruction indicated that total pollen and grass pollen concentrations were low between 7.0 and 5.0 ka BP, apart from Asteraceae. In Tierra del Fuego, winds further intensified during this interval (Björck et al., 2012), but conditions remained dry, which may explain this unique interval with abundant Asteraceae taxa. In the absence of tall grasses, increases in light availability will increase herbaceous and shrub forms of Asteraceae taxa. After a disturbance, for example, perennial grasses are slow to recolonize while herbaceous ruderal taxa, common in the Asteraceae family, often perform best at recolonizing (Tilman, 1997; Lavorel et al., 1998).

There is evidence for a second dry interval between 5.5 and 4.5 ka BP, as indicated by abundant Asteraceae taxa and *Empetrum* shrubs (Fig. 1.6). Interestingly, Wilson (1994) examined sand accumulations (aeolian and alluvial) at Blue Mountain, West Falkland Island during the Holocene and found major aeolian erosion between 5.0 and 4.5 ka BP along with lower lake levels. Results from our work and Wilson (1994) coincide with a dry interval from southern South America that lasted until ~5.0 ka BP, and increased warming of SSTs at 53 °S (known as the Hypsithermal), which ended between 5.5 and 5.0 ka BP at the onset of neoglaciation (Hodell et al., 2001). Together, these environmental data provide regional evidence for greater warmth, aridity, and more

intense winds. Seabirds arrived at the onset of neoglaciation, suggesting that the conditions during the warm, dry, and windy interval were not suitable for seabirds.

It is clear a change in the environment occurred at ~5.0 ka BP. Changes in seabirds, fire, and vegetation may have each responded to climate alone, or may have been influenced by feedbacks with nutrient inputs from seabirds to coastal grasslands. A significant gradual increase in grasses began at 5.0 ka BP and peaked at 1.7 ka BP, then declined to present. Some have suggested that grass pollen on sub-Antarctic islands should not be used as a climate proxy, due to grasses' changing position relative to dynamic sea levels (Barrow, 1978; Van Zinderen Barker, 1985). Alternately, we propose that grass pollen may be responding more strongly to seabird activity. We cannot attribute the grass pollen increase after 5.0 ka BP to sea level change because global sea levels did not fluctuate substantially between 6.0 ka BP and 0.15 ka BP (Lambeck et al., 2014). No relative sea level curve for the Falkland Islands exists today due to preservation issues with proxies i.e. testate amoeba (Newton, 2017).

Seabirds in the Southern Ocean are sentinels of environmental change and ocean health (Barbraud et al., 2012), and our work provides the first evidence of the impact of warming sea surface temperatures on seabirds in the South Atlantic. Barrow (1978) produced the first pollen studies from South Georgia and West Falkland Island and showed that peat formation began ca. 10.0 ka BP and the vascular flora of today flourished before 9.5 ka BP. On West Falkland Island, a drying period ca. 7.0 to 6.0 ka BP is reflected by vegetation changes and a second period of low *Baccharis* (Asteraceae; Christmas bush) pollen may reflect the neoglacial period (Barrow 1978). Barrow (1978) indicated that there are no signs of neoglacial cooling (5.0-4.5 ka BP) in pollen diagrams

from either South Georgia, because the flowering of plants did not decline during the cooling. However, in our study of coastal grasslands from East Falkland Island, there is a clear neoglacial signal indicated by the near-absence of *Empetrum* and Asteraceae taxa and the increase in seabird bioelemental assemblage of As, Cd, Cu and Zn after ~5.0 ka BP (Fig. 1.5).

Prior to this investigation, the natural fire regime for the Falklands was unknown. Fire activity at the end of deglaciation and the early Holocene was lower and less frequent than during the late Holocene (Fig. 1.6). Since 5.0 ka BP, fire activity was greater than previous fire activity and the number of plant taxa became more abundant (Fig. 1.6). We found a mean fire return interval (number of years between fires) of 250 years. In peatlands, especially, Huber et al., (2004) suggested that fire signals may be dampened or underestimated in peat cores because the processes that focus charcoal in sediments are lacking, versus, e.g., lake sediments. Recent work (Turney et al., 2016) to reconstruct the past 5.0 ka BP of wind in the Falkland Islands identified a 250-year periodicity in westerly wind behavior using long distance transported pollen and microscopic charcoal accumulation rates from charcoal assumed to be blown from South America. Because Turney et al. (2016) found negligible amounts of macroscopic charcoal in their record, we suggest that the 250-year periodicity of the westerly winds based on microscopic charcoal may be a consequence of local fire return intervals near their coring site on East Falkland Island. Further evidence for local fire activity is based on 1) the extremely high counts of macroscopic charcoal particles (>125 µm) in our record and 2) previously estimated source areas for macroscopic charcoal fractions

burned in grasslands have a maximum dispersal distance of 5 km (Leys et al., 2015; Leys et al., 2017; Vachula et al., 2018).

Conclusion

In the mid to late Holocene, the Falkland Islands may have been a refuge for displaced seabirds when neoglacial oceanic conditions occurred around Antarctica. Recently, globally important seabird populations in the Falkland Islands have been declining (Crofts & Stanworth, 2017). Sub-Antarctic SSTs have been cooler in the past decade compared to the long term annual mean (Fig. 1.2B). Similar to neoglacial time, marine productivity should be high and seabirds should be increasing like they did after 5.0 ka BP; however, with the influence of fisheries and other anthropogenic activities, seabirds are declining.

Tussac grasslands may have been important habitat for seabirds during biogeographic redistributions in the past or tussac grasslands directly expanded as a result of the redistribution of seabirds and the marine-derived nutrient subsidies, which can be further investigated using phytolith analysis. Whether natural or anthropogenic, fire was a component of seabird habitat in the past and does not seem to have had a long-term negative impact on coastal peatlands or seabird populations. Providing a significant baseline of the response of fauna breeding on the Falkland Islands to changes in the marine environment and the nutrients deposited into tussac grasslands can be used to inform habitat restoration ecologists who are currently working to restore tussac grasslands.

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Table 1.1. Radiocarbon results for Falkland Islands cores SUBA16. Samples submitted to the UCIAMS are listed with the identification number, depth in core, sample type, radiocarbon age (BP) \pm error, and calibrated age range (95% confidence). UCIAMS is the Keck Carbon Cycle AMS Facility at UC Irvine, California, USA.

Core ID	UCIAMS	Depth (cm)	Sample type	^{14}C age (BP)	\pm	Calibrated age range
SUBA16	171842	3.5	Grass leaf	140	15	4-253
SUBA16	171843	174.5	Grass leaf	3,430	15	3,575-3,693
SUBA16	171844	319.5	Grass leaf	6,075	20	6,795-6,957
SUBA16	171845	472.5	Grass leaf	12,275	30	14,007-14,287

Table 1.2. Zonation for SUBA16 vegetation and climate.

Zone	ka BP	Vegetation	climate
Z1	14.0 to 11.2	Grasses dominate; few exotics; Herb total declines; <i>Colobanthus</i> abruptly declines at 11.7 kcal;	
Z2	11.2 to 10.7	Grasses decline (<30%); Shrub (<i>Empetrum</i>) peaks (>60%)	dry
Z3	10.7 to 9.9	Ferns increase to 60%; <i>Empetrum</i> declines to 15%; Grasses begin to increase;	dry to wet transition
Z4	9.9 to 7.0	Grasses dominate; Asteraceae begin to increase; Exotics increase to 5%; <i>Empetrum</i> declines to < 2%; UNK45 peaks and declines;	windy, wet
Z5	7.0 to 5.7	Grasses begin to decline; Asteraceae increases to 20%; Ferns increase; <i>Empetrum</i> begins to increase; Herbs increase to 10%;	windy, dry
Z6	5.7 to 4.5	Grasses decline; Asteraceae peaks at 30% and declines to <1%; <i>Empetrum</i> reaches 40%; Ferns fluctuate between 2 to 20%; UNK45 peaks at 5.7 kcal; <i>Colobanthus</i> disappears after 5 kcal;	dry
Z7	4.5 to pres	Abrupt large peaks between grasses and ferns; Herbs reach a high at 3.7 kcal	

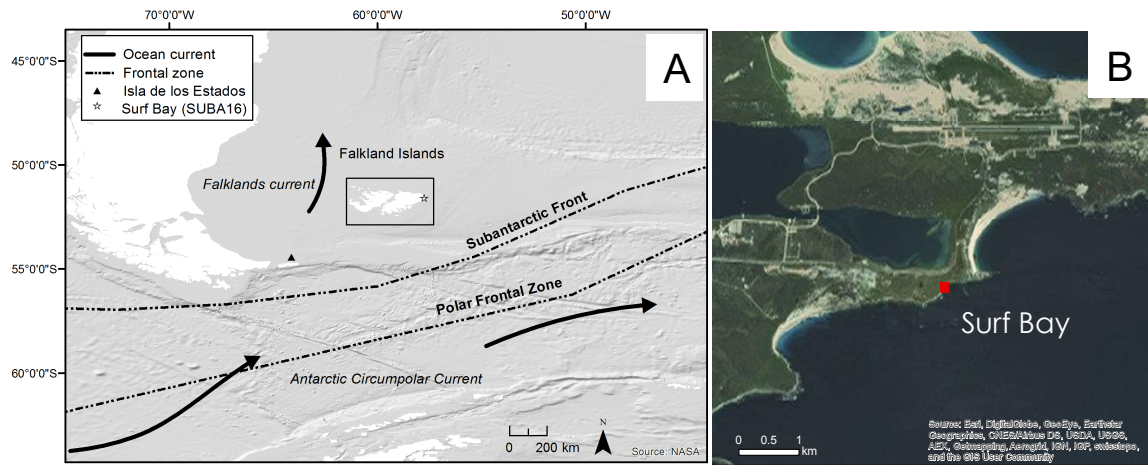


Figure 1.1. Study area. A) Geographic location of the Falkland Islands with with regionally important oceanic currents and frontal zones. Coring sites are demarcated by stars at Surf Bay, East Falkland Island. Isla de los Estados, Tierra del Fuego, Argentina is the site of wind reconstruction (solid triangle). Location of peat collection site B) Surf Bay, East Falkland Island (red square).

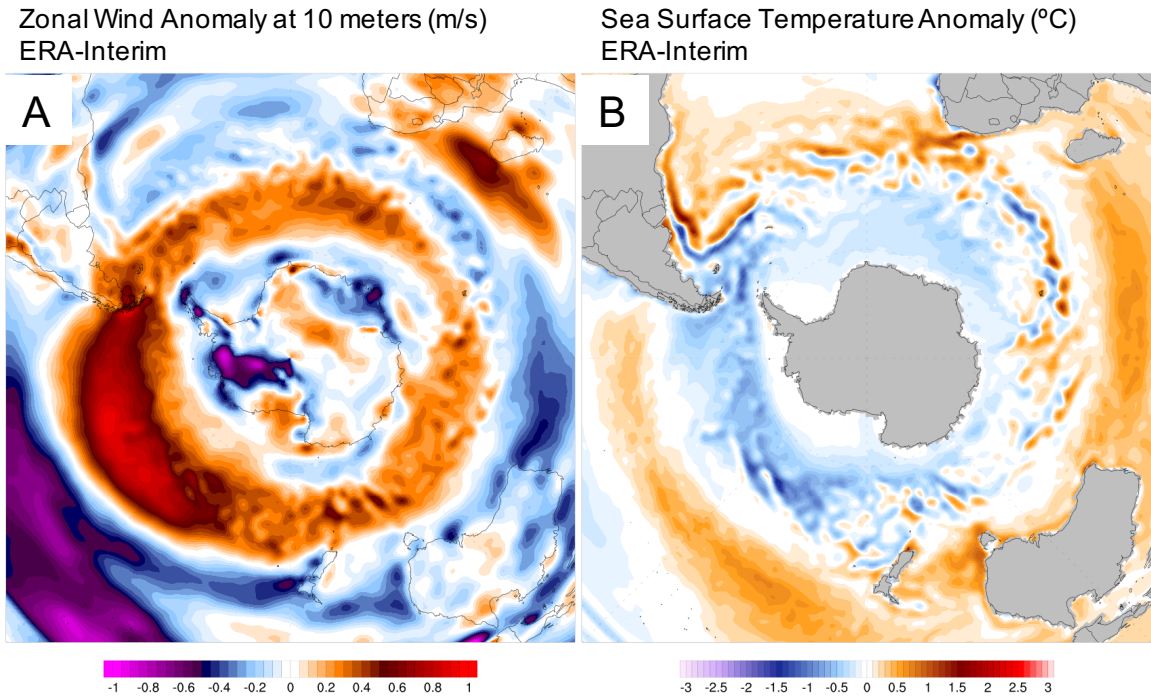


Figure 1.2. Southern Hemisphere westerly wind and sea surface temperature anomaly. Wind intensity increased in the past 10 years relative to 1979-2007; A) ERA Interim reanalysis difference maps of 2007-2017 minus 1979-2007 wind speed anomaly at 10 meters (m/s) and B) sea surface temperature (°C) anomaly. Images obtained using Climate Reanalyzer (<http://cci-reanalyzer.org>), Climate Change Institute, University of Maine, USA.

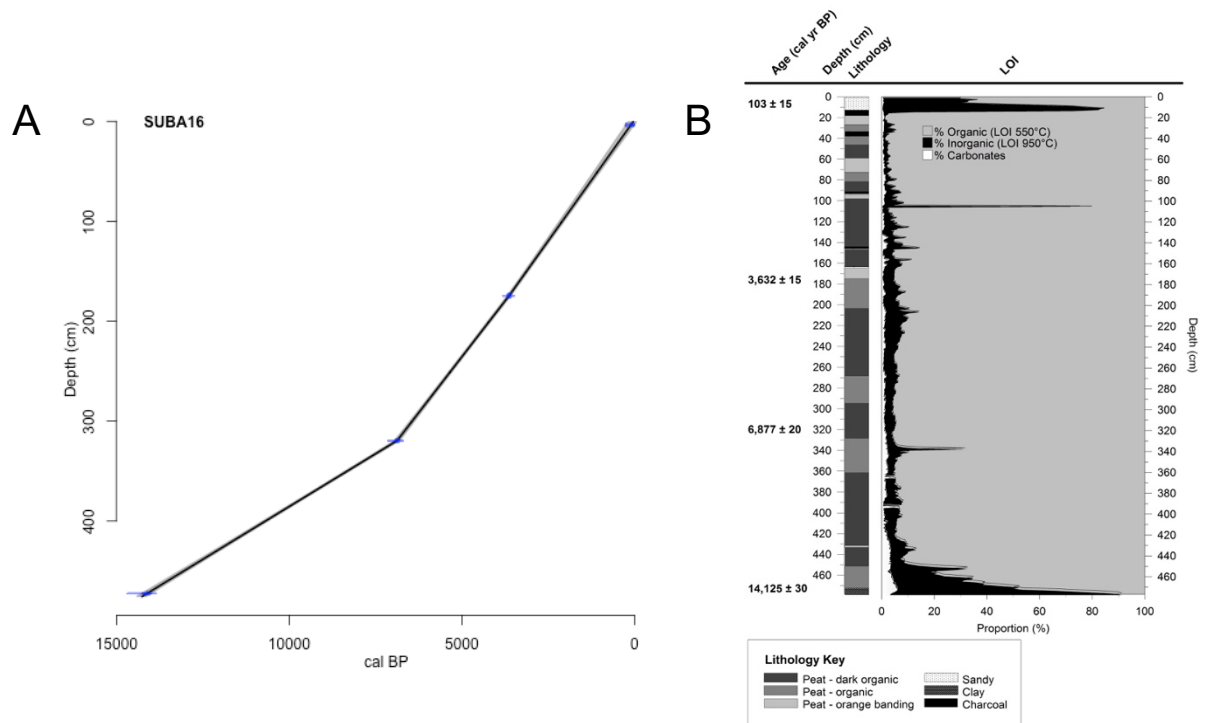


Figure 1.3. Age models and lithology for peat core SUBA16. **A)** Age-depth model (linear interpolation) created using clam (Blaauw 2010) with ^{14}C radiocarbon dates indicated and weighted by calibrated probabilities, performing 1000 iterations using SHcal13 calibration curve (Hogg et al. 2013). **B)** Lithology against depth of SUBA16 peat monoliths with the calibrated age in cal yr BP, and summary of loss on ignition (LOI) proportions (%) for organic (gray) LOI at 550 °C, inorganic (black) LOI at 950 °C, and carbonates (white). Ages were calculated at each depth, from 0 to 476 cm.

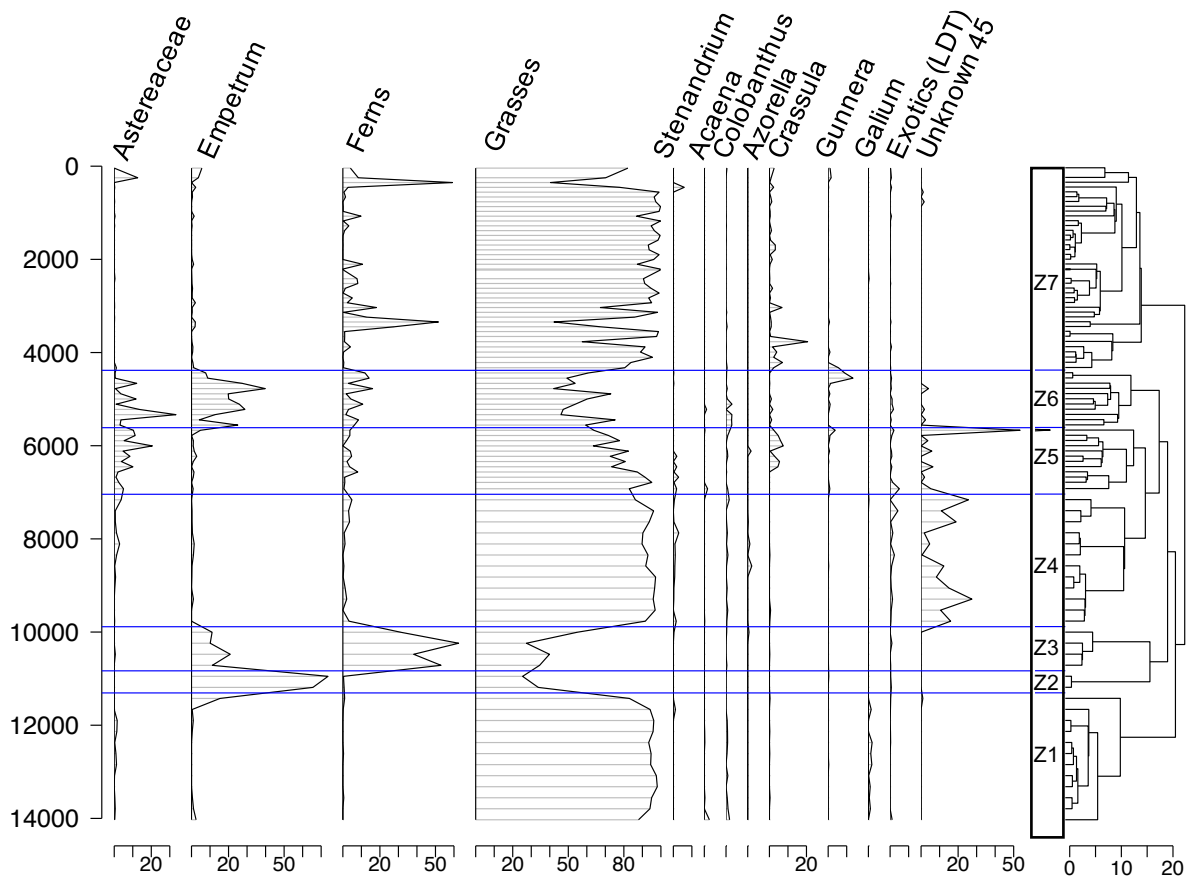


Figure 1.4. Stratigraphic plot of paleovegetation with % abundances for all abundant types in SUBA16 peat core. Zonations are delineated by the horizontal lines (blue) and CONISS (sum of squares) cluster analysis is on the far right.

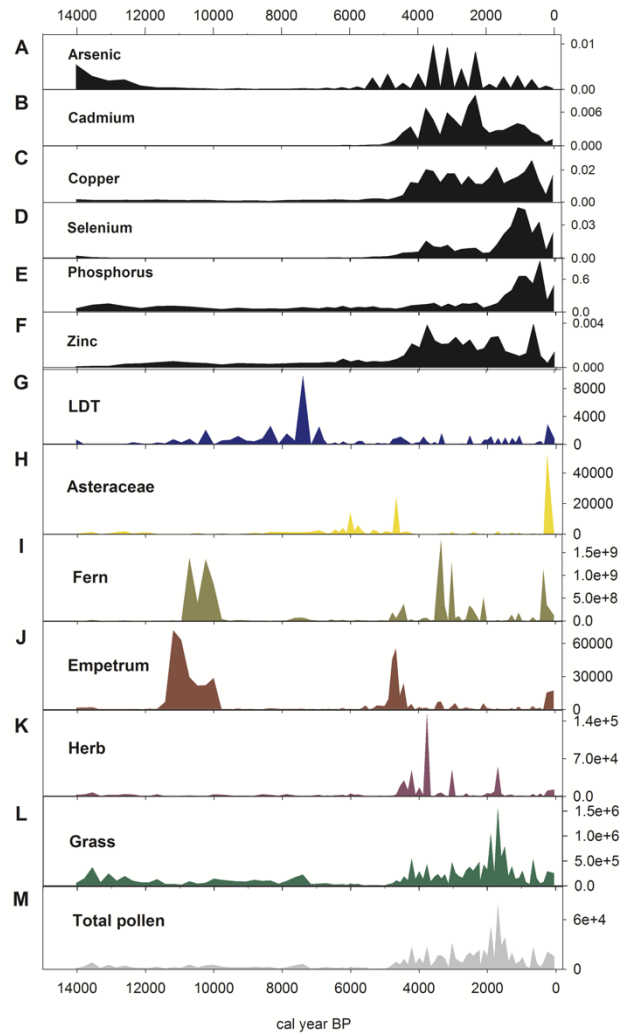


Figure 1.5. SUBA16 Falkland Islands paleoecological reconstruction. A-F) bioelemental seabird proxy concentrations (mg/kg or ppm normalized using aluminum); SUBA16 pollen concentrations for relevant plant taxa G) Long distance transported pollen (SUBA16) concentrations peat at 7.5 ka BP; H) Asteraceae include herbaceous and shrub; I) fern spores; J) *Empetrum* shrub; K) Herb total; L) Grass; and M) total pollen concentration (grains/cm³).

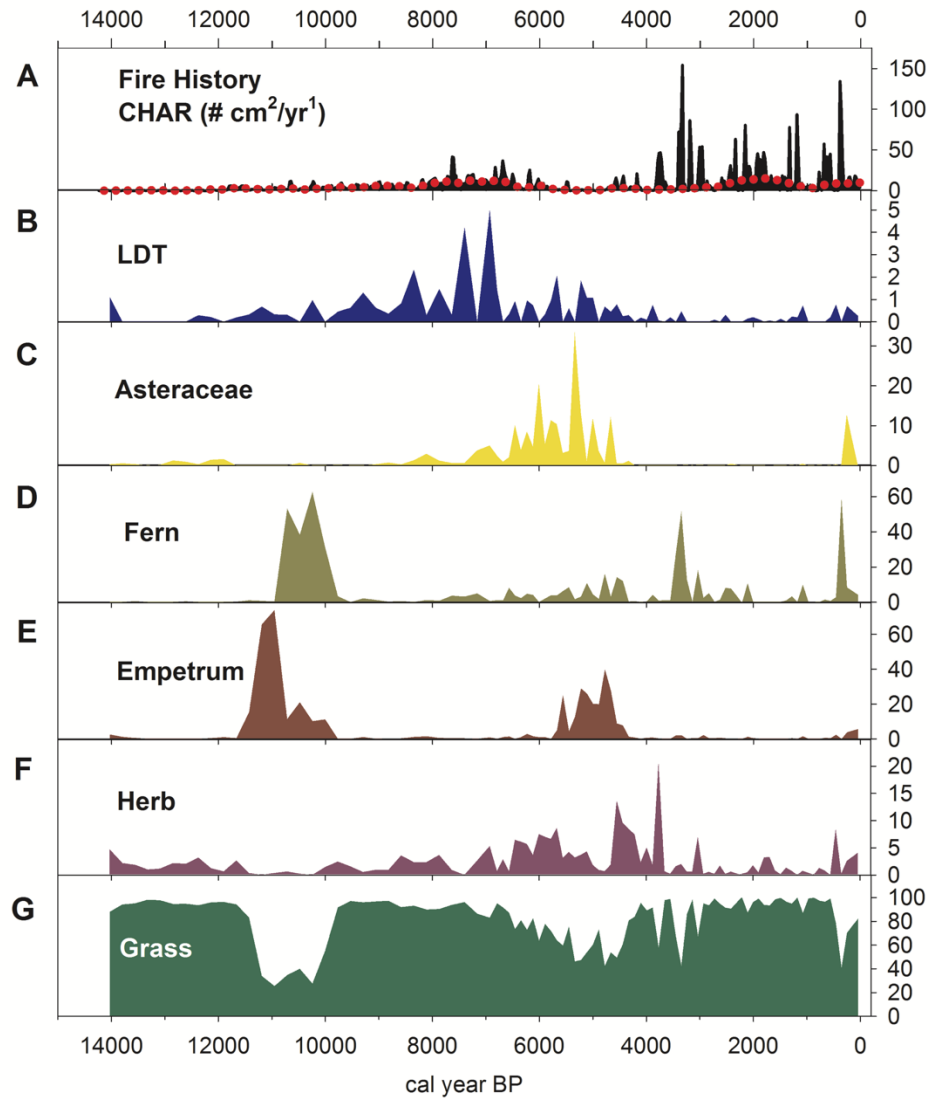


Figure 1.6. Stratigraphic plot of SUBA16 from the Falkland Islands. A) Fire accumulation rate (CHAR in # cm⁻² yr⁻¹) with red dashed line indicating charcoal background levels; B) proportion of long distance transported (LDT) pollen as a proxy for the westerly winds; C-G) proportion (%) abundance) of pollen from SUBA16.

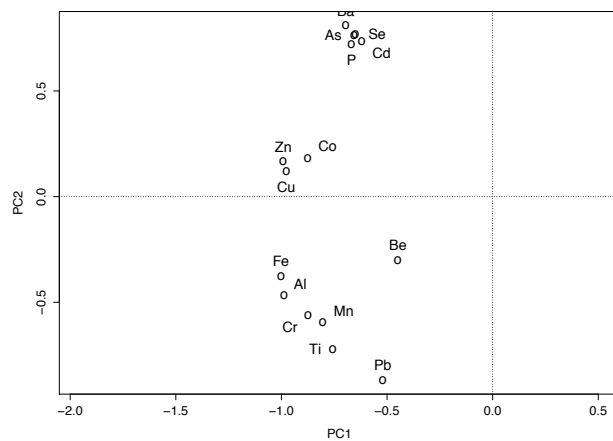


Figure 1.7. PCA of all bioelements analyzed in SUBA16 representing both seabird indicators and all elements analyzed via ICP-MS. The PCA suggests there are two potential groups of bioelements, (Cu and Zn; As, Cd, P and Se), as well as a group of local lithologies (Al, Fe, Ti, Pb, Mn, Cr, and Be).

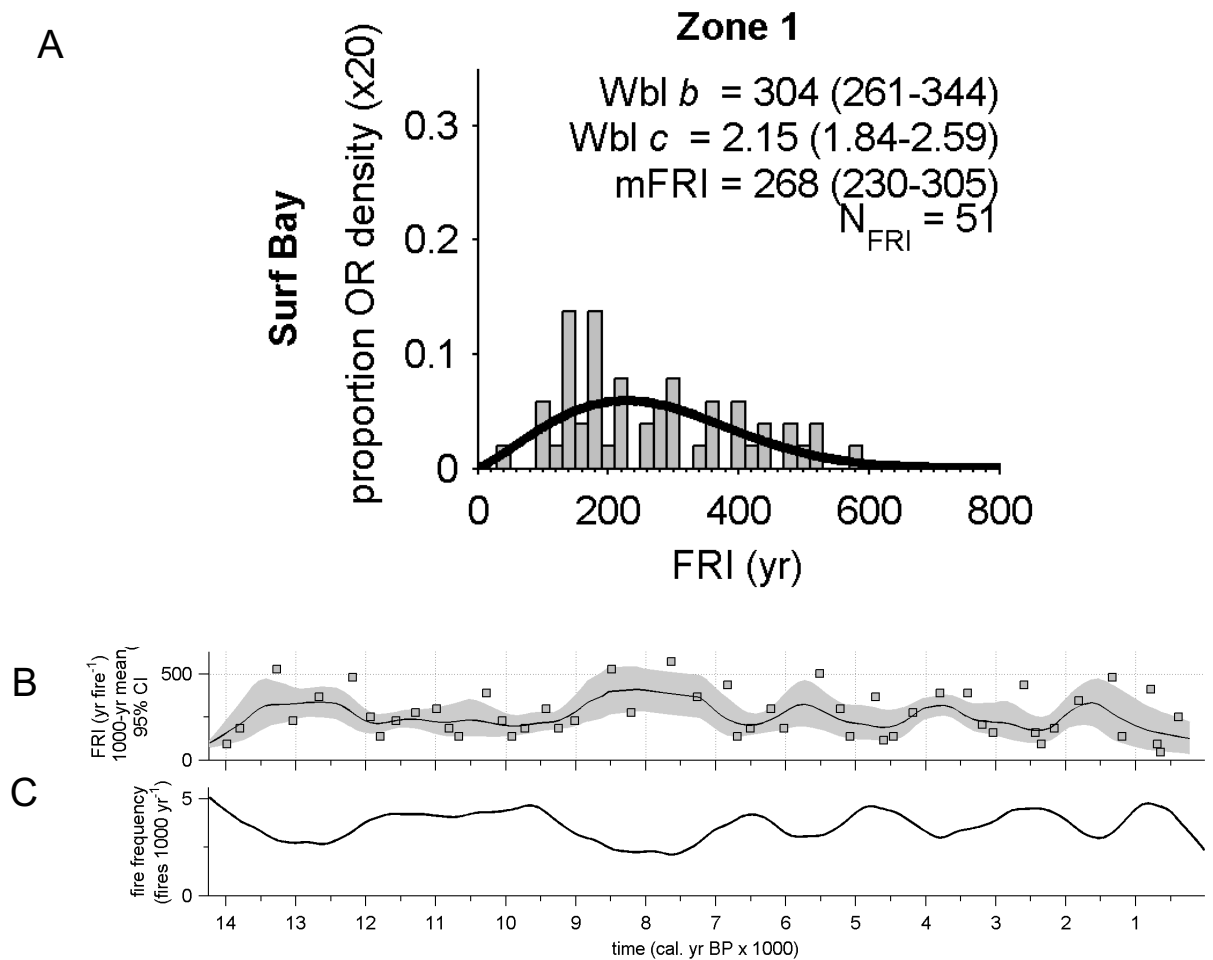


Figure 1.8. Fire history of SUBA16 analyzed using charcoal. A) The mean FRI (mFRI) is 268 years between fires ranging from 230-305 years between fire events. B) Fire return interval is the number of years between fire events using a 1000 year mean and 95% confidence intervals (gray shading); C) Fire frequency (black line is the number of fires per 1000 years) ranges between 2 and 5 fires per 1,000 years.

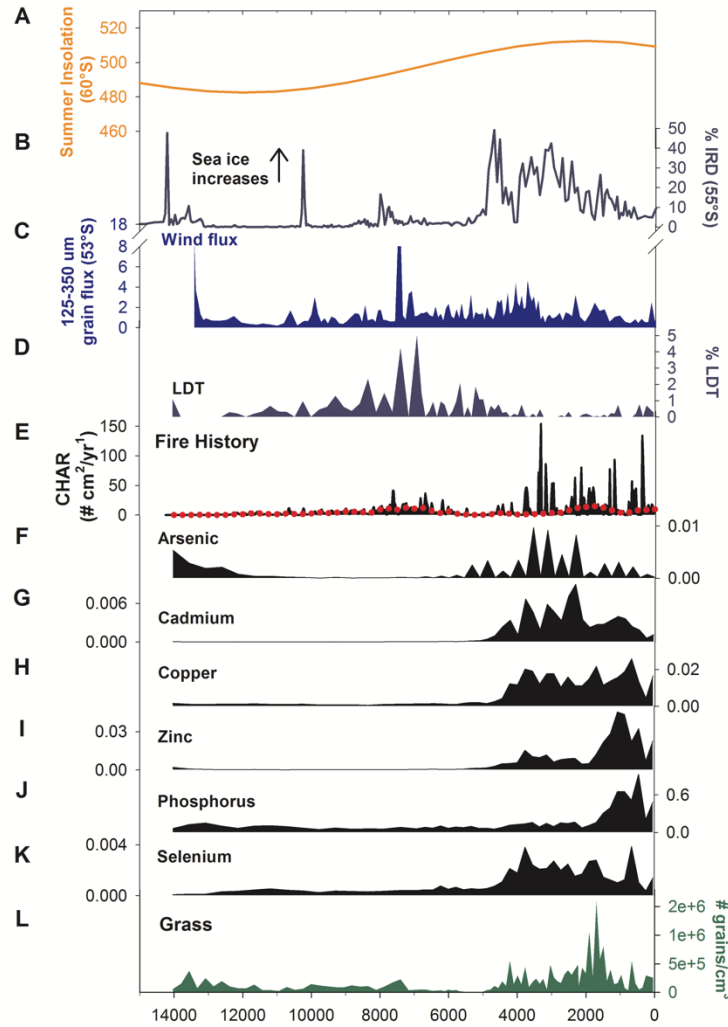


Figure 1.9. Regional and Southern Hemisphere proxies. A) February SST (°C) at 53 °S South Atlantic Ocean (Nielsen et al. 2004); B) Ice rafted debris at 53 °S South Atlantic Ocean (Hodell et al., 2001); C) wind flux (125-300 um grain flux) from grain size analysis at 55 °S (Isla de los Estados, Tierra del Fuego; Björck et al., 2012); D) proportion (%) of long distance transported pollen (LDT) from SUBA16 (Falkland Islands); E) Fire history (CHAR # cm²/yr) in black, and red dashed line indicates charcoal background levels from SUBA16 (Falkland Islands); F-K) influx of seabird-derived bioelements from SUBA16 (Falkland Islands) normalized using Al (mg/kg); L) Grass pollen accumulation rate from SUBA16 (grains/cm²/yr).

CHAPTER 2

POLLEN AND PHYTOLITHS OF THE GRASSES (POACEAE) OF THE FALKLAND ISLANDS

Abstract

Grasses are notoriously difficult to distinguish in paleovegetation reconstructions, and are often identified to family or subfamily. In the Falkland Islands, one grass species, *Poa flabellata* (tussac grass) is regarded as a keystone species forming coastal breeding habitat for seabirds and seals, and produces deep peat deposits that are useful paleoecological archives. To understand how tussac grass responded to variations in environmental change in Quaternary fossil records, we investigated morphological variations of pollen and phytoliths of native grasses to determine whether *P. flabellata* was distinctive at the species level. We found that while pollen is not distinguishable to species, phytoliths are a useful proxy for differentiating tussac grass from other native grasses. These findings reveal the potential for phytoliths to shed light on questions about the response of grasslands in the South Atlantic to environmental change using multi-proxy analyses.

Introduction

Grasslands occur in many types of environments, from the tropics to high latitude regions (Dixon et al., 2014). When reconstructing past ecosystems using paleoecological approaches, we are generally limited to family level taxonomic identification of grasses, which hampers our ability to address important ecological questions. Grass pollen are

particularly abundant and difficult to distinguish when reconstructing past vegetation from sediments. Identification of their pollen is commonly limited to the family or subfamily level due to morphological homogeneity (Bush, 2002). On sub-Antarctic islands where grasslands are a dominant feature of landscapes, the ability to identify different species of grasses could provide useful information about environmental change and biodiversity in the Southern Ocean through time. Grass species are known to have varying tolerances to disturbance from animals and fire, biogeochemical changes, and nutrient and water stress (Craine et al., 2012).

Even though grass species are ecologically variable, grass pollen are generally combined into a single category, undermining information relevant to a species' ecology. Interpretations of grass pollen in paleoecological and archaeological studies commonly include reconstructing shifts between closed forests and open grasslands (Shuman, 2012), and identifying anthropogenic landscape change marked by domesticated grasses, such as *Cerealia* and *Zea mays*, which are typically much larger in size than non-crop grasses (Delcourt et al., 1986). Analysis of phytoliths, silica particles produced by plants, is another commonly used approach to identify grasses to species (Piperno, 2006). When used in paleoecological reconstructions, phytoliths can also identify domesticated grasses (Pearsall & Piperno, 1990), as well as different types of grassland communities (Fredlund & Tieszen et al., 1994).

Grasses of the Falkland Islands

As in most sub-Antarctic islands, grasses dominate the Falkland Islands; there have been no trees on the islands since at least pre-Quaternary times (Macphail &

Cantrill, 2006). Intense grazing since the 18th century introduction of livestock (Wilson, 2016) has altered plant communities, such as the coastal tussock- and peat-forming grasslands once along the fringe of most islands in the archipelago (Kerr, 1997; Groff, 2018). These grasslands are primarily formed by one grass species, *Poa flabellata*; this grass is an ecologically and culturally important species in the Falkland Islands, primarily, because it forms habitat for seabird and marine mammal species (Otley et al. 2008). *Poa flabellata* is endemic to the South Atlantic, and can only be found on Tierra del Fuego, Diego Ramirez Islands, the Falkland Islands, Gough Island, and South Georgia (Kew Royal Botanic Garden, 2018). A century of overgrazing by introduced livestock has decimated *P. flabellata* grasslands (Wilson, 2016; McAdam & Walton, 1990). Restoration and conservation efforts to restore *P. flabellata* grasslands have largely been unsuccessful (Kerr, 1997). A greater understanding of the ecology of how *P. flabellata* grasslands respond to environmental change in the past is important to their restoration. *Poa flabellata* grasslands provide a unique opportunity to contribute to our understanding of the paleoecology and paleoclimates of the Falkland Islands and across its geographic distribution.

There are fourteen native grasses in the Falkland Islands. However, only a few other native plants are typically found growing in the mature remnant stands of *Poa flabellata*, one of which is the grass *Hierochloë redolens* (cinnamon grass; Upson & Lewis, 2014; Moore, 1983). Nutrient-poor acid grasslands are the most widespread type of grassland in the Falkland Islands, dominated by *Cortaderia pilosa* (white grass) in the interior of the Falkland Islands. *Deschampsia flexuosa* is also found within acid grasslands. *Poa alopecurus* (blue grass) forms dense, but low growing, stands along

coastlines and in dune areas (Upson & Lewis, 2014). The other native grasses occur in sandy areas, including dunes, scree slopes, and among heathland shrubs, but do not form extensive grasslands (Upson & Lewis, 2014; Moore, 1983). To determine whether native species of grasses in the Falkland Islands are distinguishable, we conducted a morphometric analysis of pollen and phytoliths from modern plants.

Materials and Methods

Study Area

The Falkland Islands are ~ 500 km east of southern South America, and have a cool temperate climate with a mean January temperature of 9.4 °C (summer) and mean July temperature of 2.2 °C (winter) (Upton & Shaw, 2002). The climate of the Falkland Islands is influenced by its latitudinal position (51°0.5' S to 52°28.0' S), the prevailing westerly winds, and the cold Antarctic Circumpolar Current (Lister & Jones, 2015).

Sampling

We used living native grasses identified, grown, and harvested in January 2016 by Falklands Conservation at the Native Seed Hub in Stanley, East Falkland Islands. We used these samples, along with additional living native grass samples collected in 2018 for pollen and phytolith extraction (Table 2.1). To comply with USDA import requirements for plants, the samples were frozen for eight days at the Falkland Islands Department of Agriculture prior to shipping to the University of Maine, USA. The native grass species used in this study include *Poa alopecurus*, *Poa flabellata*, *Cortaderia pilosa*, *Deschampsia flexuosa*, *Elymus magellanicus*, *Festuca contracta*, *Festuca magellanica*, *Hierochloë redolens*, and *Trisetum pheloides*. We used each of these species for phytolith and pollen analysis, except *Festuca magellanica* was not used for

pollen. For this analysis, we present phytoliths extracted only from leaf material, not flowering parts or roots. Grass species used in this study are described in Table 2.1, using data from Falklands Conservation vascular plant list (Upson & Lewis, 2014) and Moore (1983). Native grasses found in the Falkland Islands not included in this study are in Table 2.2.

Pollen

Reference pollen preparation and identification

We concentrated reference pollen from flowers using a modified protocol of (Faegri & Iversen, 1989) at the University of Maine, USA. Each plant sample was processed with 10% potassium hydroxide (KOH), sieved through 250 μm mesh to remove large particles, followed by glacial acetic acid to dehydrate pollen grains. Following the removal of organics with acetolysis (concentrated sulfuric acid and acetic anhydride), we rinsed each sample with deionized water and 95% ethanol, and dehydrated with tertiary butyl alcohol. We prepared a subset of the pollen for electron microscopy, which remained in DI water (described below), and a second subset was processed for archiving using 1000 cs silicone oil.

Sample preparation for scanning electron microscopy

We used scanning electron microscopy (SEM) to identify sculptural distinctions and finer-scaled measurements for the modern reference pollen collected for each species. At the University of Maine School of Biology and Ecology Electron Microscopy Laboratory, we first folded Whatman filter paper (Grade 50, hardened) into small envelopes, and using a glass pipette, we pipetted the subset of reference pollen in DI

water into the envelope. We folded the envelopes to ensure pollen did not escape. Using ethanol (EtOH), we dehydrated the pollen in the envelopes using the following increasing increments: 10%, 20%, 30%, 50%, 2 x 70%, 80%, 85%, 90%, 4 x absolute EtOH. Pollen remained in each EtOH increment for 5 minutes. After ethanol dehydration, a Tousimis Samdri PVT-3 Critical-Point Dryer dried the pollen using carbon dioxide at critical pressure and temperature. We mounted samples on carbon tape and sputter coated with gold using the following parameters: 0.08 mBar pressure, 30 mA current, 60 seconds, at 14 nm/140A thickness (Cressington 108 Auto/SE Sputter Coater). Images were captured on an AMRay 1820 Digital Scanning Electron Microscope using a 10 kV working distance at magnifications ranging from 2,000X to 2,100X.

Light and scanning electron microscopy

Using light microscopy (40X magnification), we quantified three measurements of each pollen grain: polar axis, equatorial axis, and anulus diameter for at least 60 pollen grains per species when possible. Using a SPOT Imaging camera and software, we used photographic images of pollen grains to make each measurement. We calculated all pairwise ratios of the polar length, equatorial width, and anulus pore diameter (Schüler & Behling, 2011). We visually compared the SEM images with the light microscopy to identify diagnostic sculpturing of the exine.

Phytoliths

Phytolith extraction

We used a dry ashing method adapted from Yost and Blinnikov (2011) to extract phytoliths from plant materials. We first combined the plant material in a 1% Liquinox solution. To remove unwanted debris, we sonicated the samples in liquinox solution for one hour. We sonicated the samples again for 30 minutes after soaking overnight in the Liquinox solution. Afterwards, we rinsed the samples with deionized water and dried them at 80 °C overnight. The dried plant material was transferred to crucibles, weighed, and ashed in a 500 °C muffle furnace for 6 hours. After allowing the samples to cool, we transferred the plant samples from the crucibles to test tubes using 10 mL of 10% HCL, and heated using a dry heating block for 40 minutes at 80 °C, followed by centrifugation at 3500 rpm for 5 minutes, and rinsed with deionized water three times. The rinsed samples were transferred to 1 dram vials using 1 mL of EtOH and dried overnight. Phytolith samples were mounted on microscope slides with silicone oil.

Phytolith classification

We used a Nikon Eclipse C-i light microscope at 20X and 40X magnification to view the phytoliths. Rare and unique phytolith images were taken from a SPOT Imaging camera attached to the microscope at 40X magnification. For each species, we counted and classified at least 300 phytoliths. Using the International Code for Phytolith Nomenclature (ICPN), we classified extracted phytoliths based on morphology (Madella et al., 2005). Where applicable, phytoliths were given both a shape and texture name. In some instances, if the phytolith was rare and distinctive, such as trilobate, it was not

given a texture name. Unclassified phytoliths were characterized as unknowns during counting. These were not reclassified as they made up a small subsample of the results. We calculated the cumulative frequency of phytolith shapes and textures for each species.

Pollen data analyses

A Shapiro-Wilk test for normality indicated that the data for the polar and equatorial axes measurements, and the P/E ratio did not meet the assumption of having a normal distribution ($p = <0.05$). We transformed data for the polar axis ($W=0.9833$, $p = 0.035$), equatorial axis ($W=0.977$, $p = 0.006$), and P/E ratio ($W=0.966$, $p = 0.0003$) using an inverse method ($1 / (x + 1)$). We used the inverse transformed data of the polar length, equatorial width, and P/E ratio for a multivariate analysis of variance (MANOVA) to test for an overall significant difference of means followed by Tukey's post hoc test of significance. We performed hierarchical cluster analysis (Ward's method) in R (R Core Team, 2013) for the eight species since all pairwise comparisons were not significant, and to visualize homogenous groupings.

Results

Pollen

The results of our pollen analysis indicated that *Poa flabellata* cannot be meaningfully distinguished from other native grasses using either the polar length, equatorial width, or the polar to equatorial ratio (Fig. 2.1A-C). The MANOVA (Wilks's $\lambda = 0.30$, $F = 28.416$, $P < 0.0001$) indicated that overall the polar and equatorial axes and P/E ratio were significantly different among species. However, the Tukey post hoc test did not detect a significant difference between *Poa flabellata* and other species. The

hierarchical cluster analysis confirmed that *Poa flabellata* is indistinguishable from other native Falklands grasses using pollen (Fig. 2.2). Summary statistics of the morphometric measurements for the eight species are found in Table 2.3. Visual inspection of pollen surface textures from SEM images did not reveal differences that would be evident using light microscopy at 40X or 100X.

Phytoliths

Phytolith production

The nine species analyzed for phytoliths belong to two subfamilies of native grasses: Pooideae and Danthonioideae (Table 2.4). We classified 41 morphotypes of phytoliths from the nine species of native grasses. Broadly, four phytoliths were common to all the species analyzed in the study: globular, elongate psilate, elongate short cell, and cuneiform. We classified 14 types of phytoliths that were unique to a single species: crenate dumbbell straight end (*Poa flabellata*), trilobate (*Hierochloa redolens*), trapeziform sulcate (*Trisetum pheloides*), trapeziform scrobiculate (*Cortaderia pilosa*), tabular scrobiculate (*Cortaderia pilosa*), tabular laminate (*Cortaderia pilosa*), square ruminant (*Poa alopecurus*), scutiform papillae-like (*Deschampsia flexuosa*), scutiform granulate (*Cortaderia pilosa*), scutiform cavate (*Cortaderia pilosa*), rondel trapeziform (*Trisetum pheloides*), elongate ruminant (*Cortaderia pilosa*), cuneiform granulate (*Cortaderia pilosa*), and bulliform reticulate (*Hierochloa redolens*).

The phytolith classified as crenate dumbbell straight end distinguishes *Poa flabellata* from the other eight grass species (Fig. 2.3). *Poa flabellata* shares most phytolith types with *Poa alopecurus* and *Festuca magellanica* (Fig. 2.4). These three species had a large percentage of ovate papillae-like phytoliths: *Poa flabellata* (75%),

Poa alopecurus (41.5%), and *Festuca magellanica* (34.5%; Fig. 2.5). In total, we classified 11 types of phytoliths for *Poa flabellata*. Five of these made up ~1% of the cumulative frequency (rare), four made up between 1-3% of the cumulative frequency, and globular and ovate papillae-like types made up ~ 89% of the cumulative frequency (Fig. 2.6).

Discussion

Distinguishing grasses of the Falkland Islands is important because it enables future work to address interesting ecological questions. Our work shows that distinguishing native grasses is not possible with pollen, but it is possible with phytoliths. Analysis of phytoliths can compliment pollen analyses of paleo reconstructions and add interesting ecological information. For example, using a multi-proxy paleoecological reconstruction which includes both phytoliths and pollen, we can decipher the causes and effects of grassland declines prior to and after the arrival of seabirds at the onset of neoglaciation in *P. flabellata* grasslands (Groff, 2018). Through the analysis of phytoliths from peat records, future paleoecological investigations will be able to distinguish *P. flabellata* from other native grasses across its geographic range of *P. flabellata* in the South Atlantic. In addition to *P. flabellata*, other native grass species in this study (*Hierochloë redolens*, *Trisetum pheloides*, *Poa alopecurus*, *Deschampsia flexuosa*, and *Cortaderia pilosa*), are distinguishable to species-level using phytoliths. Identification of these grass species in the fossil record can address recent observations from native grassland restoration trials (Smith et al., 2017) regarding plant succession on eroded habitats, as well as *C. pilosa*, an indicator species of widespread acid grasslands.

Future work to understand the dispersal of phytoliths in modern soils may be

useful to determine whether homogenization of phytolith assemblages occurs over large areas. However, work on sub-Antarctic Campbell Island (near New Zealand) suggests that phytolith assemblages are very localized in soils where grasslands dominate (Thorn 2004; Thorn, 2008). The acidic soils and peatlands of grasslands in the Falkland Islands should also ensure the preservation of phytoliths for paleo reconstructions, as preservation of phytoliths is usually compromised in high pH soils (Muerk et al., 1994). A phytolith analysis using acidic peat records (Smith & Clymo, 1985) from the Falkland Islands will likely not be hindered by post deposition processes.

Conclusions

Phytoliths are a valuable tool to add to multi-proxy paleoecological reconstructions of grasslands in the Falkland Islands. Our results showed that at least six species of native grasses have unique phytoliths. The ratio of phytoliths unique to widespread (or once widespread) and ecologically important taxa like *C. pilosa* and *P. flabellata* will facilitate interpretation of past fluctuations by these plant communities in response to climate and other environmental change. Information about past grassland responses at the species-level provides a potentially promising way forward to improve our understanding of the resilience and response of grass species targeted for restoration and conservation in the Falkland Islands.

Acknowledgements

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Table 2.1. Grasses of the Falkland Islands used in analyses and associated habitat, taxa, and geographic distribution. a. Fuegia, b. Falkland Islands, c. Andean Patagonia, d. New Zealand, e. Eurasia, f. Ecuador, g. SE Australia, h. North America, i. South Georgia

Grass species	Common name	Falklands Conservation-named habitat	Associated habitat	Geographic distribution	Botanical history
<i>Cortaderia pilosa</i>	White grass	Acid Grassland	covers vast areas; dislikes swampy or dry shallow soils	a, c, , S. Chile (39dS), W. Patagonia	(D'Urv.) Hack 1900, in Dusen, Wiss Ergebn schwed Exped Magellansland., 3, No. 5, p.222
<i>Deschampsia flexuosa</i>	Wavy hair-grass		Dwarf shrub heath, dry <i>Cortaderia</i>	a, c, e, h, E. Patagonia	(L.) Trin. 1836, Mem Acad Sci Petersb, Ser. 6, 4, p. 9
<i>Elymus magellanicus</i>	Fuegian couch grass	Strandline Vegetation; Coastal (Saline) Grasslands			
<i>Festuca contracta</i>	Land-tussac	Coastal Cushion Heath (Fuegian fescue <i>Festuca magellanica</i>)	Feldmark, screes and rocks by streams, <i>Sphagnum</i> bogs, <i>Marsippospermum</i> communities	a, b, i, Iles de Kerguelen; Macquarie Island	T. Kirk 1895, Trans Proc. NZ Inst 27:353
<i>Festuca magellanica</i>	Fuegian fescue				
<i>Hierochloë redolens</i>	Cinnamon grass	Neutral Grassland (Greens)	Damp ground, near running water; fairly common	a, b, c, d, f, W. Patagonia, Chiloe, Chile, New Guinea	(Sol. ex Vahl) Roem. & Schult. 1817, Syst Veg 15, 2, p.514
<i>Poa alopecurus</i>	Blue grass (coastal ecotype)	Acid Grassland; Sand Dunes, Other Coastal (Saline) Grasslands	Common except with <i>Poa flabellata</i> , and <i>Cortaderia</i> is dominant, most common in rocky dwarf shrub heath, often with <i>Bolax</i> and locally sub- or co-dominant at higher elevations	a, b, Andean Patagonia near Straits of Magellan	(Gaudich.) Kunth 1829, Revis. Gram. 1, p.116
<i>Poa flabellata</i>	Tussac grass	Tussac	Coastal areas on rock and shingle, forms dense stands	a, b, i, Straits of Magellan	(Lam.) Raspail 1829, Ann. Sci. Obs. 2:86
<i>Trisetum phleoides</i>	Spiked Oat-grass		Sandy or shallow and open soils, especially in dwarf-shrub heath, usually by the sea	a, b, c, d, e, h, Andes	<i>Trisetum spicatum</i> var. <i>phleoides</i> (D'Urv.) Hack

Table 2.2. Native grasses of the Falkland Islands not included in this study. Species name, common name, and occurrence status using the Falklands Conservation updated vascular plant list (Upson & Lewis 2014).

Species	Common name	Occurrence status
<i>Deschampsia antarctica</i>	Antarctic Hair-grass	Occasional
<i>Deschampsia parvula</i>	Dwarf Hair-grass	Rare
<i>Koeleria permollis</i>	Berg's Hair-grass	Very rare (1937-1938)
<i>Poa robusta</i>	Shore-Meadow grass	Frequent
<i>Puccinellia pusilla</i>	Dwarf Saltmarsh-grass	Very rare

Table 2.3. Summary of pollen morphometric statistics. Measurements were made for the polar length in μm (P), equatorial width in μm (E), and polar to equatorial ratio (P/E) of eight native grasses (Poaceae) in the Falkland Islands; average \pm 1SD.

	<i>Poa flabellata</i>	<i>Deschampsia flexuosa</i>	<i>Trisetum pheloides</i>	<i>Poa alopecuras</i>	<i>Hierochloe redolens</i>	<i>Cortaderia pilosa</i>	<i>Festuca contracta</i>	<i>Elymus magellanicus</i>
	n = 60	n = 61	n = 61	n = 61	n = 21	n = 24	n = 61	n = 61
P (μm)	29.0 \pm 2.3	24.2 \pm 2.2	26.0 \pm 2.2	26.8 \pm 2.0	27.3 \pm 2.6	28.9 \pm 3.9	30.0 \pm 2.9	37.2 \pm 3.8
E (μm)	28.3 \pm 2.2	23.8 \pm 2.3	26.3 \pm 2.6	26.2 \pm 2.2	27.4 \pm 2.7	28.8 \pm 3.3	30.7 \pm 3.3	37.0 \pm 4.4
P/E	1.027 \pm 0.053	1.018 \pm 0.068	0.993 \pm 0.078	1.027 \pm 0.074	1.004 \pm 0.128	1.009 \pm 0.119	0.981 \pm 0.093	1.011 \pm 0.100

Table 2.4. Taxonomic classifications for Falkland Islands native grass species processed for pollen and phytolith analyses.

Family	Subfamily	Species
Poaceae	Danthonioideae	<i>Cortaderia pilosa</i>
	Pooideae	<i>Deschampsia flexuosa</i>
	Pooideae	<i>Elymus magellanicus</i>
	Pooideae	<i>Festuca contracta</i>
	Pooideae	<i>Festuca magellanica</i>
	Pooideae	<i>Hierochloe redolens</i>
	Pooideae	<i>Poa alopecuras</i>
	Pooideae	<i>Poa flabellata</i>
	Pooideae	<i>Trisetum pheloides</i>

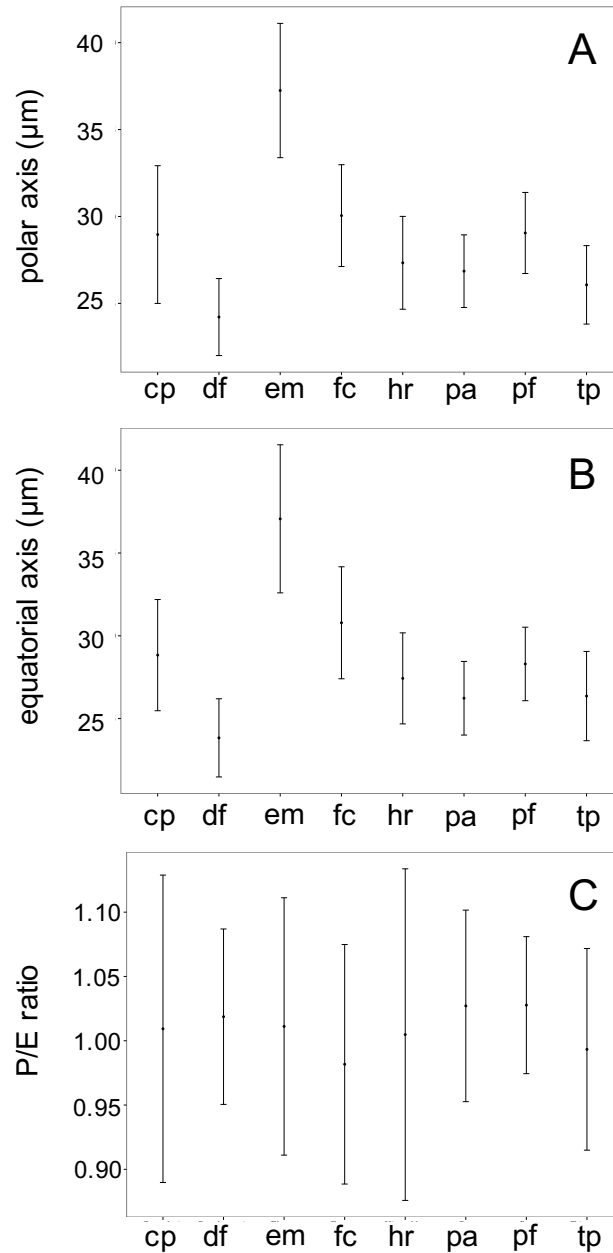


Figure 2.1. Morphometric results of reference pollen (mean \pm 1SD) for eight grass species measured using light microscopy. **A)** The polar axis length (μm), **B)** equatorial axis width (μm), and **C)** the polar/equatorial ratio are represented for each of the following: cp, *Cortaderia pilosa*; df, *Deschampsia flexuosa*; em, *Elymus magellanicus*; fc, *Festuca contracta*; hr, *Hierochloë redolens*; pa, *Poa alopecurus*; pf, *Poa flabellata*; tp, *Trisetum pheloides*.

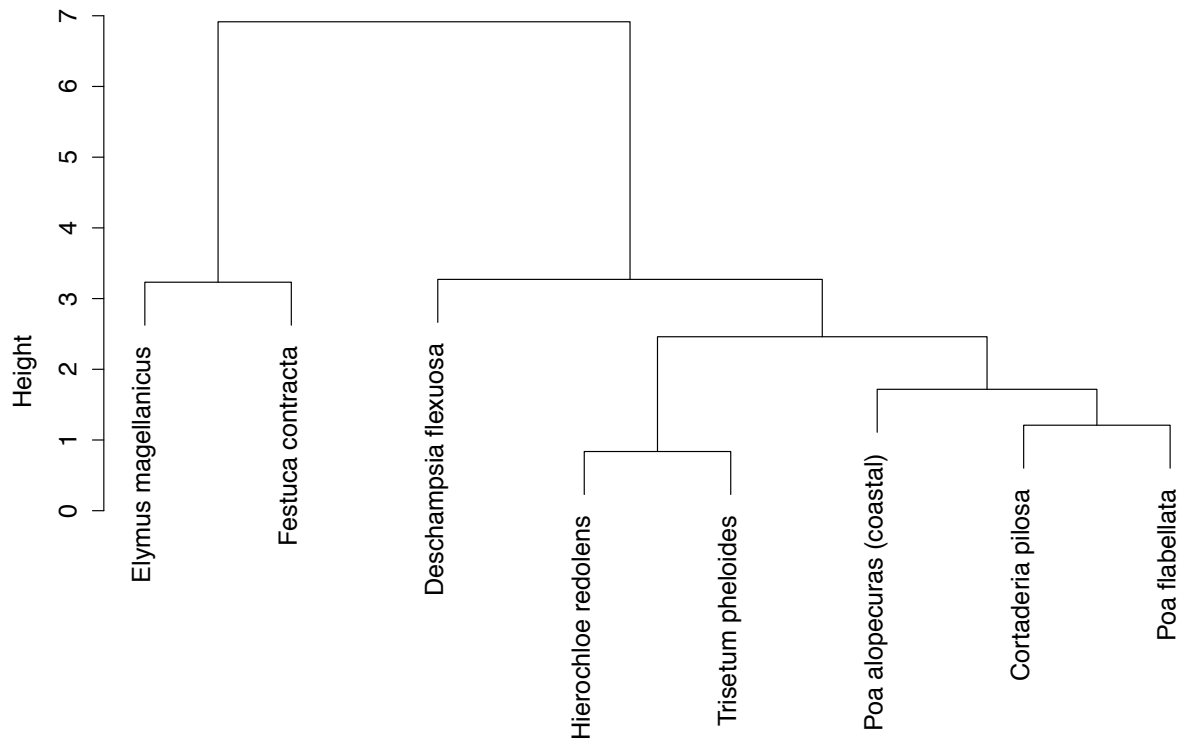


Figure 2.2. Dendrogram showing the relationship among pollen morphometric data for eight native grass species. The hierarchical cluster analysis used the Ward's method of no prior assumptions.

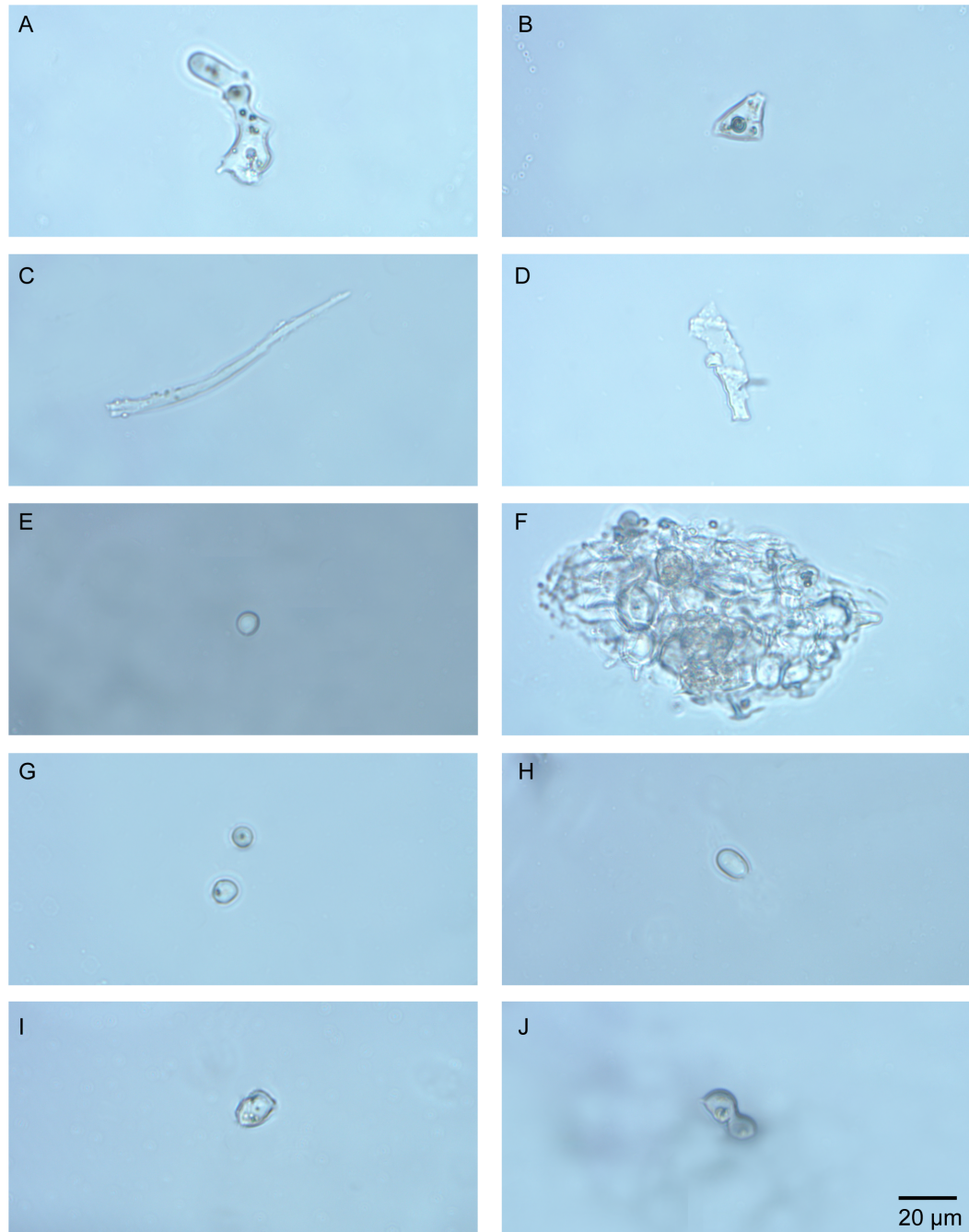


Figure 2.3. Phytoliths of *Poa flabellata* from the Falkland Islands. A) crenate dumbbell straight end; B) cuneiform; C) elongate psilate; D) elongate short cell; E) globular; F) multi-ovate to sub-polygonal; G) ovate papillae-like; H) ovate; I) rondel; J) bilobate.

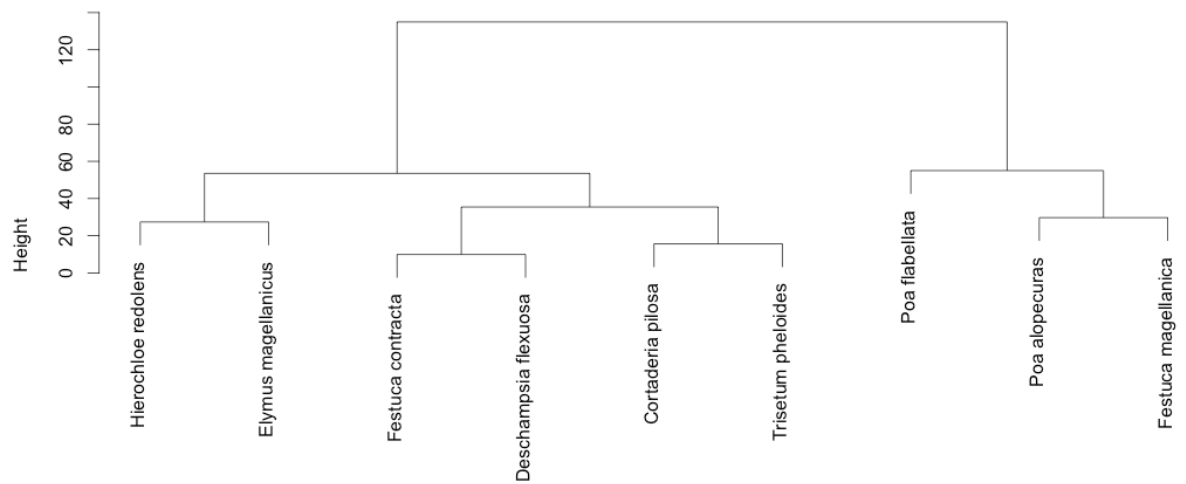


Figure 2.4. Dendrogram showing the relationship among phytolith morphotypes for nine native grass species. The hierarchical cluster analysis used the Ward's method of no prior assumptions.

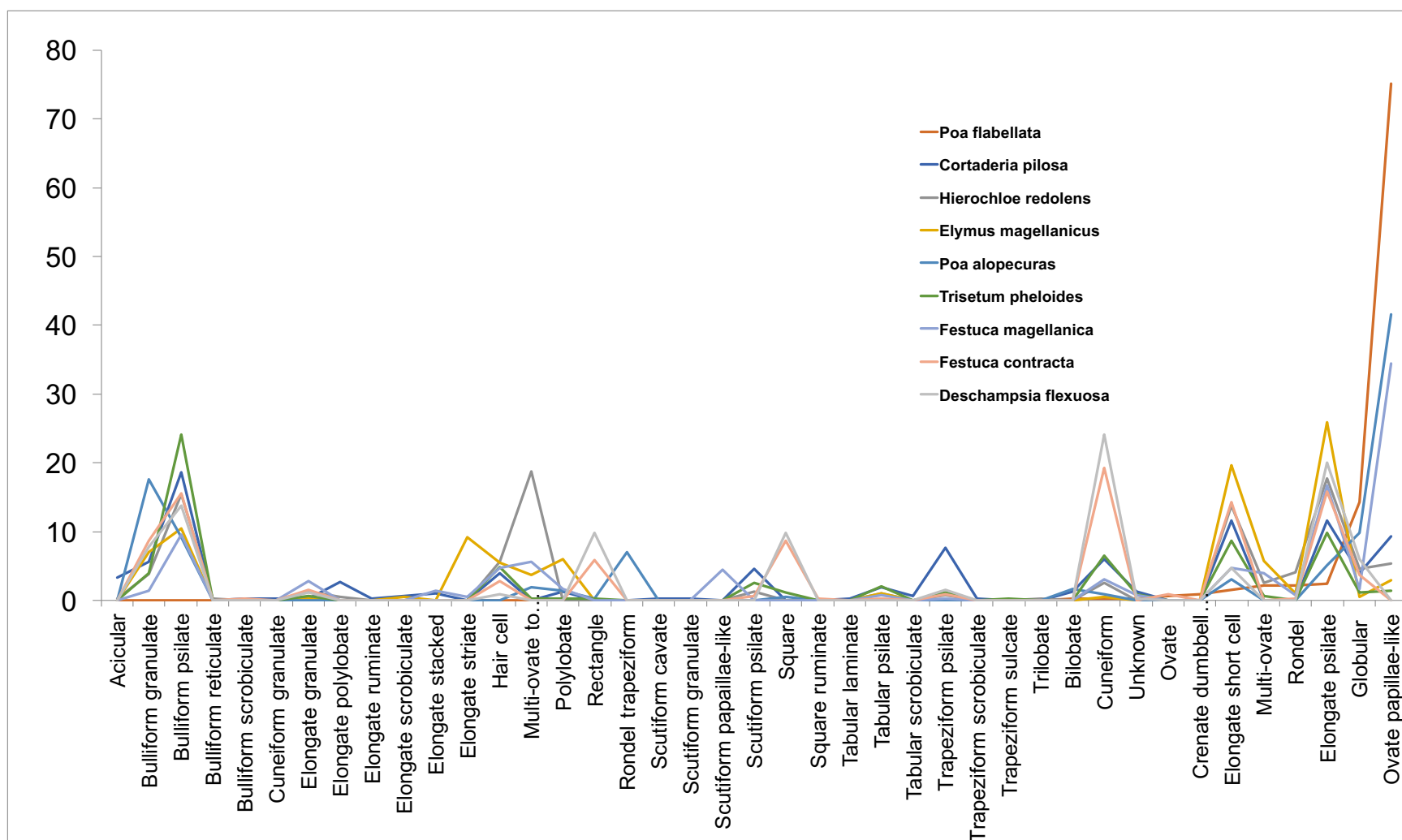


Figure 2.5. Cumulative frequencies for phytoliths classified using shape and texture for nine species of native grasses in the Falkland Islands.

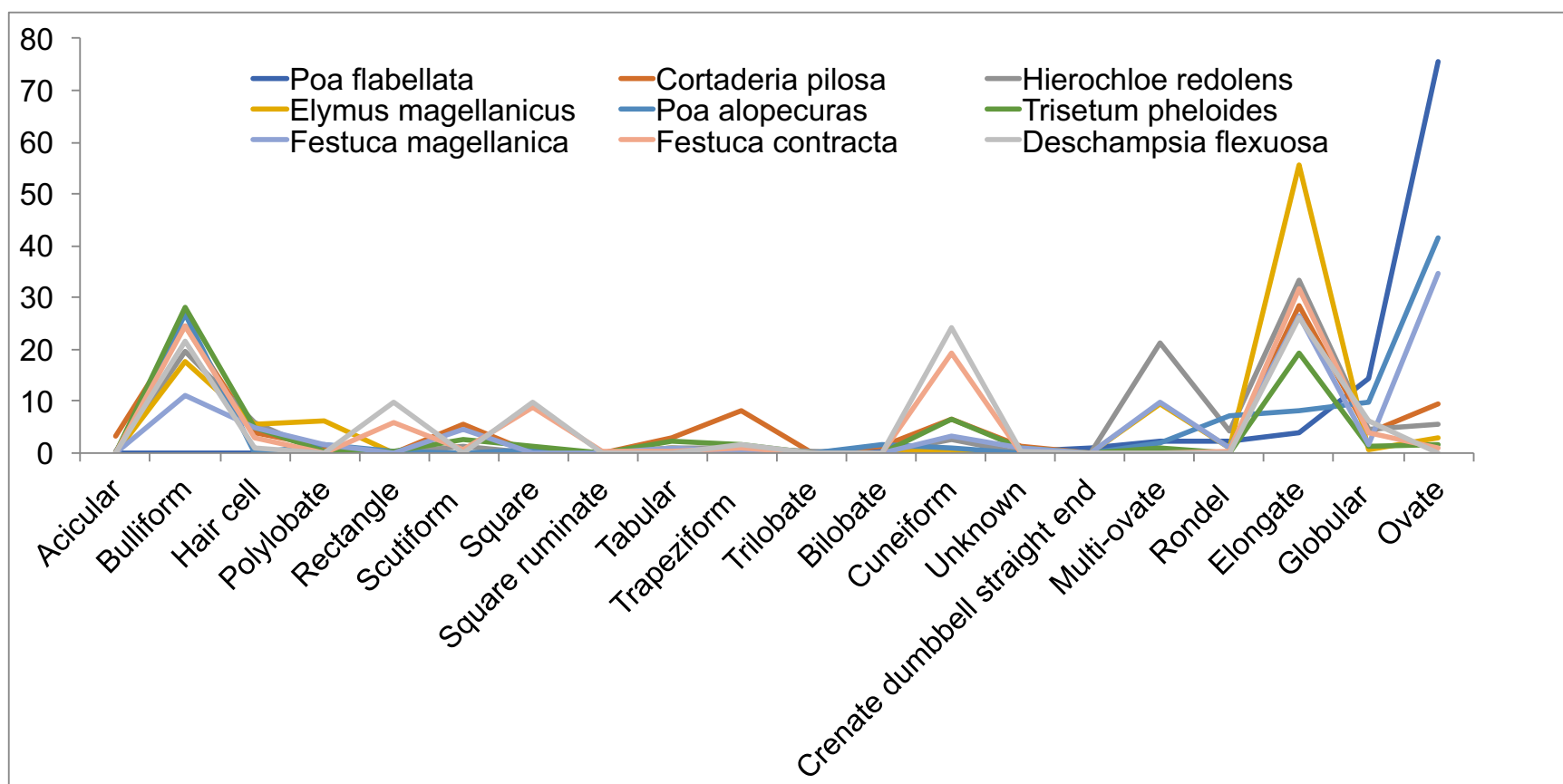


Figure 2.6. Cumulative frequencies for phytoliths classified using shape only for nine species of native grasses in the Falkland Islands.

CHAPTER 3

MODERN CALIBRATION OF *POA FLABELLATA* (TUSSAC GRASS) AS A NEW PALEOCLIMATE PROXY IN THE SOUTH ATLANTIC

Abstract

Terrestrial paleoclimate records are rare in the South Atlantic, which limits opportunities to place current global changes in a prehistoric context. Tussock grass (*Poa flabellata*), which grows abundantly along the coastal margins of the Falkland Island and other sub-Antarctic islands, forms extensive peat records from its leaves and roots, and provides a promising opportunity to reconstruct high-resolution regional paleoclimate records. The isotopic composition of leaf and root tissues in peatland vegetation has the potential to record variation in precipitation and relative humidity, but this relationship is unknown for *P. flabellata*. We found that inter-seasonal differences in oxygen and carbon stable isotopes of leaf α -cellulose of growing tussocks at four locations in the Falkland Islands significantly correlated with monthly mean temperature and relative humidity. Weak correlations between $\delta^{18}\text{O}$ in monthly composite precipitation and $\delta^{18}\text{O}$ of leaf and root cellulose require further investigation. This study supports the use of peat records formed by *P. flabellata* to fill in a significant gap in our knowledge of the long-term geographic and temporal patterns of Southern Hemisphere westerly wind dynamics.

Plain Language Summary

Leaves and roots of tussock grasses growing along coastlines of the Falkland Islands and other islands in the southwestern Atlantic Ocean are slow to decay and hence build up as peat over thousands of years. The isotopic composition of grass fragments in peat can be used to decipher how temperature, humidity, and rain patterns changed in the

past, because tussock grasses record these changes in their tissues as they grow. The challenge is that different plant species record these patterns in slightly different ways. We tested whether modern living plants of the Tussac grass (*Poa flabellata*) in the Falkland Islands record temperature, humidity and precipitation. We found that Tussac grass leaves reliably record temperature and humidity in their leaves. It is less clear whether tussac grass leaves and roots record the origin of air masses that transport moisture to the Falkland Islands, which may be either from the northwest or southwest. Our study demonstrates that tussac grass leaves found in peat can be used to tell us how humidity changed in the past in response to global change.

Introduction

High latitude environments of the South Atlantic are changing rapidly. Over the last century mean annual temperature in the Falkland Islands has increased by 0.5 °C (Lister and Jones 2014). This warming has corresponded with an intensification and poleward shift of the southern westerly winds (Gillette and Thompson 2003; Thompson and Solomon 2002), and more northerly air masses are expected to increase aridity. The impact of these changes have already altered the distribution of some marine animal species in the Southern Ocean (Weimerkirsch et al., 2012), and warming of the western South Atlantic is projected (Jones et al., 2013) to alter the distribution of plants on islands as well (Upson et al., 2016). Paleoecological archives, such as high-resolution lake sediments and trees rings, can provide useful long-term records documenting and quantifying changes (Dietl and Flessa 2011; Dietl et al., 2015; Willis et al., 2007), but such records are lacking for the South Atlantic. The absence of trees across many sub-Antarctic islands especially limits high-resolution, independent paleoclimate

reconstructions, which are essential for detecting past abrupt changes in temperature, precipitation, and humidity caused by shifts in the intensity and position of the westerly wind belt. However, many sub-Antarctic islands support widespread communities of peat-forming tussock grasses (*Poa flabellata*), which provide important habitat and shelter for breeding marine animals such as seals and seabirds. Peat records formed by *P. flabellata* present a promising avenue for paleoclimate reconstructions; peatland vegetation has been used to reconstruct hydrological change and temperature in mid- to high latitudes (Chambers et al., 2012; Pendall et al., 2001, Amesbury et al., 2015).

Tussac grass (*Poa flabellata*) stands in the South Atlantic accumulate substantial amounts of peat (Lewis Smith and Clymo 1985) (Fig. 3.1). Endemic to the South Atlantic, *P. flabellata* only occurs on Tierra del Fuego, the Falkland Islands, Gough Island, and South Georgia in the Southern Hemisphere (Fig 1). *P. flabellata* stands were once widespread throughout the Falkland Islands, but are now greatly reduced because of land-use change and introduced grazers (Strange et al., 1988; Wilson et al., 1993).

Tussac peatlands are bogs that are formed by a single-species dominant community of *P. flabellata*, which allows very little light or space for other plants to co-occur in the absence of disturbance. The term “tussock” is used to describe the clumping growth form of *P. flabellata*, while the grass itself is commonly known as “Tussac.” Individual tillers of *P. flabellata* grow on top of a pedestal of decaying roots and leaves, known as a bog, which can reach up to 3-4 meters in height (Fig. 3.2A). Because *P. flabellata* tillers grow on top of peaty pedestals (Lewis Smith and Clymo 1984), plants may be hydrologically isolated from other sources of water and thus likely primarily use water from precipitation. This, along with the abundance of macrofossil *P. flabellata*

leaves in peat deposits spanning the Holocene period, supports the potential use of tussac as a record of precipitation, relative humidity, and temperature. Tussac grass forms extensive peat deposits of up to 13.3 m deep, with accumulation rates of dry matter far greater ($430\text{--}720\text{ g m}^{-2}\text{ yr}^{-1}$; Lewis Smith and Clymo 1984) than Northern Hemisphere peatlands ($18.6\text{ g C m}^{-2}\text{ yr}^{-1}$) of similar latitude, as well as peatlands in the tropics ($12.8\text{ g C m}^{-2}\text{ yr}^{-1}$) or Patagonia ($22\text{ g C m}^{-2}\text{ yr}^{-1}$) (Yu et al., 2010). Tussac peat is predominantly comprised of grass leaves and roots, and often makes up thin sheets of well-preserved leaves that are locally referred to as ‘bible peat.’

Grasses exhibiting the tussock growth form often have evergreen leaves and exhibit a profligate/opportunistic water use strategy, due to the high evaporative conditions and pulses of water availability in semi-arid habitats (Sala et al., 1989; Schwinning and Ehleringer 2001; Moreno - Gutiérrez et al., 2012). Carbon and oxygen stable isotope ratios record species’ water-use strategies in water-limited environments because of the role of stomatal conductance (Moreno-Gutierrez et al., 2012; Farquhar and Sharkey 1982). Tussock grasses typically occur in water limited environments where a lower water-use efficiency and greater stomatal conductance are common functional traits that allow tussac grasses to take advantage of pulses of water (Moreno-Gutierrez et al., 2012). The $\delta^{18}\text{O}$ of leaf water is a primary driver of $\delta^{18}\text{O}$ in leaf cellulose, and may be influenced by water source and atmospheric vapor pressure, as a function of air temperature and humidity (Helliker and Ehleringer 2002). Correlations between $\delta^{18}\text{O}$ of plant cellulose and air temperature and humidity provide information about environmental conditions in the season the cellulose tissue formed. Apart from water source, $\delta^{18}\text{O}$ of cellulose can also be influenced by internal exchange among organic

molecules and other plant waters (Sternberg et al., 1986). $\delta^{18}\text{O}$ reflects source water, and thus temperature of the environment (Libby et al., 1976). The $\delta^{18}\text{O}$ of leaf water, and that of cellulose in leaves records information about source water and humidity (Roden and Ehleringer 1999), and δD is expected to have similar patterns as $\delta^{18}\text{O}$ in cellulose (Barbour et al., 2001, Barbour et al., 2007; Fig. 3.2B). Leaf $\delta^{13}\text{C}$ of leaf cellulose discrimination records changes in the supply of CO_2 through stomatal pores and demand for CO_2 by photosynthetic biochemistry (Cernusak et al, 2013; Farquar et al., 1982; Ferrio et al., 2002; Fig. 3.2B). The climate signal recorded in the cellulose of plant tissues (roots, shoots, and leaves) is deciphered using stable isotopes $\delta^{18}\text{O}$, δD (Araguas-Araguas et al., 2000) and $\delta^{13}\text{C}$. Different species of plants vary in the way they record precipitation and temperature, which is reflected in stable isotope measurements; therefore, peat comprised of a single species is more desirable over a mixture of species (van Geel and Middelborg 1988).

To test the potential of *P. flabellata* peatlands as a paleoclimate proxy, we conducted a modern calibration study to determine whether living *P. flabellata* is sensitive to precipitation, relative humidity, and temperature. We measured oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) stable isotopes temporally and spatially across the Falkland Islands. To address this, we used $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ to calibrate and validate the use of α -cellulose from *P. flabellata* leaves as a proxy for precipitation, temperature, and relative humidity in the Falkland Islands (51° S, 59° W; Fig. 3.1). By applying the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ record of *P. flabellata*-dominated peatlands endemic to the region, we aim to improve our understanding of Southern Hemisphere westerly wind dynamics through time with a new paleoclimate proxy that leverages the unique properties of *P. flabellata*.

Methods

Study location description

The Falkland Islands are located approximately 500 km east of southern South America, between 51°0.5' S to 52°28.0' S and 61°22.0' W to 57°40.5' W. The cool-temperate (mean temperature: January 9.4 °C and July 2.2 °C) climate of the Falkland Islands is driven by the cold Antarctic Circumpolar Current, the waters surrounding the Antarctic Peninsula, the Falklands Current, and the Andes of southern Patagonia to the west (Turner and Pendlebury 2000). The persistent winds of the southwesterly wind belt average 8.5 m s⁻¹, with gale force winds averaging 70 days per year (Jones et al., 2013; Lister and Jones 2015). Study sites were selected to reflect 1) climatic diversity, and 2) the availability of an able volunteer to collect monthly samples for one year. We ultimately selected four study locations (Fig. 3.1B): Bleaker Island, Cape Dolphin, Surf Bay, and West Point Island.

Meteorological data analyses

Precipitation, temperature and relative humidity

Precipitation was collected at each site using a Palmex monthly composite precipitation collection sampler (Palmex d.o.o., Zagreb, Croatia). The Palmex collector is designed to prevent evaporation and evaporative enrichment of ¹⁸O in precipitation samples without the use of paraffin oil, and has been recommended by the Global Network of Isotopes in Precipitation (GNIP). Samples were shipped to the University of Maine, Orono, Maine, USA prior to analysis. Oxygen (δ¹⁸O) and hydrogen (δD) stable isotope ratios of water samples were measured at the University of Wyoming Stable Isotope Facility (UWSIF), Laramie, Wyoming, USA using a Thermo Scientific Delta V

Plus that is run in continuous flow mode and connected to high-temperature conversion elemental analyzer (TCEA) via a ConFlo IV. The technique used injections of 1 μ l of water into the TCEA column filled with glass carbon heated to 1420°C. Water reacts with the glassy carbon to produce carbon monoxide and hydrogen gas, which is then separated via a gas chromatographic column. Precipitation samples were extracted using cryogenic distillation prior to TCEA analysis to remove aeolian debris, including marine salts. Internal quality control (UWSIF-301 and UWSIF-303) and assurance (UWSIF-E) materials were analyzed with each batch of samples with analytical precision typically better than 0.3 and 2.5 ‰ for $\delta^{18}\text{O}$ and δD , respectively. Isotope values are reported with respect to VSMOW in parts per thousand (per mil, ‰).

To record temperature and relative humidity we placed iButton™ DS1923 loggers (Maxim Integrated, Dallas, TX, USA) in the Palmex precipitation samplers, such that they were protected from direct contact with precipitation, but were open to ambient temperature and humidity. The temperature accuracy resolution of iButton is 0.5 °C and 0.0625 °C, respectively, and a resolution of 0.04% for relative humidity. Temperature and humidity were logged every two hours (12 measurements/day) and averaged to daily values for analysis. Daily average temperature (°C) & relative humidity (%) were calculated from two hour measurements using iButton loggers at Bleaker Island, Cape Dolphin, Surf Bay, West Point Island sites (Fig. 3.2), and daily average temperature of 15 minute measurements using MetPak II (Gill Instruments, UK) at Bleaker Island.

Wind speed, direction, and HYSPLIT analyses

We analyzed data from a Bleaker Island weather station (MetPak II supplied by Gill Instruments, UK), to explore variation in sources of air masses between summer and

winter seasons, which recorded wind speed and wind direction at ground level from September 2015-August 2016. The frequency of counts by wind direction (%) was measured at Bleaker Island WSD (MetPak II) across four seasons, from September 2015 to August 2016. Mean seasonal wind speed (m s^{-1}) and % calm were calculated and a wind rose was constructed using the package *openair* in R (version 3.1.0). We explored variation in sources of air masses at 1000 m above ground level from September 2015 to August 2016, using the Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPLIT) model (NOAA Air Resources Laboratory; Draxler et al., 1999). We selected global reanalysis data sets from the National Centers for Environmental Prediction (NCEP) and the National Center for Atmospheric Research (NCAR; Kalnay et al., 1996; Kistler et al., 2001) as the NCEP/NCAR reanalysis model is suitable for the Southern Hemisphere based on previous work of back trajectory modeling to determine the origin of air masses (Gasso and Stein 2007; Schwank et al., 2017; Dixon et al., 2011; Markle et al., 2012.) Five-day (120 h) 3-D back trajectories were created for a central point over the Falkland Islands (51.79 °S, 59.52 °W) from 1 December 2015 to 29 February 2016 (summer) and 1 June 2016 to 30 August 2016 (winter).

Temperature comparison among iButton and weather stations

To determine the validity of the iButton temperature data, we compared temperature (°C) measurements logged every two hours with an iButton at Bleaker Island with those from a local weather station taken every 15 minutes (MetPak II supplied by Gill Instruments, UK; hereafter referred to as Bleaker WSD). The elevation at Bleaker WSD is approximately 1.74 meters above sea level, and ~10 meters higher than the iButton, which was positioned 350 meters to the northwest. These measurements were

compared to data from the Mt. Pleasant Airport weather station, located 50 km northeast of Bleaker, which records temperature, wind speed, and wind direction downloaded from the Global Summary of the Day (GSOD) hosted at the National Climate Data Center (Downloaded at <https://www7.ncdc.noaa.gov/CDO/cdoselect.cmd>). To detect differences in the median values of the seven-day running average across these three series of measurements, we analyzed the data using a Kruskal-Wallis *H*-test.

Field collection and laboratory analyses

***Poa flabellata* leaf collections, cellulose extraction, and measurements**

Poa flabellata plants were collected at the start of each month at each site from October 2015 through September 2016, from relatively uniform habitats that were undisturbed by grazing or tilling. Up to six *P. flabellata* plant tillers (leaves, stem, and roots) were collected near each of the four stations each month. All plant samples were stored in paper envelopes in a cool, dry location until frozen for eight days at the Falkland Islands Department of Agriculture. Plant samples were dried at 50 °C and pulverized using a Retsch ball mill at the University of Maine. Variation in environmental conditions during the growth of a leaf blade can lead to isotopic variations along the gradient of a single leaf as has been shown with $\delta^{18}\text{O}$ of cellulose (Helliker and Ehleringer 2002; Helliker and Ehleringer 2000); therefore, we collected and homogenized whole leaves. For each sample, we used 20 mg of leaf or root material for extraction and purification of α -cellulose, following an adapted procedure prepared by A.D. Beloso, Jr. for Dr. M. Berkelhammer (Version 1.0, March 2015) of Brendel et al., (2000). As an internal quality control, one leaf sample was selected for extraction and

purification of α -cellulose throughout the sample processing in batches of 10 to 12 samples.

Oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) stable isotope ratios of α -cellulose samples were measured at the University of Wyoming Stable Isotope Facility. Oxygen was analyzed with Temperature Conversion Elemental Analyser, Pyrolysis coupled to a Thermo Delta V IRMS; isotope values are expressed with regard to VSMOW in parts per thousand (per mil) (Craig 1961; Gonfiantini 1978). Quality control standard reference material includes USGS-42 and IAEA cellulose, and internal UWSIF α -cellulose. Carbon isotopes were analyzed using a Costech 4010 Elemental Analyzer coupled to a Thermo Delta Plus XP-IRMS; units are expressed with regard to VPDB in parts per thousand (per mil). Oxygen sample weights ranged from 0.206 to 0.289 mg and were loaded into silver capsules. Carbon sample weights ranged from 1.937 to 2.194 mg and were loaded into tin capsules. We measured % nitrogen (%N) of α -cellulose as a check for purity, after visual inspection for purity, and %C.

Statistical analysis

To test whether $\delta^{18}\text{O}_{\text{LEAF}}$ samples reflects the isotopic value of precipitation, we used simple linear regression of $\delta^{18}\text{O}_{\text{LEAF}}$ and precipitation samples to detect a significant correlation. Using simple linear regression, we tested for a relationship between $\delta^{13}\text{C}_{\text{LEAF}}$ and measures of temperature, relative humidity, and soil moisture using the package *Rmisc* in R version 3.1.0 (R Core Team 2013).

A two-way analysis of variance (ANOVA) was conducted to compare the main effects of season (summer vs. winter) and the four study locations on the carbon and oxygen stable isotopes of α -cellulose of *P. flabellata* leaves and roots grown in the

summer versus winter, followed by a post hoc test (Tukey's multiple comparison of means). P-values < 0.05 are considered significant. Descriptive and multivariate statistical analyses were calculated in SigmaPlot 12.5.

Results

Meteorological analyses

Environmental measurements

Across all sites, summer (DJF) daily average temperatures range from 3.48 °C – 15.6 °C (mean = 10.04 °C) and relative humidity ranged from 64.18 % - 98.07 % (mean = 81.05 %). Winter (JJA) daily average temperatures range from -1.78 °C – 7.56 °C (mean = 3.67 °C), and relative humidity ranges from 73.65 %-100 % (mean 94.29 %). Seasonal temperature (°C) and relative humidity (%) minimum and maximum ranges for individual study locations are found in Table 3.1. Between study locations, the daily average temperatures over the year ($F(3,44) = 0.316$, $p = 0.813$; Fig. 3.3A) and relative humidity were not significantly different ($F(3,44) = 0.674$, $p = 0.573$; Fig. 3.3B).

iButton and weather stations comparison

A test for normality (Shapiro-Wilk) failed ($P < 0.050$), and a non-parametric Kruskal-Wallis one way analysis of variance on ranks indicated there are significant differences ($p\text{-value} < 0.05$) in the median values among the three groups ($n = 365$, $H = 21.131$, $df = 2$, $P < 0.001$). A Tukey test of all pairwise multiple comparisons indicated that the median running average of the Bleaker iButton (5.78 °C) is significantly greater ($P < 0.05$) than Bleaker WSD (5.09 °C) and Mt Pleasant GSOD (5.65 °C; Fig. 3.8).

Wind

The wind rose (Fig. 3.9) shows that winds at Bleaker Island during winter primarily blew from the west and northwest. In winter (JJA), two spokes in the west and NNW direction comprise >30% of the total recorded 15-minute wind directions. In summer (DJF), three spokes in the west, WSW, and SW directions comprise >45% of all 15-minute wind directions. The wind rarely blew from the east, SE, or north. Examining winds from the west in winter, >10% of wind speeds recorded were between 5 and 10 m s⁻¹, and the frequency of strongest winds came from the NNE. In summer, >20% winds from the SW were between 5 and 10 m s⁻¹, and there was a higher frequency of 10-15 m s⁻¹ wind speeds than in winter. Over the year the study was conducted, seasonal wind variation deviated from the long-term average (1979-2015). Reanalysis data (ERA Interim; Fig. 3.10) indicated that the wind speeds during summer (DJF 2015 to 2016) were stronger over the Falkland Islands (5-6 m/s) and weaker during winter (JJA 2016).

Seasonal HYSPLIT air mass trajectory analyses

The daily back trajectory HYSPLIT analysis indicated that during the summer months, 89% of the air masses had originated ($n = 344$) W of the Falkland Islands. Approximately 11% of summer air masses originated south of the Falkland Islands near the Antarctic Peninsula. In winter, the air mass back trajectories ($n = 332$) were from the west, NW, and SW, while 21% of air masses had backward trajectories south of the Falkland Islands near the Antarctic Peninsula (Fig. 3.11).

Monthly composite precipitation, $\delta^{18}\text{O}$ and δD

Each study location had $n = 12$ samples over the year, except for Surf Bay ($n = 11$), as it is missing the September 2015 sample. Monthly composite $\delta^{18}\text{O}$ and δD

isotopes in precipitation ranged from -12.3 ‰ to -4.8 ‰, and from -86 ‰ to -23 ‰, respectively. Monthly composite precipitation at each location was used to construct a local meteoric water line using $\delta^{18}\text{O}$ and δD isotopes ($y = 7.571x + 5.527$; Fig. 3.4) from monthly composite precipitation ($n = 47$). The range for winter $\delta^{18}\text{O}$ and δD was from -8.6 ‰ to -6.6 ‰ and -61 ‰ to -40 ‰, respectively. Summer values of $\delta^{18}\text{O}$ and δD in precipitation ranged from -12.3 ‰ to -5.3 ‰ and -86 ‰ to -38 ‰, respectively, and fit within the range of historical isotopes in precipitation from the Falkland Islands (GNIP; Fig. 3.12). There was no significant difference between summer and winter $\delta^{18}\text{O}$ ($t = -1.73$, $df = 5.312$, $p = 0.139$) isotopes in precipitation. There was a significant difference between summer and winter δD isotopes ($t = -2.65$, $df = 5.559$, $p = 0.041$) in precipitation, and no significant difference among sites in $\delta^{18}\text{O}$ ($F(3,43) = 0.323$, $p = 0.809$) or δD isotopes ($F(3,43) = 0.361$, $p = 0.785$) in precipitation.

$\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of leaf and root α -cellulose

Leaf oxygen and carbon stable isotope values for α -cellulose extracted from leaf tissues (hereafter abbreviated as $\delta^{18}\text{O}_{\text{leaf}}$ and $\delta^{13}\text{C}_{\text{leaf}}$) passed tests for normality (Shapiro-Wilk; $p = 0.173$ and $p = 0.385$, respectively) and equal variance (Fisher's F test; $p = 0.865$ and $p = 0.196$, respectively). Thus, a two-way analysis of variance was conducted on the influence of independent variables (season and study location) on both $\delta^{18}\text{O}_{\text{leaf}}$ and $\delta^{13}\text{C}_{\text{leaf}}$. Season included two levels (summer and winter) and study location consisted of four levels (Bleaker Island, Cape Dolphin, Surf Bay, and West Point Island).

Analysis of $\delta^{18}\text{O}_{\text{leaf}}$ had an annual mean of $28.9 \text{ ‰} \pm 1.3 \text{ SD}$, and ranged from 26.3 ‰ to 31.8 ‰ (difference of 5.4 ‰; Table 3.2). The main effect for season yielded an F ratio of $F_{(1, 16)} = 183.2$, $p < 0.001$, indicating that the effect for season is significant for

$\delta^{18}\text{O}_{\text{leaf}}$, with a 2.6 ‰ difference of means between summer (mean = 30.1 ± 0.8 SD) and winter (mean = 27.5 ± 0.6 SD; Fig. 3.5A; Table 3.2). The main effect for study location yielded an F ratio of $F_{(3, 16)} = 4.8$, $p = 0.014$, indicating a significant difference in $\delta^{18}\text{O}_{\text{leaf}}$ between study locations. Pairwise multiple comparison (Tukey's post hoc test) of study locations indicated that Surf Bay is significantly more depleted in $^{18}\text{O}_{\text{leaf}}$ than Cape Dolphin ($p = 0.016$), Bleaker Island ($p = 0.029$); Fig. 5B). The interaction effect was not significant ($p = 0.552$).

The annual mean $\delta^{13}\text{C}_{\text{leaf}}$ value was $-25.4 \text{ ‰} \pm 1.31$ SD; The annual mean of $\delta^{13}\text{C}_{\text{leaf}}$ ranged from -30.4 ‰ to -21.9 ‰ (range = 8.4 ‰ ; Table 2). For $\delta^{13}\text{C}_{\text{leaf}}$, only the effect for season was statistically significant, and not the study location factor or the interaction. The main effect for season yielded an F ratio of $F_{(1, 16)} = 40.8$, $p < 0.001$, indicating that the effect for season is significant, summer (mean = $-24.2 \text{ ‰} \pm 1.05$ SD) and winter (mean = $-26.8 \text{ ‰} \pm 1.3$ SD; Fig. 5C; Table 2). The main effect for study location was not statistically significant ($p = 0.861$; Fig. 5D). The interaction effect was not significant ($p = 0.638$).

The mean $\delta^{13}\text{C}$ in root α -cellulose (hereafter abbreviated as $\delta^{13}\text{C}_{\text{root}}$) samples for summer months ($n = 18$) is $-25.3 \text{ ‰} \pm 1.27$ SD, and a mean of $-26.6 \text{ ‰} \pm 1.38$ SD in winter months (see Table 2 for ranges). After $\delta^{13}\text{C}_{\text{root}}$ data passed tests for normality (Shapiro-Wilk test; $p = 0.085$), but not equal variance ($p < 0.05$), the two-way ANOVA indicated that for $\delta^{13}\text{C}_{\text{root}}$, the effects for season ($p = 0.201$) and study location ($p = 0.521$) were not statistically significant. The interaction effect was not significant ($p = 0.886$).

The mean $\delta^{18}\text{O}$ in root α -cellulose (hereafter abbreviated as $\delta^{18}\text{O}_{\text{root}}$) samples for summer months ($n = 18$) is $28.8 \text{ ‰} \pm 1.04$ SD, and a mean of $28.3 \text{ ‰} \pm 0.5$ SD for winter

months (see Table 2 for ranges). The $\delta^{18}\text{O}_{\text{root}}$ data passed tests for normality (Shapiro-Wilk test; $p = 0.483$) and equal variance (Fisher's F test; $p = 0.897$), the two-way ANOVA indicated that for $\delta^{18}\text{O}_{\text{root}}$, the study location effect was statistically significant, whereas season was not. The difference in the mean values among the season factor is statistically significant ($F_{(1, 8)} = 5.4$, $p = 0.049$). The main effect for study location was statistically significant ($F_{(2, 8)} = 8.7$, $p = 0.010$). Pairwise multiple comparison (Tukey's post hoc test) of study locations indicated that Cape Dolphin is significantly greater than Bleaker Island ($p = 0.012$), and West Point Island ($p = 0.049$). The interaction effect was not significant ($p = 0.397$).

$\delta^{13}\text{C}_{\text{leaf}}$ and $\delta^{18}\text{O}_{\text{leaf}}$ – temperature, humidity, precipitation

Across all sites, measurements of $\delta^{13}\text{C}_{\text{leaf}}$ and $\delta^{18}\text{O}_{\text{leaf}}$ positively correlated with monthly average temperature (Pearson's $r = 0.82$ and $r = 0.89$, respectively) and negatively correlated with relative humidity (Pearson's $r = -0.76$ and $r = -0.88$, respectively; Table 3.3; Fig. 3.6A-D). Measurements of $\delta^{18}\text{O}$ in precipitation had a weak negative correlation with $\delta^{18}\text{O}_{\text{leaf}}$ (Pearson's $r = -0.20$) and $\delta^{18}\text{O}_{\text{root}}$ (Pearson's $r = -0.30$) across all sites (Table 3.3). Further analysis indicated that there was a strong positive correlation between $\delta^{18}\text{O}_{\text{leaf}}$ and $\delta^{13}\text{C}_{\text{leaf}}$ (Pearson's $r = 0.88$ Fig. 3.7) and segregation between winter and summer values.

Discussion

Significant inter-seasonal differences in $\delta^{13}\text{C}_{\text{leaf}}$ and $\delta^{18}\text{O}_{\text{leaf}}$ suggest that *P. flabellata* may be used as a proxy for environmental change. The negative correlation between $\delta^{13}\text{C}_{\text{leaf}}$ and vapor pressure deficit suggests higher relative humidity increases stomatal

conductance and lower relative humidity causes a large leaf-to-air vapor pressure deficit (Ferrio et al., 2002). The observed positive correlation between $\delta^{13}\text{C}_{\text{leaf}}$ and temperature suggests higher temperatures led to an increased assimilation rate and reduced discrimination against $\delta^{13}\text{C}$ as shown in other vascular plant studies (Ferrio et al., 2002; Ménot & Burns 2001). $\delta^{13}\text{C}_{\text{leaf}}$ is driven by changes in the ratio of internal leaf partial pressure of CO_2 to that of ambient air, and can be explained by a greater influence by either stomatal conductance or increased photosynthetic capacity (Scheidegger et al., 2000). As the internal partial pressure of CO_2 decreases, the $\delta^{13}\text{C}_{\text{LEAF}}$ increases (Farquhar et al., 1982) and plant stomata close in response to arid conditions (Williams and Ehleringer 1996).

The $\delta^{18}\text{O}_{\text{leaf}}$ is influenced by soil water, leaf water enrichment from transpiration, and biochemical fractionations. Leaf water enrichment due to transpiration, which is reflected in $\delta^{18}\text{O}_{\text{leaf}}$ (DeNiro and Epstein 1979; Sternberg 1989; Yakir 1992; Farquhar et al., 1998; Roden and Ehleringer 1999a), depends on relative humidity (Helliker and Ehleringer 2002). Diffusion limitation by stomatal resistance is primarily driven by relative humidity (White et al., 1994). The $\delta^{18}\text{O}_{\text{leaf}}$ and relative humidity were negatively correlated, which is consistent with other studies showing that low relative humidity increases $\delta^{18}\text{O}_{\text{leaf}}$ (Barbour & Farquhar 2000; Helliker & Ehleringer 2002).

Previous work on leaf water and cellulose isotopes in *Eucalyptus* leaves demonstrated that the atmospheric-leaf vapor conditions are a strong predictor of $\delta^{18}\text{O}_{\text{leaf}}$ (Munksgaard et al., 2016), and can be used as a proxy for atmospheric humidity conditions during leaf growth. Our work supports this finding, and expands the use of such paleoclimate proxies to tussock grasslands forming peat, which opens up new possibilities for reconstructing

paleoclimates across the South Atlantic and beyond, in other tussock grasslands. The relationship between relative humidity and $\delta^{18}\text{O}_{\text{leaf}}$ deteriorates at relative humidity > 90% (Helliker and Ehleringer 2002) and < 21% (Munksgaard et al., 2016). At the higher relative humidity range, the $\delta^{18}\text{O}_{\text{leaf}}$ is more of a reflection of source water, while the $\delta^{18}\text{O}_{\text{leaf}}$ at low humidity differed greatly from source waters because of stomatal closure.

The positive correlation between $\delta^{13}\text{C}_{\text{leaf}}$ and $\delta^{18}\text{O}_{\text{leaf}}$ (Pearson's $r = 0.88$) suggests that stomatal conductance is the driving force acting on these two proxies, which is a likely scenario when water is not limiting (Scheidegger et al., 2000; Sauer et al. 1997). Measurements of relative humidity allowed us to determine whether photosynthetic capacity or stomatal conductance was more influential, as possible causes of a change in partial pressure of CO_2 within the leaf. In our study, stomatal conductance is likely driving both $\delta^{13}\text{C}_{\text{leaf}}$ and $\delta^{18}\text{O}_{\text{leaf}}$ due to relative humidity. This pattern fits well with the Barbour and Farquhar (2000) model.

In the Falkland Islands, precipitation amount is not highly seasonal, but tends to vary the most in the summer (Fig. 3.12; data from Jones et al., 2013). Over the year of our study, summer $\delta^{18}\text{O}$ in precipitation varied more than winter $\delta^{18}\text{O}$; however, our data indicate that summer $\delta^{18}\text{O}$ in precipitation was more depleted. This is supported by the wind rose data from Bleaker Island, which indicated that most wind came from the SW (Fig. 3.9). In the winter, precipitation was more enriched in $\delta^{18}\text{O}$, and most of the wind came from the west and NW where $\delta^{18}\text{O}$ in precipitation should be enriched because precipitation originating from the north (equatorward) is more enriched in $\delta^{18}\text{O}$, than polar precipitation (Fig. 3.10). If the relationship between root cellulose reflected isotopes in precipitation, and the latitudinal origin of storm tracks, then the negative correlation

between $\delta^{18}\text{O}$ and $\delta^{18}\text{O}_{\text{root}}$ found at Cape Dolphin would support the evidence found in the precipitation and wind data. The pattern found at Bleaker Island is less clear, and warrants further investigation.

The observed weak negative correlations between measurements of $\delta^{18}\text{O}$ in precipitation and $\delta^{18}\text{O}_{\text{leaf}}$ (Table 3.3) indicated that leaves do not reflect the source of precipitation. However, the observed relationship between $\delta^{18}\text{O}$ in precipitation and $\delta^{18}\text{O}_{\text{root}}$ appeared to be less clear in part due to low sample number from only two study locations (Bleaker Island and Cape Dolphin). At Bleaker Island, there was a weak positive correlation between $\delta^{18}\text{O}$ in precipitation and $\delta^{18}\text{O}_{\text{root}}$, while Cape Dolphin had a strong negative correlation. At Cape Dolphin, enrichment of the heavy isotope $^{18}\text{O}_{\text{root}}$ occurred in summer when $\delta^{18}\text{O}$ precipitation was lower. In contrast, $\delta^{18}\text{O}_{\text{root}}$ was lower during the winter months when $\delta^{18}\text{O}$ of precipitation was higher at Cape Dolphin. Despite the strong relationship between $\delta^{18}\text{O}$ precipitation and $\delta^{18}\text{O}_{\text{root}}$ at Cape Dolphin, we propose that *P. flabellata* ‘bogs’ may not be ombrotrophic, and may potentially source water from fog, sea-spray, groundwater, or a mix. However, the relationship found at Cape Dolphin warrants further analysis of $\delta^{18}\text{O}_{\text{root}}$ and source waters.

An alternative explanation for a lack of correlation is that our precipitation sampling density was not sufficient to establish a relationship between $\delta^{18}\text{O}_{\text{leaf}}$ and precipitation $\delta^{18}\text{O}$. However, the growth rate of *P. flabellata* leaves may not be in sync with shorter precipitation sampling intervals (less than monthly composite precipitation). Examination of leaf waters post precipitation events would improve our understanding of $\delta^{18}\text{O}_{\text{leaf}}$. Amesbury et al. (2015) found evidence of a similar relationship between $\delta^{18}\text{O}_{\text{root}}$ and $\delta^{18}\text{O}$ in precipitation and proposed that shoots/leaves and roots in *Empodisma* peatlands

in New Zealand. Proposed mechanisms for the negative relationship between source water and cellulose assume enrichment of the heavy isotope in summer precipitation while leaves are water stressed and roots are saturated.

Further work needs to be done to understand the relationship between $\delta^{18}\text{O}_{\text{root}}$, $\delta^{18}\text{O}$ of precipitation, and internal root and leaf waters extracted using cryogenic vacuum distillation. Sources of potential water are also an interesting avenue of future research, especially considering anecdotes of local differences in the frequency of fog, which may be an important source of water for *P. flabellata*. Tussock grasslands most likely increase local water by two physical mechanisms: through low evaporation from the tussock itself via protection from wind, and via storage through fog interception by the leaves (Davie et al., 2006).

iButtons indicated that there was not a difference in temperature or humidity across all the sites; however, the Bleaker iButton indicated warmer temperatures than both the Bleaker WSD and Mt Pleasant GSOD (Fig. 3.8). iButton mean annual temperatures (Table 3.1) were similar to the mean annual temperature long term/historical MPA observations ($^{\circ}\text{C}$), 6.5°C and similar to MPA GSOD. The Bleaker Island iButton temperatures were correlated with Bleaker WSD and Mount Pleasant. Weekly running averages generally follow each other during the year. Cape Dolphin is the most equatorward site, but had the lowest mean annual and mean summer temperatures. West Point Island is at a similar latitude as Cape Dolphin (Table 3.1), yet, had the warmest mean annual temperature of the four study sites, and the warmest mean winter and summer temperatures. West Point Island also had the largest range in % RH and the lowest % RH.

Among the four study sites, Cape Dolphin had the highest RH in summer and winter (Table 3.1).

Conclusions

Coastal grasses are an important resource of inter-seasonal hydrological information in the South Atlantic region where paleoclimate inferences derived from tree ring records are lacking, and can be considered analogous to tree ring reconstructions (Helliker and Ehleringer 2002). The observed relationships between temperature and moisture, and $\delta^{13}\text{C}_{\text{LEAF}}$ and $\delta^{18}\text{O}_{\text{LEAF}}$, along with the abundance of macrofossil *P. flabellata* leaves in peat deposits spanning the Holocene, supports the use of coastal grasslands formed by *P. flabellata* in the Falkland Islands as a paleoclimate proxy in the South Atlantic region. On Beauchene Island, Lewis Smith and Clymo (1984) described the *P. flabellata* stands as “extraordinary peat forming communities” in the South Atlantic, storing large amounts of carbon. With high accumulation rates, *P. flabellata* peat has the potential as a proxy unique to high-resolution (sub-decadal) *P. flabellata* cores. A loss of these communities and peat also means a loss of irreplaceable peat and past environmental information, especially during a time when there is a need for more records to understand past climate. The use of carbon and oxygen stable isotopes in alpha cellulose demonstrates that geochemical studies and climate reconstructions using *P. flabellata* is a promising avenue for independent paleoclimate proxies in a region experiencing rapid change. Future work will decipher whether $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of cellulose from *P. flabellata* macrofossils correspond with other regional proxies for changes in atmospheric temperature and relative humidity during the Holocene.

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Table 3.1. Summary of sites. Elevation (m) above sea level, geographic coordinates, mean annual and seasonal (summer and winter) temperature (°C) and relative humidity (%) measured with iButton data loggers every two hours.

Site information			Temperature (C) mean (min-max)			Relative humidity (%)		
Site (elevation)	Lat (S)	Long (W)	Mean annual	Mean summer	Mean winter	Mean annual	Mean summer	Mean winter
Surf Bay (4 m)	-51.7012	-57.7858	6.32	9.94 (4.30-15.30)	3.30 (-1.33-6.51)	87.97	80.47 (64.87-95.17)	94.37 (79.07-100)
West Point Is. (30 m)	-51.3505	-60.6875	6.96	10.55 (5.26-15.60)	4.54 (-0.57-7.56)	86.99	80.09 (64.17-98.07)	91.77 (73.65-100)
Cape Dolphin (33 m)	-51.3420	-58.8425	5.95	9.52 (3.48-13.81)	3.20 (-1.78-6.31)	90.14	82.79 (69.94-96.27)	95.70 (84.51-100)
Bleaker Is. (6 m)	-52.2065	-58.8508	6.63	10.16 (4.50-14.93)	3.63 (-0.92-6.31)	88.46	80.82 (66.32-94.44)	95.33 (79.83-100)

Table 3.2. Summary of mean summer and winter isotope analysis of α -cellulose in leaves and roots. All values are in standard per mil notation (‰) with \pm SD.

α -cellulose	Min	Max	Range	Summer	n	Winter	n	Difference of means
$\delta^{13}\text{C}_{\text{leaf}}$	-30.41	-21.95	8.47	-24.27 ± 1.05	39	-26.80 ± 1.39	36	2.55
$\delta^{13}\text{C}_{\text{root}}$	-29.83	-23.45	6.38	-25.35 ± 1.27	18	-26.67 ± 1.38	18	1.32
$\delta^{18}\text{O}_{\text{leaf}}$	26.38	31.84	5.45	30.16 ± 0.83	39	27.53 ± 0.62	36	2.63
$\delta^{18}\text{O}_{\text{root}}$	27.48	31.02	3.54	28.88 ± 1.04	18	28.39 ± 0.59	18	0.28

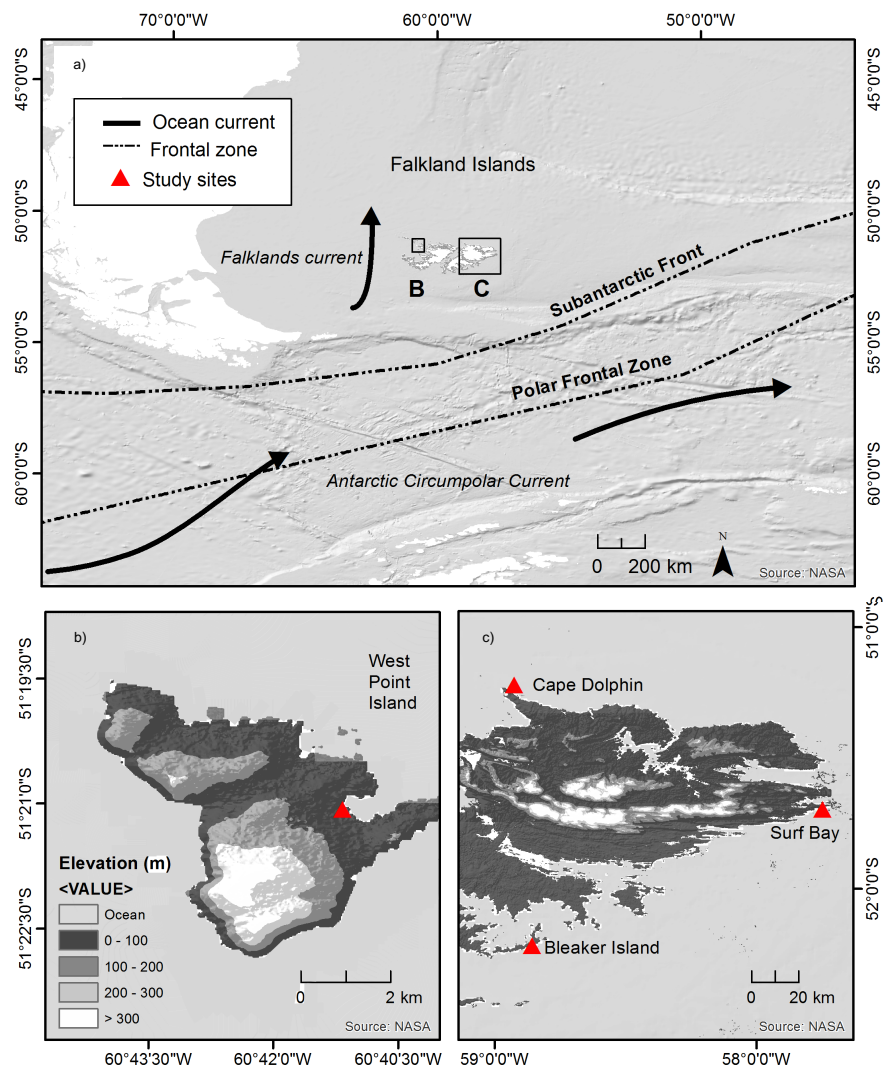


Figure 3.1. Geographic overview of study region. **a)** Map of the Falkland Islands and western South Atlantic Ocean with ocean currents (black arrows) and frontal zones (dashed lines); Locations of four study locations where samples were collected and measurements made are in **b)** West Point Island and **c)** Bleaker Island, Cape Dolphin, and Surf Bay.

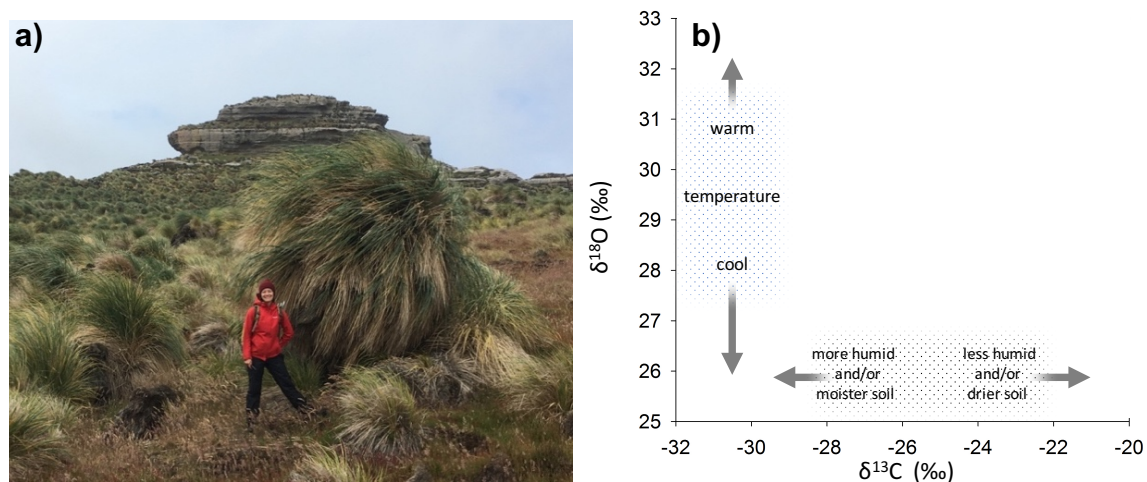


Figure 3.2. Study organism, tussock grass, and conceptual relationship of stable isotopes with temperature and humidity. **a)** A single large *Poa flabellata* bog made up of a mix of dead and living grass tillers growing on top of a pedestal of decomposing *P. flabellata* at Cape Meredith, Falkland Islands. D. Groff pictured is approximately 1.65-m tall standing next to a bog remnant of older *P. flabellata* grasslands. **b)** Conceptual figure of the relationship between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of leaf cellulose and air temperature, and humidity and/or soil moisture.

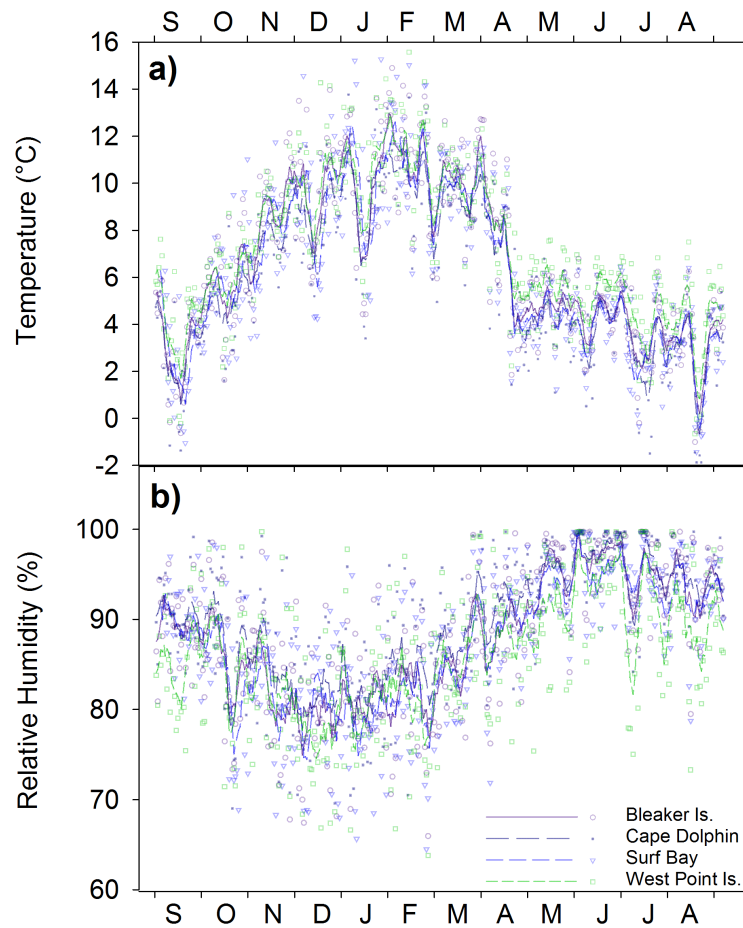


Figure 3.3. Annual environmental measurements in the Falkland Islands. **a)** Daily average temperature (°C) and **b)** relative humidity (%) from September 2015-August 2016 at the four study locations calculated from 2 hour measurements. Seven day running averages of daily average temperature and relative humidity are indicated by the lines for each study location.

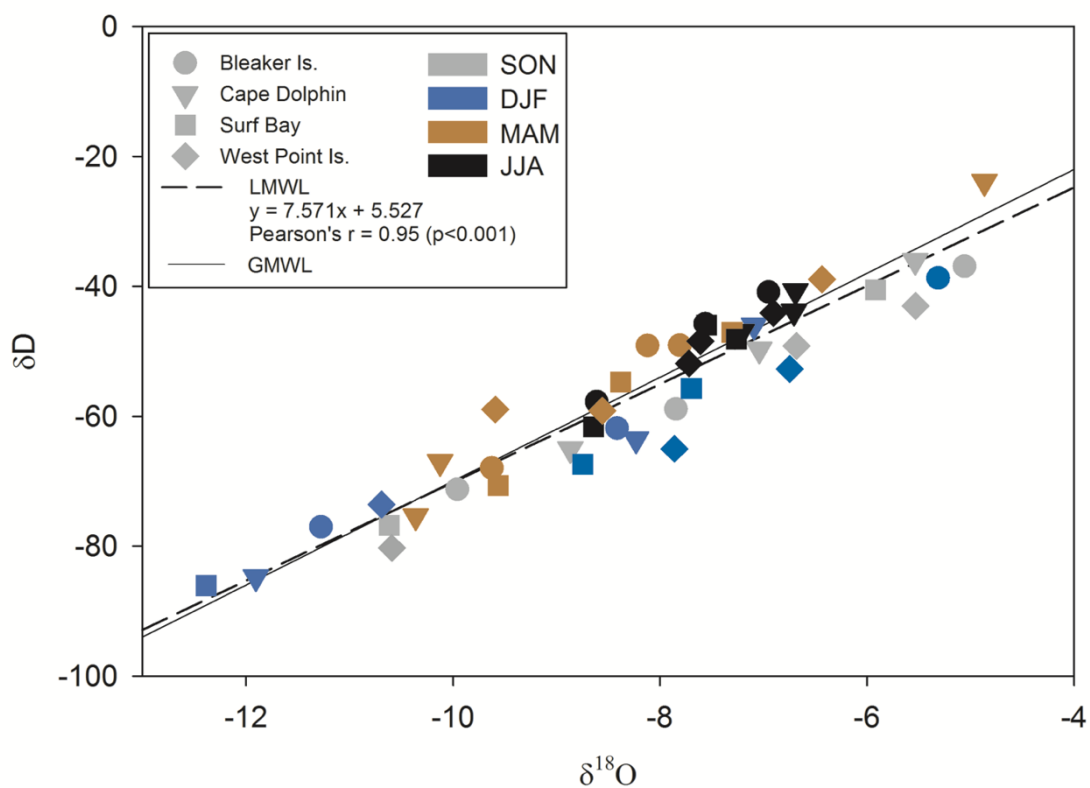


Figure 3.4. $\delta^{18}\text{O}$ and δD (‰) isotopes in precipitation for four study locations (symbol shape) during four seasons (symbol color). The constructed local meteoric water line (LMWL; $y = 7.571x + 5.527$) is shown as a dashed line and global meteoric water line (GMWL: $\delta\text{D} = 8.0 \delta^{18}\text{O} + 10$) is a solid line.

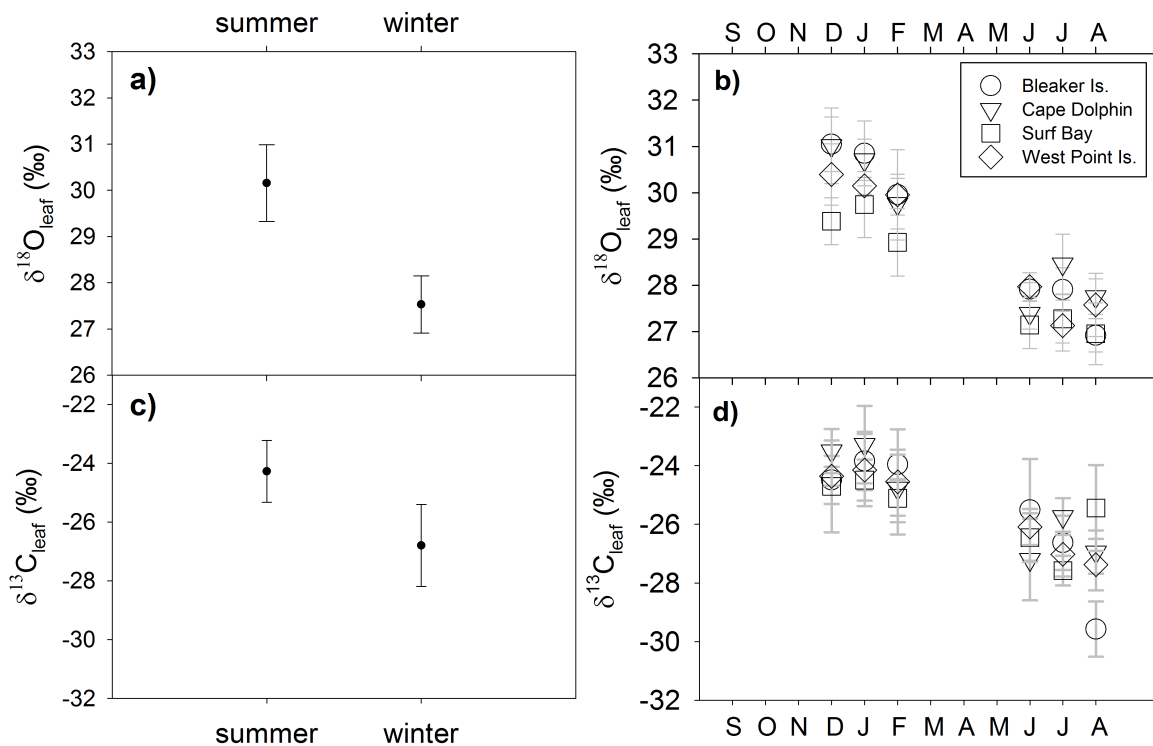


Figure 3.5. Oxygen and carbon stable isotopes of *Poa flabellata*. **a)** $\delta^{18}\text{O}_{\text{leaf}}$ (‰) at four study locations over one year and, **b)** comparison (mean \pm 1 SD) between summer (DJF) and winter (JJA); **c)** $\delta^{13}\text{C}_{\text{leaf}}$ (‰) at four study locations; and **d)** comparison (mean \pm 1 SD) between summer and winter.

Table 3.3. Correlation of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in leaf and root cellulose between $\delta^{18}\text{O}$ in precipitation, monthly average temperature, and humidity by site. Bold values indicate correlations >0.600 Pearson's r .

		$\delta^{18}\text{O}$ Precip	Temp	Humidity
$\delta^{18}\text{O}_{\text{leaf}}$	Bleaker	-0.058	0.947	-0.939
	Cape Dolphin	-0.357	0.877	-0.979
	Surf Bay	-0.378	0.952	-0.977
	West Point Is.	-0.330	0.977	-0.900
$\delta^{18}\text{O}_{\text{root}}$	Bleaker	0.222	0.219	-0.116
	Cape Dolphin	-0.868	0.701	-0.694
	Surf Bay	NA	NA	NA
	West Point Is.	NA	NA	NA
$\delta^{13}\text{C}_{\text{leaf}}$	Bleaker	0.843	0.843	-0.688
	Cape Dolphin	0.849	0.849	-0.951
	Surf Bay	0.780	0.780	-0.819
	West Point Is.	0.977	0.977	-0.816
$\delta^{13}\text{C}_{\text{root}}$	Bleaker	0.561	0.561	-0.273
	Cape Dolphin	0.778	0.778	-0.718
	Surf Bay	NA	NA	NA
	West Point Is.	NA	NA	NA

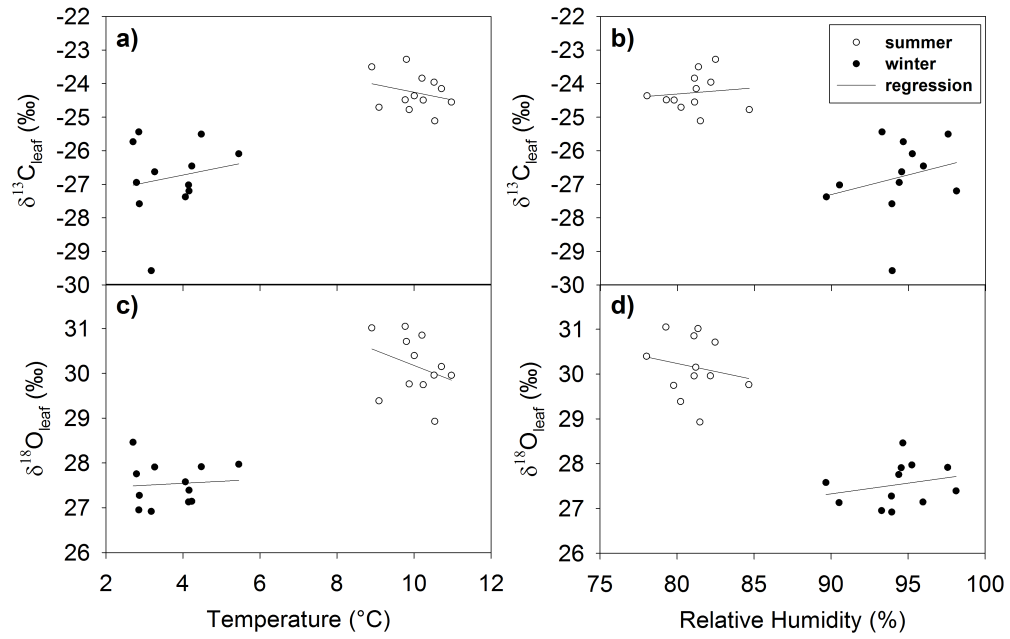


Figure 3.6. Evaluation of relationship between carbon and oxygen stable isotopes with temperature and relative humidity. Relationship between $\delta^{13}\text{C}_{\text{leaf}}$, **a)** temperature (Pearson's $r = 0.82$), and **b)** humidity (Pearson's $r = -0.76$); Relationship between $\delta^{18}\text{O}_{\text{leaf}}$, **c)** temperature (Pearson's $r = 0.89$), and **d)** humidity (Pearson's $r = -0.88$) across all sites; Lines are linear regression.

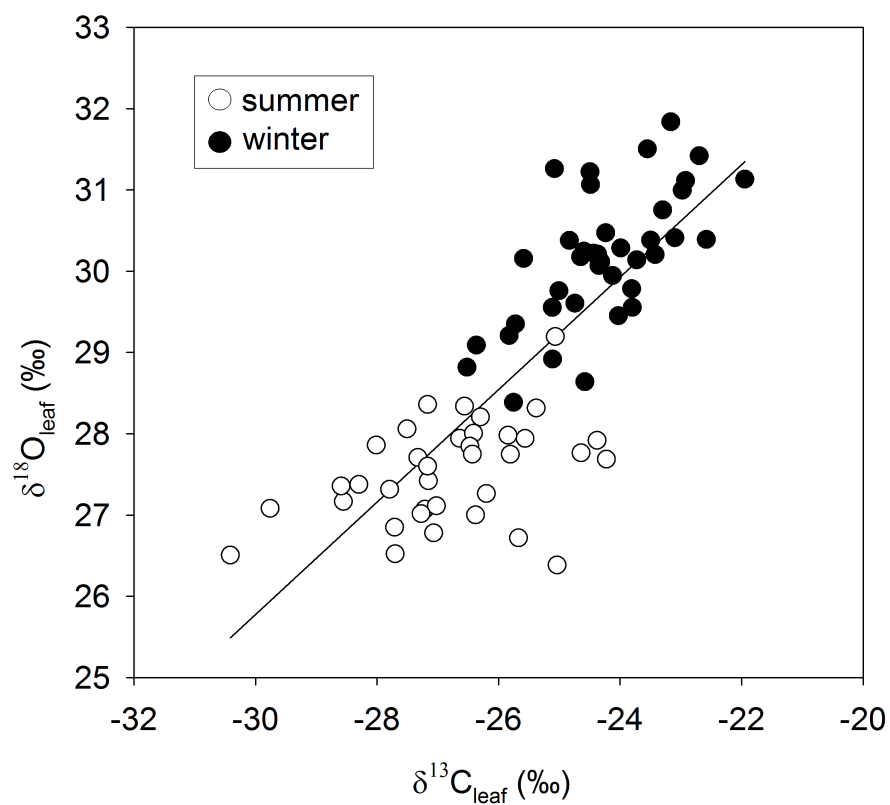


Figure 3.7. The significant positive relationship between $\delta^{13}\text{C}_{\text{leaf}}$ and $\delta^{18}\text{O}_{\text{leaf}}$ (correlation coefficient, r value = 0.88). Open circles indicate samples collected in summer and solid circles indicate winter.

Supporting Information

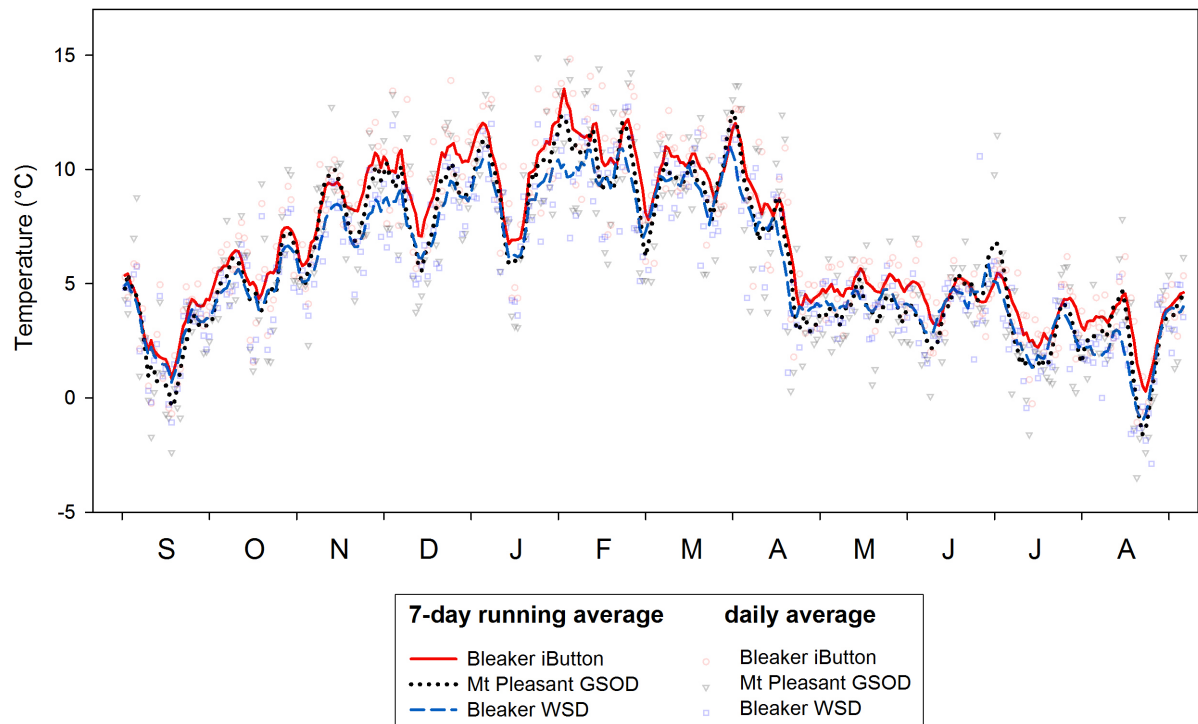


Figure 3.8. Comparison of ambient temperature measurements measured by various devices from Bleaker Island and Mount Pleasant, East Falkland Island between September 1, 2015 – August 31, 2016. Daily averages were computed using 2-hour measurements with the iButton (red circle symbol), hourly measurements for the Mt. Pleasant Global Summary of the Day (GSOD; black triangle symbol), and 15-minute measurements at the Bleaker Island weather station (WSD; blue square symbol). A seven-day running average (line) was calculated from the daily averages for each dataset. Tails of each running average were computed by appending in SigmaPlot (v. 12.5).

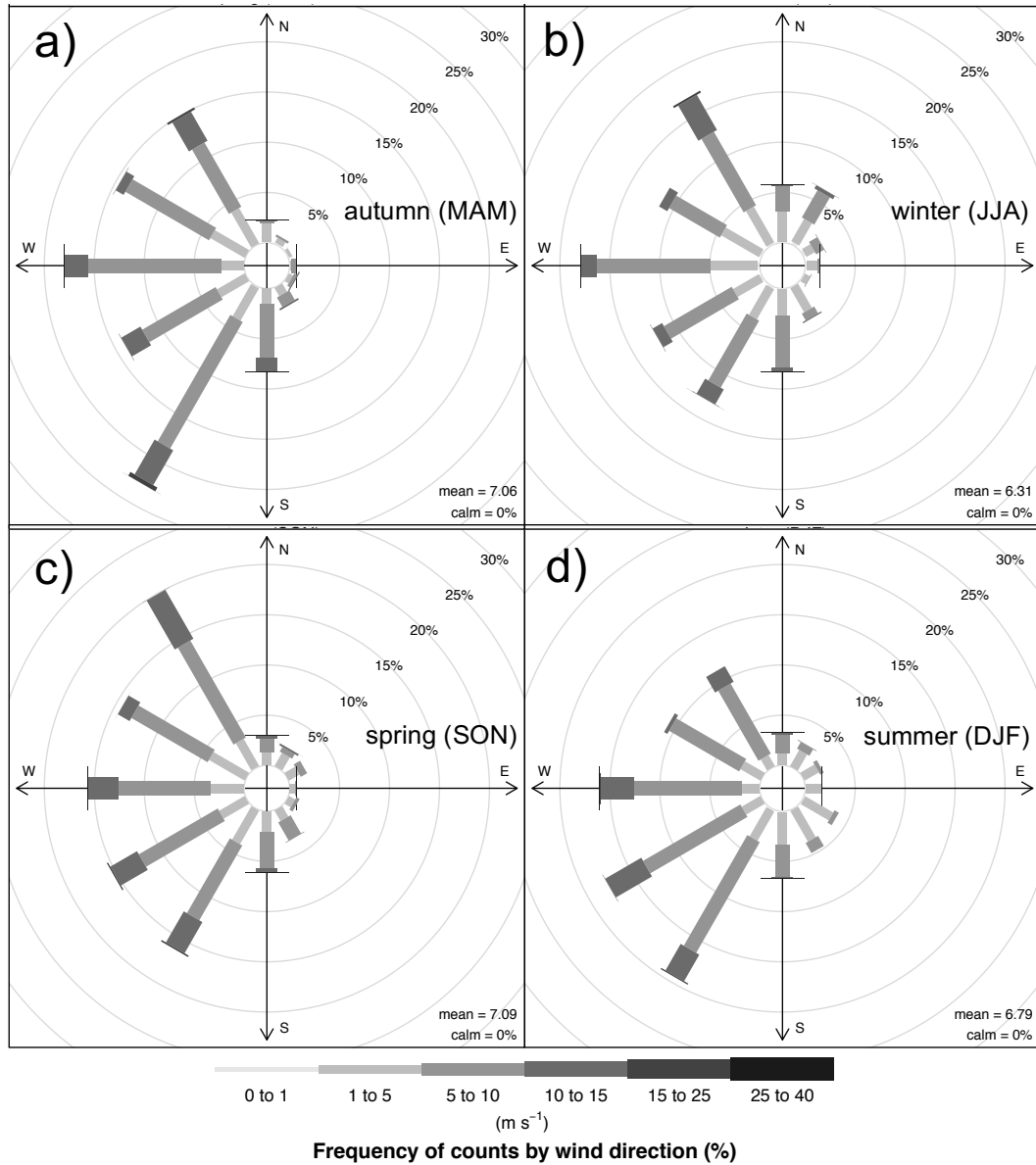


Figure 3.9. Distribution of wind speed (m s^{-1}) and the frequency of counts by wind direction (%) at Bleaker Island across four seasons. Wind data was collected in **a)** autumn (MAM), **b)** winter (JJA), **c)** spring (SON), and **d)** summer (DJF), along with mean seasonal wind speed in m/s and % calm. Measurements logged at 15-minute intervals using Bleaker Island weather station (MetPak II) from September 2015-August 2016. Wind rose was constructed using the package *openair* in R version 3.1.0.

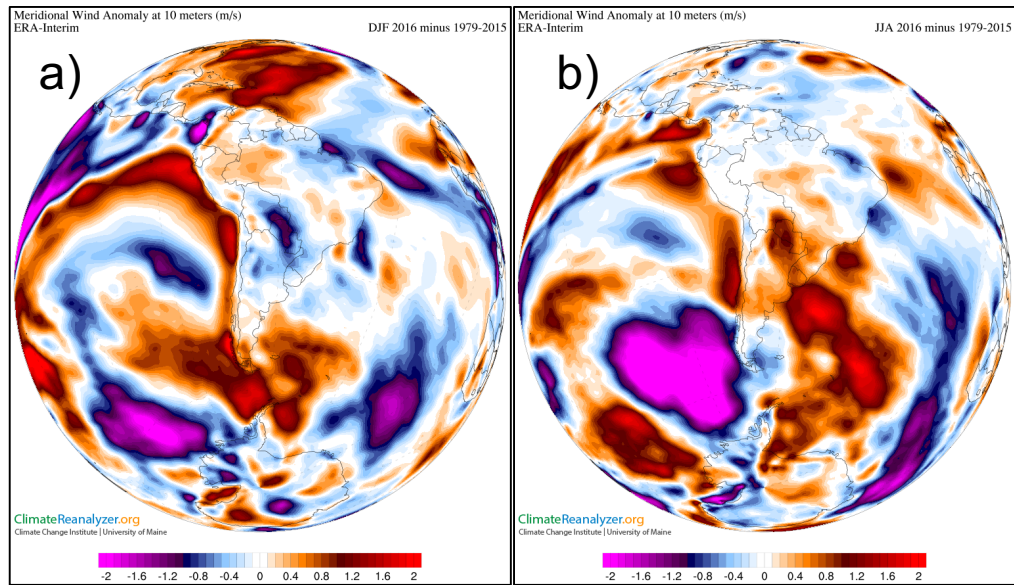


Figure 3.10. ERA-Interim reanalysis [3rd generation] data showing difference plots of meridional wind anomaly (2016 minus the 1979-2015) at 10 m (m/s). Panel **a)** illustrates the austral summer (DJF) and **b)** is the austral winter (JJA). Contour plots from Climate Reanalyzer (<http://cci-reanalyzer.org>), Climate Change Institute, University of Maine, USA.

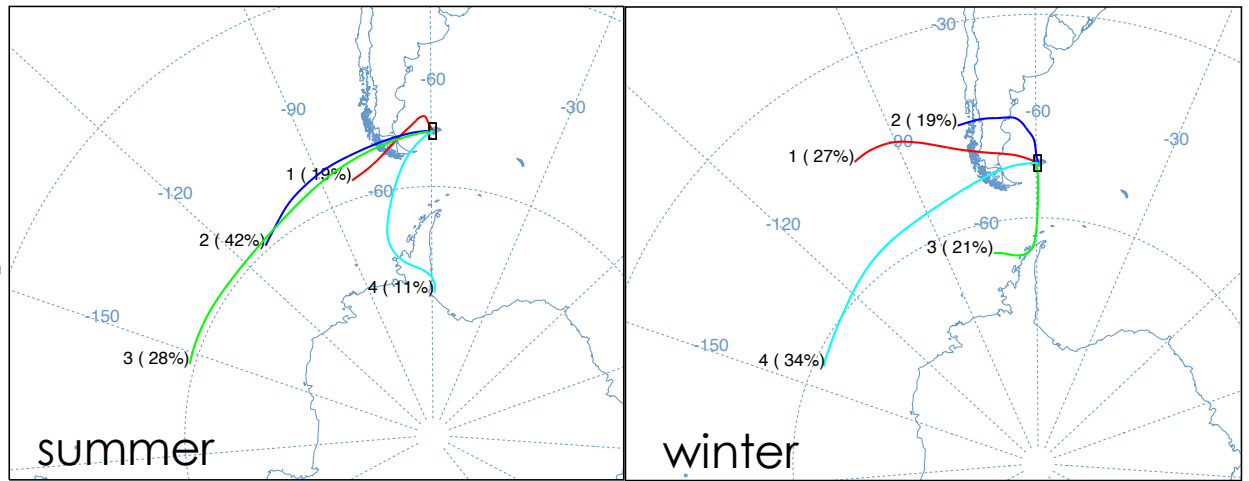


Figure 3.11. HYSPLIT seasonal cluster means of daily 5-day back trajectories from summer 2016 and winter 2015-16 at -51.79°S , -59.52°W with percentage of daily trajectories in each cluster and number of daily trajectories.

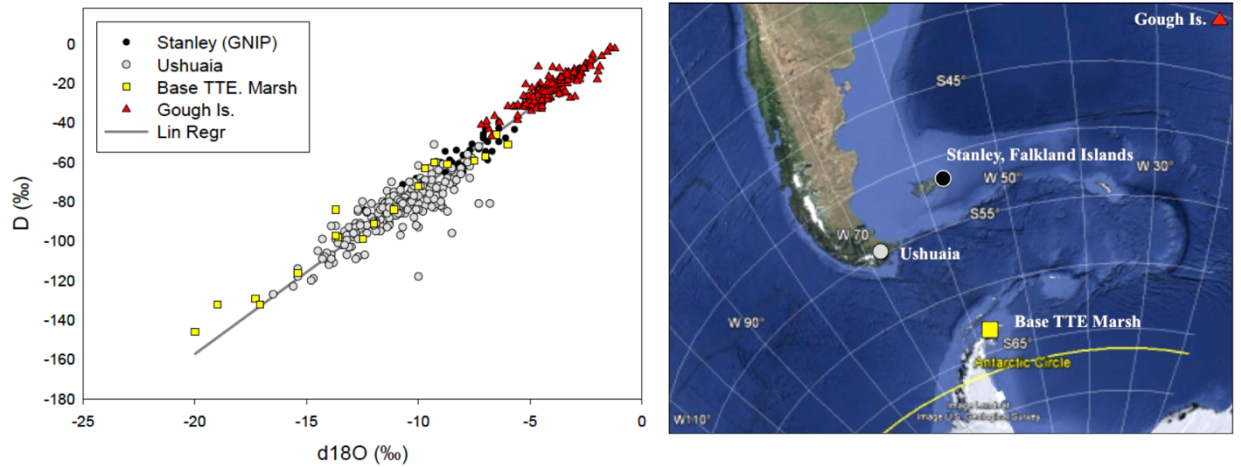


Figure 3.12. Regional variation of $\delta^{18}\text{O}$ and in δD in precipitation align along a meteoric water line illustrating the variability in precipitation isotopes and sources in Stanley, Falkland Islands. Corresponding locations of GNIP sites and potential sources of precipitation origin throughout the region over 30 years of data collection (Source: data downloaded from GNIP through the IAEA).

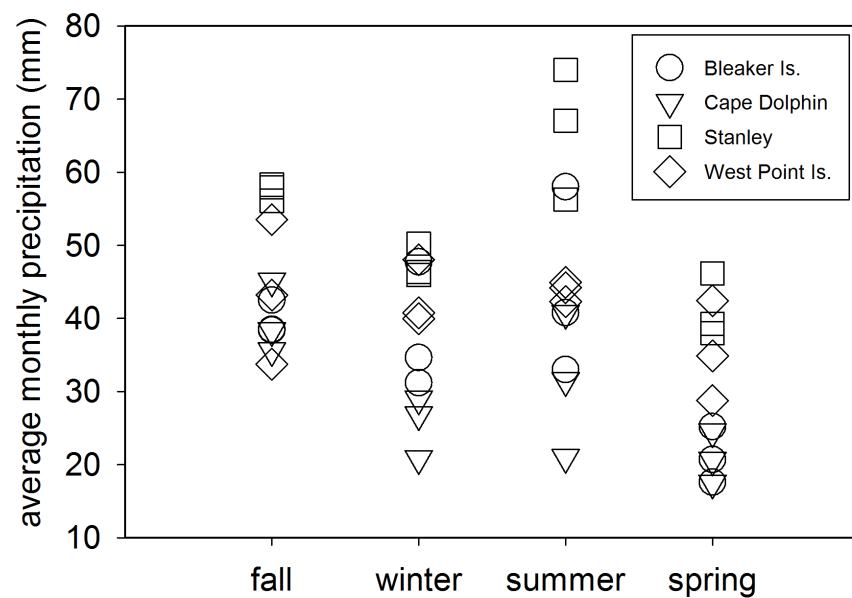


Figure 3.13. Seasonal precipitation amount from weighted monthly averages (mm) for historical climate records in the Falkland Islands from Jones et al., 2013 report for the United Kingdom Falkland Islands Trust (UKFIT; data from J. McAdam).

CHAPTER 4

SOIL AND PLANT COMMUNITY CHARACTERISTICS OF TUSSAC GRASSLANDS: AN ASSESSMENT OF GRAZING IN THE FALKLAND ISLANDS

Introduction

Coastal grasslands form a critical breeding habitat for many species of seabirds on several sub-Antarctic islands in the Southern Oceans, but have been significantly reduced in recent decades due to land use change, particularly from sheep and other livestock grazing. Endemic to Isla de los Estados, Tierra del Fuego, Gough Island, and the Falkland Islands, “tussac grass” (*Poa flabellata*, Hook. f.) forms coastal grasslands where some of the world’s most important seabird rookeries breed and take refuge from the persistent westerly winds in tussac grass. With an estimated loss of 80% of tussac grass habitat nationwide, and declines in seabird populations (Kerr, 1997; Strange, 1987; Woods & Woods, 2006; Crofts & Stanworth, 2017), understanding the importance of marine-derived nutrients to tussac grasslands is critical for land use management efforts and to the conservation of vegetation and wildlife alike. There is a long history of over-exploitation dating back to sealing and whaling in the 17th century, and the introduction of livestock grazing in the 18th century (Wilson, 2016). The combination of no native herbivores (aside from the upland goose, *Chloephaga picta*) in the Falkland Islands and the high palatability of tussac grass to livestock has led to the degradation of coastal tussac grasslands. Tussac grass is important for storing carbon both aboveground in

amounts comparable to temperate and boreal forests (Smith & Karlsson, 2017), and belowground as deep peatlands (Smith & Clymo 1984), which also aid in preventing property loss via coastal erosion.

Tussac grasses exhibit several characteristics of a species adapted for high nutrient ecosystems. First, roots are abundant within the pedestals of mature ungrazed tussac bogs, and the skirt of leaves within and around the pedestal accumulate rapidly to eventually form peat (Woods, 1970). Second, the stems of tussac grasses are tender, starchy, and palatable, all of which suggest that the tussac grasses do not invest energy into developing dense stems or leaves and are adapted to high nutrient ecosystems. A third indicator that tussac grasslands are adapted to high nutrient input is the clear ability to outcompete other plant species for light, which is evident in mature tussac grasslands that are nearly pure stands of tussac grass.

Comprehensive action plans are in place to protect threatened tussac grasslands in the Falkland Islands (Otley et al., 2008). Past efforts to restore degraded tussac grasslands include native seed planting and mitigating soil erosion using locally sourced materials (Smith et al., 2017). Further conservation efforts resulted in several designated landholdings as National Nature Reserves (NNRs), and several private landholdings exclude grazing livestock in tussac grasslands or limit grazing to a short winter period (K. Ross, personal communication). These efforts have yielded mixed results to date, due in part to a lack of information on tussac ecology and the impact of grazing on tussac grassland soils and plant community structure. Conservation and restoration efforts to restore tussac grasslands seek to improve seabird and seal breeding habitat, but whether the winter-only grazing practice is a compromise between these efforts and the

livelihoods of farmers remains to be tested. It is debated whether seabirds and seals play a role in maintaining these habitats in the Falkland Islands, because the impact of physical disturbances and guano enrichment varies among plants.

Seabirds and seals have a biologically important role in coastal ecosystems by influencing vegetation through nutrient transfers from marine to terrestrial ecosystems, which are often nutrient poor (Liu et al., 2013; Pizzaro et al., 2012; Polis & Hurd, 1996; Polis et al., 1997; Anderson and Polis, 1999). Thus, primary and secondary producers on oceanic islands must rely on a transfer of nutrients from the adjacent ecosystem for nutrient enrichment. The influence of manuring as a nutrient subsidy to islands varies depending on the species and the vegetation, ranging from enhancing vegetation through nitrogen and phosphorus inputs to reducing plant cover through scorching from guano (Mulder et al., 2011). In the Falkland Islands, different seabirds species can have different impacts on their habitat. For example, King penguins (*Aptenodytes patagonicus*) occupy large scorched lawns, whereas sooty shearwaters (*Ardenna grisea*) burrow into soft tussac (Woods & Woods, 1997). In terms of biogeochemical mechanisms, characterizing how seabird guano changes the edaphic conditions through fluctuations of soil nutrients is important for understanding enrichment of coastal tussac grass ecosystems.

It is important to document the characteristics in tussac grasslands as both land use and climate are changing in the Falkland Islands. It is unknown how marine biota, such as seabirds and seals, will change in the future and how a subsequent change in nutrient subsidies will impact coastal tussac grasslands. Future projected increases in temperature and the uncertainty of future hydrological conditions (Lister & Jones, 2015),

combined with increased human visitation (Falkland Islands Government, 2012), escalate the risk of introduced pests and plants. In this study, we assessed the effects of seabird and marine mammal nutrient input and grazing history on soil nutrient status, plant community structure, and tussac cover in coastal sub-Antarctic tussac grasslands. We evaluated to what extent the presence, absence, and density of burrowing seabirds explain the chemical properties of soils, to shed light on the importance of marine-derived nutrient transfers to tussac grasslands to inform ongoing land management, conservation, and restoration efforts to restore eroded grasslands.

We hypothesized that grasslands with greater marine-derived nutrient inputs will have higher *P. flabellata* cover. To assess the impacts of grazing, we combined field observations, soil nutrients, and plant surveys to test the following hypotheses: (1) Physical disturbances from grazing increase plant species richness in coastal tussac grasslands. (2) Plant species richness is lowest in ungrazed tussac grasslands. We compared nutrient levels between currently grazed, previously grazed (not now) and ungrazed grasslands. Previously grazed sites ranged in time since last grazed by livestock, which we used to evaluate nutrient changes over time since released by grazing.

Methods

Study area

The Falkland Islands (Malvinas) (51.7963° S, 59.5236° W, Fig. 4.1) main climates are polar tundra and warm temperate, fully humid with cool summers (Köppen-Geiger climate classification for 1986-2010; Rubel et al. 2017; Kottek et al. 2006)

dominated by shifting of the sub-Antarctic polar and polar frontal boundaries (Fig. 4.1A). The southwesterly winds are persistently high (Upton and Shaw 2002), and there is little wet/dry seasonality with only ~600 mm of total annual precipitation (Lister and Jones 2015). Over the last 50 years, the climate has become drier and warmer; long-term regional climate models predict increases in average annual temperature and little change in precipitation, yet a short-term climate prediction is likely to change to cool and wet (Jones et al. 2013). Generally, the inland vegetation is similar to tundra and subpolar classifications (Kottek et al. 2006). There are 181 native species in the Falkland Islands, and 251 introduced (non-native) species (Upson and Lewis 2014). Coastal tussock grasslands grow up to 300 m inland from the shore, and some uninhabited, ungrazed islets are completely covered. The inland distribution (300 m) may have more to do with nutrient subsidies than any other intrinsic limiting factor. Mature tussock grasslands are single species dominant stands that occur along the coasts of many islands, particularly in places that have not historically been grazed by introduced livestock (e.g. steep slopes, islets without fresh water for livestock), and in small enclosures where restoration of tussock grasslands have occurred. The soils of tussock grasslands on farms with hen runs are known to have higher nutrient concentrations available to plants (Fuller, 1996).

We surveyed tussock grasslands from private landholdings, National Nature Reserves (NNRs), and on inhabited and uninhabited islands (Table 4.1; Fig. 4.1B-C). We chose tussock grassland sites based on accessibility, i.e. access by boat or car, and landowner permission. We classified and compared sites using three treatments “ungrazed”, ‘previously grazed’ and ‘grazed’. The time since each site was last grazed was considered to be an important environmental variable of land use history (Table 4.1).

Disturbances to vegetation across surveyed sites includes grazing by livestock (sheep, cattle, or horses), burrowing by seabirds, and trampling by seabirds and pinnepeds. Sites where winter-only or current grazing by cattle or reindeer were grouped as ‘*grazed*’ and include Albemarle, Cape Dolphin, and West Point Island; we grouped sites permanently released from grazing, which ranged from the past 6 to 44 years, as ‘*previously grazed*’ and include Bleaker Island, Ear Island, New Island, Port Harriet, Sea Lion Island, and Surf Bay; and the third group, ‘*ungrazed*’, includes two sites: Kidney Island and ‘Cobb’s stand’ at Bleaker Island. Kidney Island is a NNR today. Livestock were never stocked on Kidney Island but during the mid 20th century, tussac grass was clipped by hand, harvested, and then transported by boat to feed livestock near Stanley. On Bleaker Island, “Cobb’s stand’ has been enclosed to prevent grazing for ~100 years (*M. Rendell, personal communication*).

Survey methods

At each site, we randomly chose six to twenty quadrats (25-m²) surveyed from the coast up to 300 m inland during 2016 (n = 88) and 2018 (n = 103). To minimize bias, we randomly generated numbers between one through eight to represent cardinal directions and randomly generated numbers between 10 to 300 to represent distance (meters) to measure between plot centroids in the randomly generated cardinal direction. Land cover maps are not available at the scale we used, thus a stratified random sampling design in advance was not possible. When the randomly generated number resulted in a direction and distance leading outside of the tussac grassland (e.g. cliff edge), we repeated the random number generator over. GPS coordinates and elevation were collected at each quadrat centroid. Surveys of quadrats included 1) plant community structure (total

number of plant species and % cover, including % cover of native and non-native species); 2) soil characteristics (% organic matter, pH, Ca, P, Cu, Zn, B, Mn, Na, Mg, and nitrogen stable isotopes); and 3) the number of seabird burrows built primarily by Magellanic penguins (*Spheniscus magellanicus*), sooty shearwaters (*Ardenna grisea*), and thin-billed prions (*Pachyptila belcheri*).

Plants

We recorded percent (%) cover of each vascular plant species in each of 88 plots in January-February 2016 at Kidney Island, Bleaker Island, Cape Dolphin, Kidney Island, Surf Bay and West Point Island; during January-February 2018, 103 plots were surveyed at Albemarle, Bleaker Island, Ear Island, New Island, Port Harriet, and Sea Lion Island. Mean summer temperatures over the Falkland Islands and surrounding ocean were slightly cooler (~0.5 °C), during summer (DJF) 2016, while 2018 was similar to the long-term mean of 1981-2010 (<https://www.ncdc.noaa.gov/sotc/global/>). When determining % cover, at least two people estimated % cover and came to a consensus. Height was not measured. Plants were identified using field guides (Liddle, 2007; McAdam & Olave, 2009). Unknown specimens were photographed and later verified against vouchers from the New Island Conservation Trust herbarium and the Falklands Conservation herbarium. Data were recorded in a matrix containing 46 species x 191 plots. Non-vascular plants, lichen, algae, liverworts, moss, and fungi were noted but not included in our analyses because they never exceeded 5% cover. Species were classified as native, introduced, or uncertain according to local vascular plant checklists (Upson & Lewis, 2014).

Animals

The number of seabird burrows (habitation not determined) within each plot, and the presence or absence of non-burrowing seabirds and pinnipeds were recorded at each site. In determining the number of burrows, at least two people estimated burrow counts and came to a consensus. Although some burrows may have had multiple openings, we used the number of burrow entrances as a proxy for usage intensity.

Soil variables

At each plot, three soil samples were taken from a depth of 10 cm in a diagonal transect across each plot, and homogenized in the field; a subsample of the homogenized samples was later analyzed in the lab for nutrients. Nitrogen (N) was extracted as N-NO_3^- and N-NH_4^+ ($\mu\text{g g}^{-1}$) from wet soils using a 1M potassium sulfate (K_2SO_4 and deionized water) solution at the Falkland Islands Department of Agriculture prior to spectrophotometric determination. Nitrogen extracts in K_2SO_4 solution were frozen and shipped to the University of Maine Soil Analytical Laboratory for analysis.

Soil samples were dried and sieved to remove roots and stems at the Falkland Islands Department of Agriculture at 25 to 30 °C for up to 48 hours to comply with USDA import requirements, and then shipped to the University of Maine. Dried soil samples were extracted in a Mehlich 3 solution (for ultra acidic soils) at 1:10 (weight : volume) for five minutes. Concentrations (mg kg^{-1} or ppm) of soil macronutrients (Al, B, Ca, Cu, Fe, K, Mg, Mn, Na, P, S, and Zn) were analyzed by ICP-OES at the University of Maine Soil Analytical Laboratory. Concentrations of sodium (Na) were high enough to render analysis of cation exchange capacity as invalid.

Soil samples were further dried at 100 °C for 24 hours at the University of Maine. Loss-on-ignition (LOI) was used to quantify % organic content (550 °C) for two hours following Heiri et al. (2001). After the 550 °C treatment we weighed the samples to quantify the proportion of weight lost. The carbon content values calculated via LOI at 550 °C provide qualitative estimates of organic carbon (Santisteban et al., 2004).

We measured the pH of soil samples using a weight to volume (1:5) ratio of soil suspended in deionized water and shaken for 30 minutes. The pH meter was calibrated using a two-point calibration (pH = 4 and pH = 7). To control for quality, we checked the calibration was checked for acceptable ranges every 20 samples and monitored temperature.

Data analysis

We used box plots of the median, interquartile ranges, min-max values, and outliers to illustrate the spread and differences soil nutrients between grazing treatments. We only plotted nutrients that had at least one pair of grazing treatments with statistically significantly different medians.

We tested the null hypothesis of no difference among sites using Multi-Response Permutation Procedures (MRPP) in the R (v. 3.1.0; R Core team, 2013) package *vegan* (Oksanen et al., 2010) was applied using Bray-Curtis distance, due to our zero-inflated dataset. Groups were defined by site ($n = 17$). MRPP calculates the distance between each group (site) using percent plant cover data. We calculated *delta* (weighted mean across all groups) which indicates the average distance between each group. The probability of *delta* is determined by randomly assigning plot observations to groups

using 999 permutations. The MRPP significance test (p-value) is the ratio of permuted deltas (expected) that are less than observed deltas. The effect size (A) ($1 - \text{observed delta} / \text{expected delta}$) evaluates the magnitude of within-group homogeneity (when $A = 1$, homogeneity within groups and when $A = 0$, within-group heterogeneity is equal to expectation by chance).

Tussac grassland communities were separated by a hierarchical agglomerative cluster analysis in the R package *vegan* using percent cover data in a transpose matrix (species in rows, plots in columns). For the cluster analysis, a strict criterion was used for species inclusion. Species had to have occurred in at least six plots; thus, 23 species were removed and 22 species were used in the cluster analysis. The data matrix contained 22 species and 191 plots. Abundance data were transformed by species sums of squares to remove the influence of grouping species together by high percent cover.

We used Non-metric Multidimensional Scaling (NMDS) to identify patterns in plant community composition and soil variables, with a matrix of 22 species and 191 plots across 17 sites using the package *vegan*. To perform the NMDS analysis, we first used the function '*rankindex()*' to identify the most appropriate method to calculate the plant species dissimilarity matrix in the R-package *vegan*. We used a ranking Bray-Curtis dissimilarity matrix for the NMDS analysis after a rank test stress plot (Fig. 4.3) to evaluate stress. We also chose to use a Bray-Curtis dissimilarity matrix for the NMDS because it is an appropriate tool to handle data with missing pairwise distances and because it handles quantitative, qualitative, and mixed variables.

Because of the unbalanced design of grazing treatments and failed tests for equal variances, we used a non-parametric analysis of variance (ANOVA) based on ranks to analyze differences in soil and in the plant variables (percent cover). When the ANOVA resulted in significant differences in median values, we used Dunn's post hoc test. For correlations and treatment comparisons, we used plots nested within sites as the experimental unit. We used randomly selected plots due to the unbalanced design of 2 sites in the ungrazed grazing treatment, 10 sites in previously grazed treatment, and 5 sites in the currently grazed treatment. The history of overgrazing on the islands resulted in more previously grazed sites available to study. In addition, the few ungrazed sites available to study are more difficult to access on uninhabited islands.

Results

Floristic diversity

We identified 45 vascular plant species in the tussac grasslands (Table 4.2). Non-vascular species of liverwort, *Marchantia* spp. (Marchantiaceae), and mosses, lichen, algae, and fungi were rare and not quantified, but their presence was noted. The site New Island Precipice Hill had the highest species richness (mean 7.9) followed by Bleaker Island (mean 4.9; 15 year since last grazed). West Point Island had the lowest species richness (mean 1.4), which was below the mean for all sites (3.6). In total, 18 families were represented, and 11 families contain only one species. The most species-rich families are Poaceae (13 species) and Asteraceae (8 species) (Appendix A). The most frequent species were *Poa flabellata* (all plots), *Rumex acetosella* (86 plots, 45% of all plots), *Senecio vulgaris* (42 plots, 21.9%), *Holcus lanatus* (37 plots, 19.3%), *Empetrum*

rubrum (34 plots, 17.8%), *Stellaria media* (34 plots, 17.8%), and *Luzula alopecurus* (33 plots, 17.2%). Except for *Poa flabellata* and *Empetrum rubrum*, all of these frequent species are introduced taxa. Of the 45 species, only 12 species occurred in a single plot out of 191 study plots (26% of all species), and five species occurred in two plots (10.8%). Of the plants we surveyed, 70% were native ($n = 33$), 26% were introduced ($n = 12$), and ~4% were classified as uncertain ($n = 2$). The occurrences of the 45 species found in our surveys, classified by Upson and Lewis (2014), are as follows: 28 species occur frequently; five species are common; eight species occur occasionally, and one species each for scarce (*Urtica urens*), rare (*Cirsium vulgare*), and very rare (*Sagina filicaulis*). Species lists and status are listed in Table 4.2.

Measures of diversity

The measure of similarity from the MRPP results indicate that sites are more dissimilar to one another than expected by chance (McCune & Mefford, 2011). The observed delta value 0.4211 is less than the expected delta 0.531, thus, we reject the null hypothesis of no difference between groups (sites) ($p\text{-value} = 0.001$, $A = 0.207$). Mean alpha diversity was 3.6 for all sites. Table 4.3 reports measures of diversity for each site and all sites combined. At the plot level, the maximum species richness across all plots was 12 and the minimum was one. The New Island Precipice Hill site had the highest species richness, 20 species. Shannon diversity (Shannon and Weaver 1949) was 0.60 and accounts for abundance and evenness. The evenness index was calculated using plots with more than one species ($n = 151$) and was 0.51 for all sites. The Simpson index, the likelihood that two randomly chosen individual plants will be different species, was 0.31 (McCune and Mefford 2011). The measures of diversity also revealed inter-site

similarities and dissimilarities. New Island Precipice Hill was the most species rich (alpha) and had the highest Shannon and Simpson index values. Beta diversity was 0.52 for all sites (Table 4.3). Surf Bay and Albemarle-reindeer had the highest beta diversity of 0.45. Albemarle-cattle had the highest evenness. At the site level, West Point Island, the most northwestern island had a total of 4 species, the lowest number of species across all sites. Mean species richness at each site and time since last grazed did not show a linear relationship (Fig. 4.2A). Similarly, the number of introduced taxa at each site and time since last grazed did not show a linear relationship (Fig. 4.2B).

Plant Communities – within tussac grassland heterogeneity

The agglomerative clustering analysis produced three groups, one with tussac grass, a second with *Empetrum rubrum* and *Rumex acetosa*, and the third with 19 species grouped together (Fig. 4.3). The 'rankindex()' function in *vegan* indicated which dissimilarity matrix had the greatest separation of gradients based on higher correlations. Spearman ranks of the plant community data without rare species found Euclidian and Bray-Curtis (0.12) dissimilarity methods (0.12) rank higher over Manhattan (0.11) and Horn (0.071) methods. To run the nMDS analysis we chose the Bray-Curtis dissimilarity matrix method. Plots with similar species are displayed closest to other plots in the ordination diagram. The Shephards plot (stressplot) of the nMDS analysis is at 0.148 or 14.8% with small scattering around the line of regression, suggesting that the dissimilarities are preserved in the reduced number of dimensions (k=2). Using higher number of dimensions (k=3) resulted in reduced stress of 0.102 or 10.2% (Fig. 4.4).

Plant community similarity

The NMDS plots demonstrated a weak pattern of differentiation when grouped by grazing treatment. The lack of differentiation among tussac grassland plant assemblages in the ungrazed group versus grazed sites is shown by the large degree of overlap of plots from the three groups of time since last grazed / disturbed (Fig. 4.5). As expected, clustering of mature ungrazed plots (Fig. 4.5) occurs in plots with greater than 70% tussac cover (Fig. 4.6). Tussac with > 70 % cover in plots are also associated with Na, S, and K (Fig. 4.6).

Dense tussac stands (>70% tussac cover) are light limited and few other species tolerate such light limited conditions versus less dense tussac stands (<70% tussac cover) with more open space between pedestals allowing light for other plants to grow (Fig. 4.6). Seabird indicators (vectors), also point toward plots with highest% tussac cover (Fig. 4.6). The significant 'Latitude' vector indicated there is a north to south gradient (Fig. 4.6). The NMDS plot also demonstrated a weak pattern of differentiation when we grouped pH into three categories "< 4.08", "4.09 - 5.0", "> 5.0" (Fig. 4.7).

Nutrients

The % tussac cover in grazed sites significantly positively correlated with K ($r^2 = 0.663$), B ($r^2 = 0.548$), Cu ($r^2 = 0.572$), Na ($r^2 = 0.576$), S ($r^2 = 0.586$), and Zn ($r^2 = 0.580$), and we found no significant correlations between tussac cover (%) and nutrients in ungrazed or previously grazed tussac grasslands (Table 4.4). We found significant positive correlations between non-native % cover and nutrients P ($r^2 = 0.542$) and K ($r^2 = 0.596$) in only ungrazed plots (Table 4.4). The number of non-native species significantly

correlates with Al ($r^2 = 0.629$) and Fe ($r^2 = 0.688$; Table 4.4). Grazed plots had significantly higher median concentrations of Na ($p < 0.001$) and Mg ($p < 0.001$), and the lowest concentration of manganese ($p = 0.002$; Table 4.5; Fig. 4.8). Ungrazed stands had significantly higher median concentrations of Ca ($p < 0.001$), P ($p < 0.001$), B ($p = 0.002$), Cu ($p < 0.001$), Zn ($p < 0.001$; Fig. 4.8), and N-NO_3^- ($p < 0.001$; Fig. 4.9) than either previously grazed plots and grazed plots in tussac grasslands. Zinc was also significantly lower in grazed plots ($p < 0.05$; Fig. 4.8). Nitrate was significantly greater ($p < 0.001$) in ungrazed sites than both grazed and previously grazed sites. The median nitrate concentration was lowest in previously grazed sites, and four times higher in currently grazed sites (Table 4.5). Grazed plots had significantly lower percent tussac cover than previously grazed and ungrazed ($p = 0.012$; Table 4.5). Tussac cover did not correlate with the number of seabird burrows across all sites or grazing treatments ($r^2 = -0.034$; Fig. 4.10). The median number of burrows is zero across all plots (Table 4.5).

The correlation analyses also indicated that the number of non-native species significantly positively correlated with Al ($r^2 = 0.629$) and Fe ($r^2 = 0.688$) at ungrazed sites (Table 4.4). It's important to note that of the two sites grouped as 'ungrazed', we only found non-native species at Cobb's stand at Bleaker Island and none at Kidney Island. Thus, the number of non-native species increases as Al and Fe in soils increase. In grazed sites, the median concentrations of Al and Fe were higher than previously grazed or ungrazed plots, but not significantly. Also at Cobb's stand on Bleaker Island, the percent cover of non-native species is significantly positively correlated with K ($r^2 = 0.596$) and P ($r^2 = 0.542$) concentrations in soil.

Discussion

This work evaluated the extent to which historical and current grazing and seabirds impact tussac grassland plants and soils. Grazed stands have less tussac cover than both ungrazed and previously grazed stands. Because there are no native herbivores in the Falklands, apart from endemic geese, this result is not surprising. Other than the sites at Albemarle grazed by cattle and reindeer year-round, the grazed sites in this study were carefully managed by limiting grazing to only winter, and managers actively monitor the intensity of grazing to prevent permanent damage of tussac meristems. Despite these efforts, there is a notable impact of grazing on tussac cover, though we also found that tussac can recover to similar abundances to ungrazed tussac grasslands within just a few years.

We found that tussac cover did not increase with increasing numbers of seabird burrows. We attribute this finding to the additional presence of non-burrowing seabirds and marine mammals (i.e. sea lions) at some sites, which we did not quantify in this study. Because burrows can be abandoned and reused (sometimes by different species) it may be that our proxy for seabird use intensity did not accurately reflect bird usage. Alternatively, burrowing seabirds and pinnipeds may also act as a disturbance driving an increase in tussac grass competition for light in these high nutrient grasslands; areas with high densities of seabirds or sea lions are often trampled and appear scorched.

Our results corroborate the high-nutrient resource strategies of tussac grasses; we found that both nitrate and phosphorus concentrations were around three times higher in the soils of ungrazed tussac grasslands versus grazed grasslands. We hypothesized that soils within ungrazed tussac grasslands have higher nutrient concentrations than currently

grazed grasslands for several reasons. First, livestock can reduce nutrient input into tussac grasslands by trampling seabird burrows (K. Ross, personal communication, June 27, 2017), though it's unknown whether livestock disturb non-burrowing seabirds or sea lions. In our study, we did not find a significant difference in the number of burrows in grazed versus the historic or ungrazed treatments, indicating that other environmental variables are more important in influencing burrowing seabird habitat. It is not an uncommon sight in the Falkland Islands to see livestock, seabirds, and sea lions co-existing. Second, it's thought that plants in high nutrient ecosystems have high nutrient content in their leaves, which rapidly return nutrients to the soils, thereby increasing soil nutrient concentrations (Craine, 2009). However, Craine (2009) suggests that the plant resource strategy of returning nutrients to the soil quickly does not actually increase nutrient content in soils; rather, the strategy tends to deplete nutrients less than plants with slower growth rates and turnover of leaf matter. Even when non-native herbivores are carefully managed, we propose that removing leaf material from tussac grasslands through grazing leads to the removal of nutrients that would otherwise be rapidly recycled in this high-nutrient ecosystem. It could be useful to future management strategies to evaluate tussac grass growth in controlled environment experiments to test whether lowered nutrients or reduced competition has a detrimental impact.

Nitrogen and phosphorus are known to limit primary productivity, however, other essential nutrients can also be limiting. In tussac grasslands, the macronutrient Ca, and micronutrients B, Cu, and Zn are also significantly higher in ungrazed sites versus grazed sites. In contrast, grazed sites had significantly higher concentrations of the macronutrient, Mg, and of the non-essential element Na, which at high levels can reduce

plant growth (Brady & Weil, 2000). Specifically, high concentrations of Na can lead to reduced cation exchange capacity and inhibit root uptake of essential nutrients (Wall et al., 2012). Because of the proximity of tussac grasslands to the ocean and the dominance of the westerly winds and sea spray, it is likely that tussac grasses are adapted to soils with high salt concentrations (McAdam and Walton, 1990). At the actively grazed sites that we analyzed, tussac cover is significantly positively correlated with K, B, Cu, Na, S, and Zn. Because this pattern is not evident in the other grazing treatments, we suggest that micronutrients, B, Cu, and Zn may be higher in grazed sites because of seabirds or marine mammals that were not accounted for in our surveys. In grazed sites, the significant positive correlations between the percent cover of non-native species suggests that tussac grasses are competing with non-native taxa for K and P. Because we found a significant positive correlation between the number of non-native species and both Al and Fe, non-natives may be exploiting more mineral soils.

Soil properties of coastal tussac grasslands in the Falkland Islands are similar to the floras of other sub-Antarctic islands. The weak correlation between burrows and P suggests that many sites without burrows are still influenced by non-burrowing seabirds and marine mammals. Despite not finding a significant correlation between burrows and P in the Falkland Islands, previous work by Smith (1976) on Marion Island in the sub-Antarctic indicated that soils inhabited by burrowing petrel and prion species had higher levels of N and P. In these same areas, plants had higher levels of N, P, K, Fe, and Na than in plants not inhabited by the birds. Smith (1976) found that sites with guano inputs increased the soil inorganic P up to 25%. In Smith's study, aluminum and iron phosphate compounds that were previously unavailable in the soil dissociated and produced

mistakenly high P estimates attributable to the method of extraction. In our study, Al and Fe are also tightly correlated and likely reflect local terrigenous sources and/or atmospheric deposition.

More mature sites of coastal tussac grasslands have low species richness because they tend to form tall, dense stands where the establishment of competitors is difficult. Thus, species richness is not necessarily a meaningful metric from the perspective of ecosystem services in tussac grasslands. However, we found that tussac grasslands at differing stages of release from grazing pressure have nonlinear patterns of species richness (Fig. 4.2A). There is no clear linear decline in species richness with increasing time since last grazed (yr). We expect low species richness in maturing tussac grasslands after the release from grazing as they begin to restrict light and space for competitors. Notably, we recorded zero introduced taxa at the Kidney Island site, while Cobb's stand at Bleaker Island – the site with >100 years since last grazed – has five introduced taxa (Fig. 4.2B). While we didn't account for the impact of grazers on seabird predators, this may be important. For example, on sub-Antarctic South Georgia, recent reports suggested that reindeer grazing opened tussac grass stands allowing seabird predators, like the brown skua (*Stercorarius antarcticus*) and striated caracara (*Phalacrocorax australis*), easier access to burrowing species of prions and petrels (D. Christie, Government of South Georgia, 2010).

Ungrazed sites in this study are more similar with each other, while currently grazed plots are more dissimilar, due in part to the high abundance of non-native plants in grazed environments. The combination of grazing, acidic soil conditions, and low light availability in tussac grasslands are conditions unfavorable for most competitors, and are

likely significant barriers for colonization in established tussac stands (in addition to the climate and long distance to the mainland). Despite this, we found much higher invasion rates in grazed areas than ungrazed areas, though the overall impact of non-native plants on native communities remains unknown.

Soils in the Falkland Islands have a similar pH to terrestrial habitats on Marion Island (sub-Antarctic) described as acidic to neutral soils (mean soil pH of 5.1, ranging from 3.8 to 7.1; Smith and Steenkamp 2001); The mean soil pH across 191 plots in the Falkland Islands coastal tussac grassland soils was 4.2, and ranged from 3.2 to 7.1 pH. In our study, sites with greater % tussac cover had low pH as a result of higher organic matter, which typically leads to water retention (Wall et al., 2012). In mature tussac grassland soils, the tall peaty pedestals reduce evaporation by obstructing light and wind; surface soil moisture may also be greater, though we did not test this in our study. The peaty soils of mature tussac grass stands are more protected from the sunlight and wind and appear to be moister than more open tussac grasslands.

Our study points to the importance of marine-derived nutrient inputs coastal grasslands, as we detected a significant positive correlation between the number of seabird burrows and both exchangeable ammonium and nitrate concentrations across 86 plots (2016 data only). Furthermore, a lack of correlation between P and Burrows indicates that marine mammals and non-burrowing seabirds play an important role in fertilizing soils of coastal tussac grasslands where % tussac cover and organic matter are high. A study from sub-Antarctic South Georgia found that plants growing in seal wallows acquired high levels of all elements compared to non-guano influenced plants (Smith, 1978). The analysis of leaf saps of guano-influenced grasses, *Poa cookii* and

Cotula plumosa, showed higher N and P concentrations than uninfluenced plants. Further work using fertilization experiments in South Georgia concluded that the island soils are low in available N (Smith 1978). Thus, our findings support a growing body of literature indicating that marine-derived fecal subsidies are important for sustaining a level of soil N and P appropriate for plant growth in resource-poor environments.

Conclusions

Tussac grasslands are significantly impacted by grazing of non-native herbivores in the Falkland Islands, and should continue to be limited to winter-grazing only to improve tussac cover. Tussac grasslands released from grazing in the past 6 to 44 years had just as high tussac cover as the ungrazed stands. Unexpectedly, the number of burrowing seabirds in tussac grasslands are not correlated with tussac cover, but several factors such as other invasive species like cats, rats, and rabbits may confound these results. Conserving tussac grasslands and the fauna that inhabit them is not only biologically and ecologically important, but may prove to be economical as ecotourism has gained support in recent years (Falkland Islands Government, 2012).

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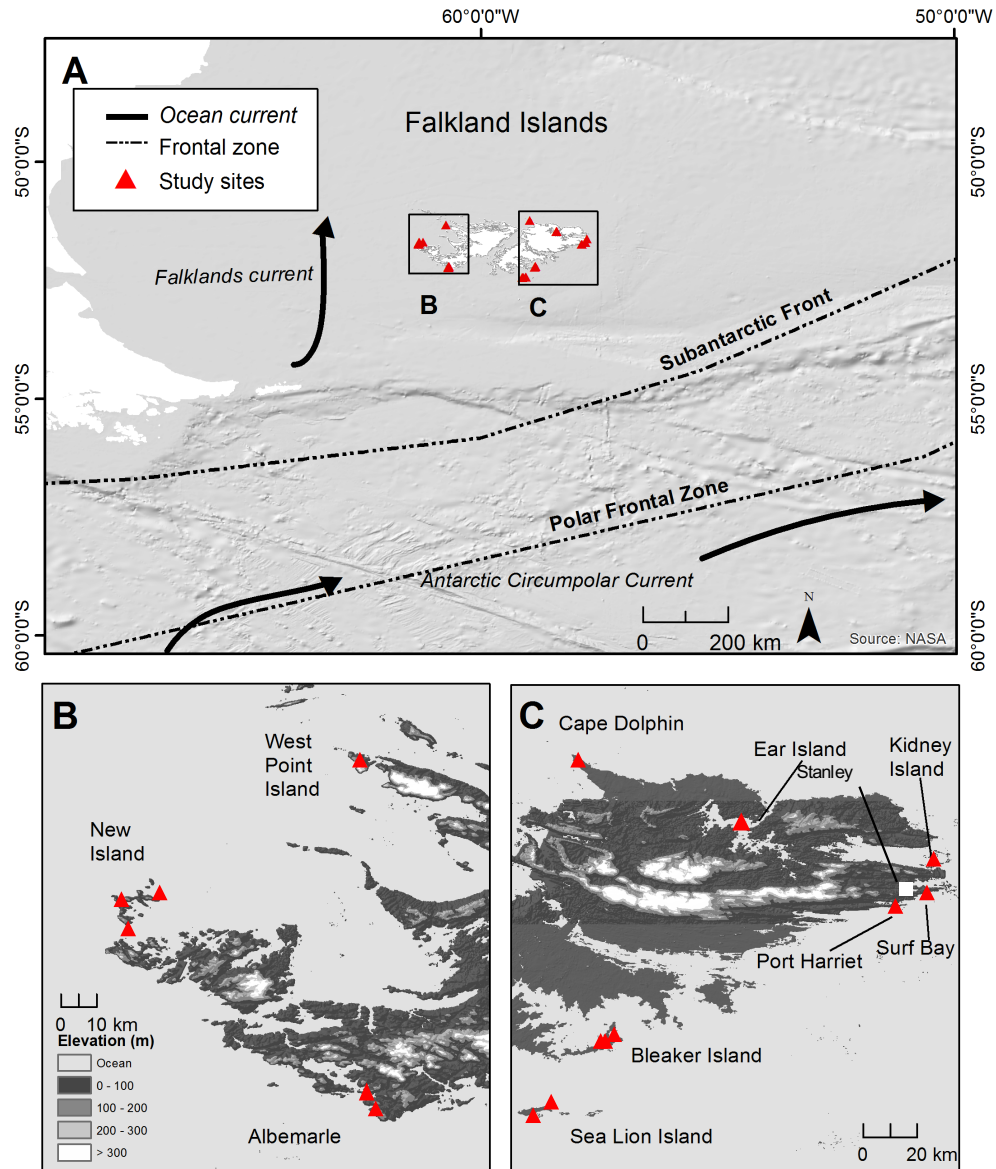


Figure 4.1. Geographic areas covered in this study. **A)** Overview of frontal boundaries and oceanic currents surrounding the Falkland Islands. The Falklands current is an offshoot of the Antarctic Circumpolar current, regarded as cold and nutrient rich. Triangle symbols indicate location of survey plots. **B)** Study sites include Albemarle of West Falkland Island, New Island, and West Point Island. **C)** Study sites of East Falkland Island include Surf Bay, Port Harriet, and Cape Dolphin, as well as nearby Ear Island (Salvador waters), Kidney Island, Bleaker Island, and Sea Lion Island.

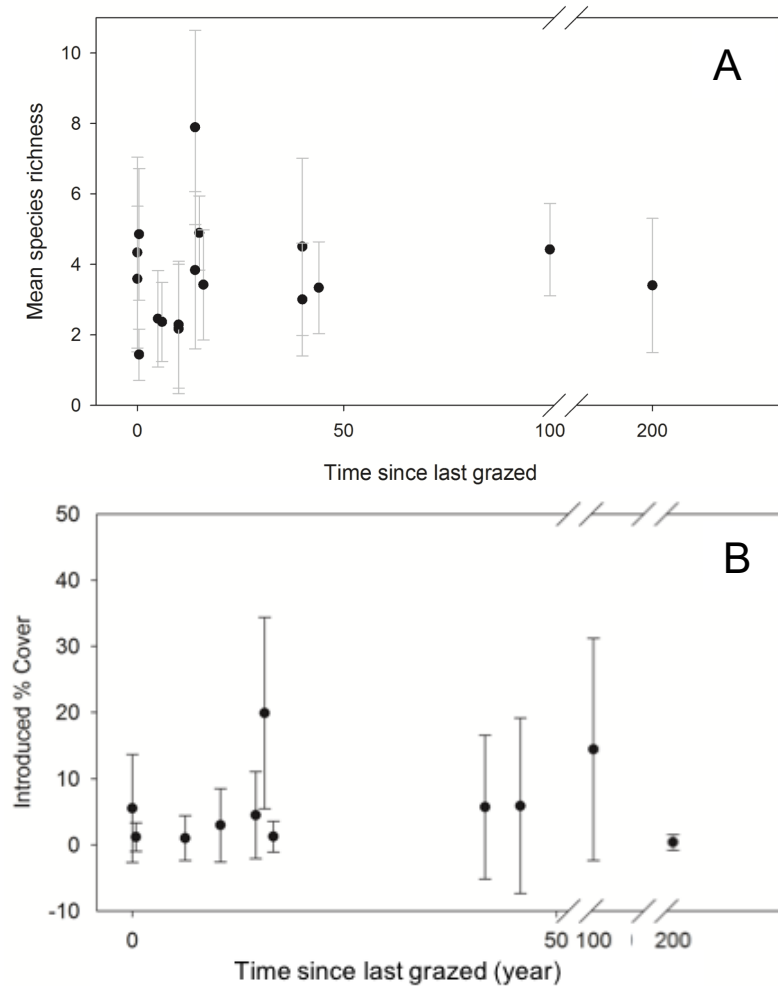


Figure 4.2. Relationships between ‘time since last grazed’ and plant metrics. **A)** Scatterplot showing the relationship between mean species richness (\pm SD) at each site (filled circle symbol; $n = 17$) and time since last grazed (x-axis). **B)** Mean total percent plant cover (%) of introduced plant taxa (y-axis) and time since last grazed (x-axis). Solid circle symbols in **B** represent sites grouped with equivalent ‘time since last grazed’ and standard deviation (\pm SD). Refer to Table 4.1 for site-level information on ‘time since last grazed’.

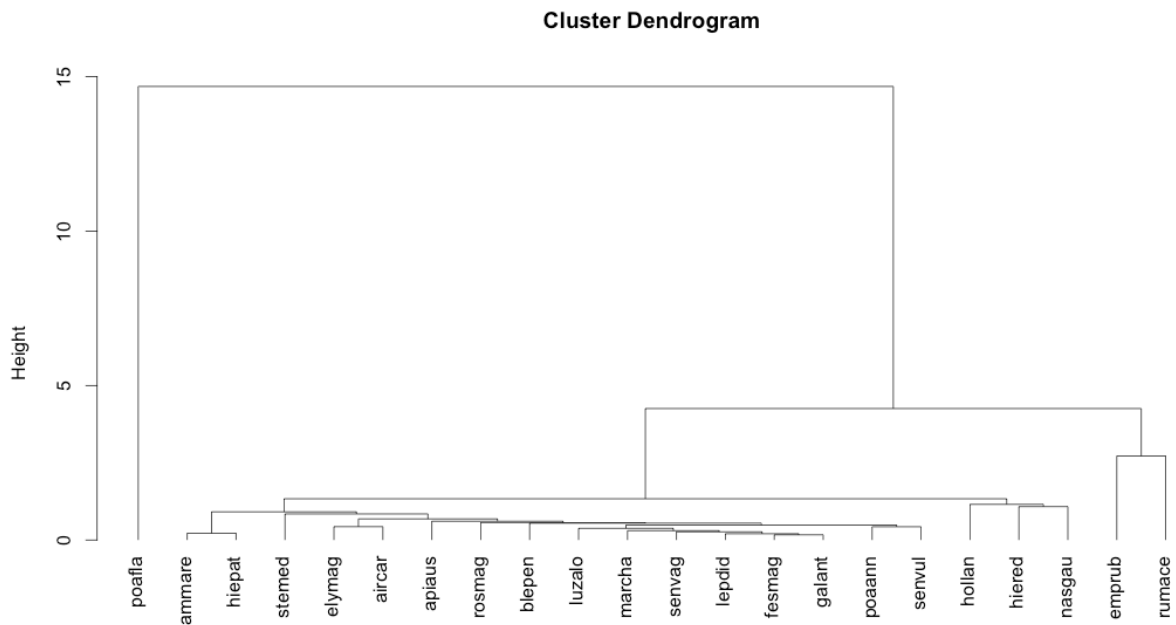


Figure 4.3. Agglomerative cluster dendrogram of tussac grassland plant communities using Bray-Curtis dissimilarity matrix. Plant taxa Refer to Table 4.2 for plant taxa abbreviations and names: poafla = *Poa flabellata*; ammare = *Ammophila arenaria*; hierant = *Hieracium antarcticum*; stemed = *Stellaria media*; elymag = *Elymus magellanicus*; aircar = *Aira caryophyllea*; apiaus = *Apium australe*; rosmag = *Rostkovia magellanica*; blepen = *Blechnum penna-marina*; luzalo = *Luzula alopecurus*; senvag = *Senecio vaginatus*; lepdid = *Lepidium didyum*; fesmag = *Festuca magellanica*; galant = *Galium antarcticum*; poaann = *Poa annua*; senvul = *Senecio vulgaris*; hollan = *Holcus lanatus*; hiered = *Hierochloe redolens*; nasgau = *Nassauvia gaudichaudii*; emprub = *Empetrum rubrum*; rumace = *Rumex acetosella*;

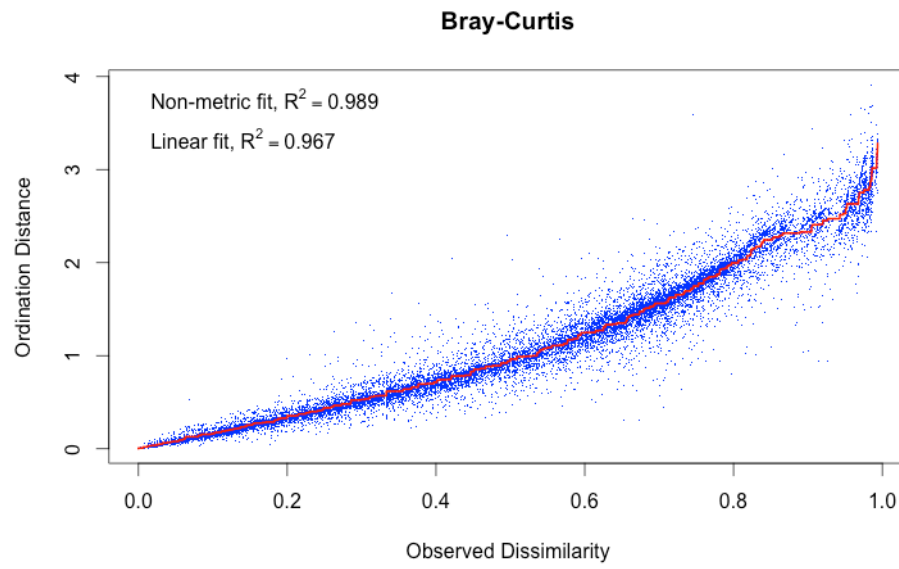


Figure 4.4. Shephard's plot. Using $k=3$ dimensions the resulting stress is 0.102 or 10.2% with high R^2 values (0.967). The line of regression is shown as the solid red line.

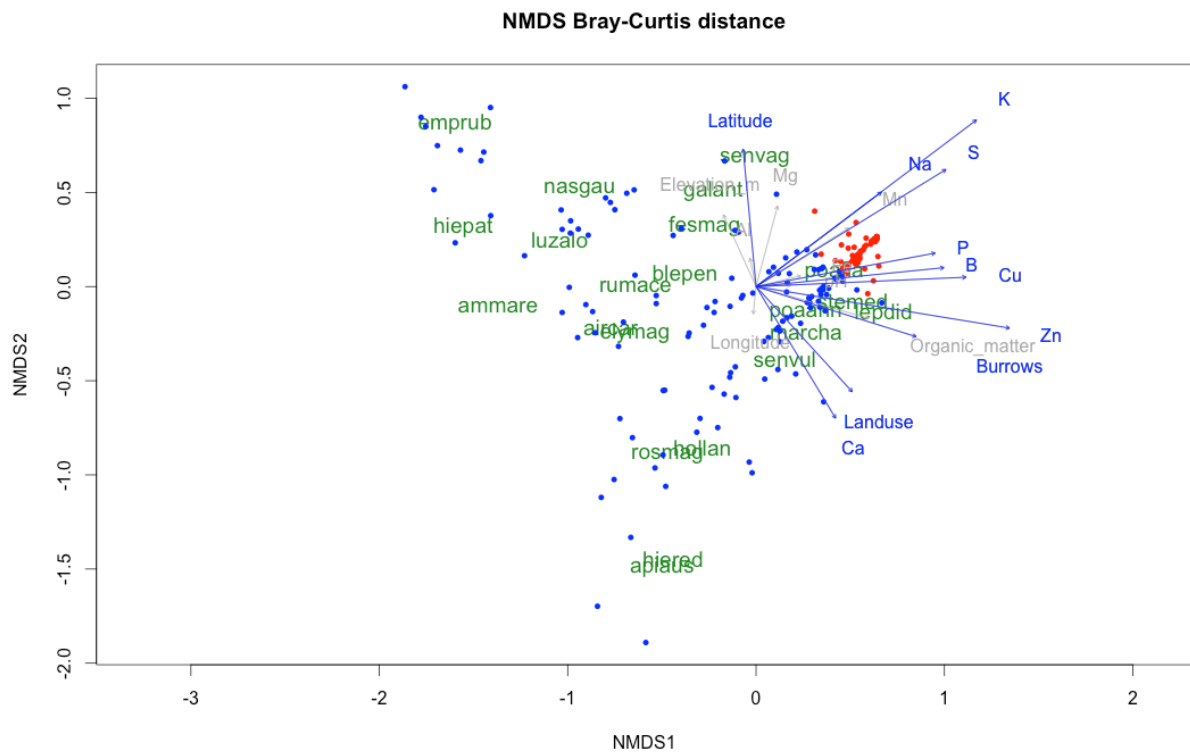


Figure 4.6. NMDS plot grouped by > 70 % tussac grass cover (●) and < 70 % tussac grass cover (●) using k=3 NMS dimensions (stress = 0.102 or 10.2 %). NMS ordination of plots in tussac grassland species space with joint bi-plots of nutrients (B, Ca, Cu, K, Na, P, S, Zn) % Organic matter, number of seabird burrows, elevation, latitude and longitude. Displayed vectors in bold (blue) have a significant $p_{max} = 0.05$, gray vectors are non-significant. Red circles represent recently grazed to currently grazed plots; blue triangles indicate grazing ceased less than 100 years ago (44 yr ago); solid black triangle are plots never grazed or grazed greater than 100 years ago by livestock.

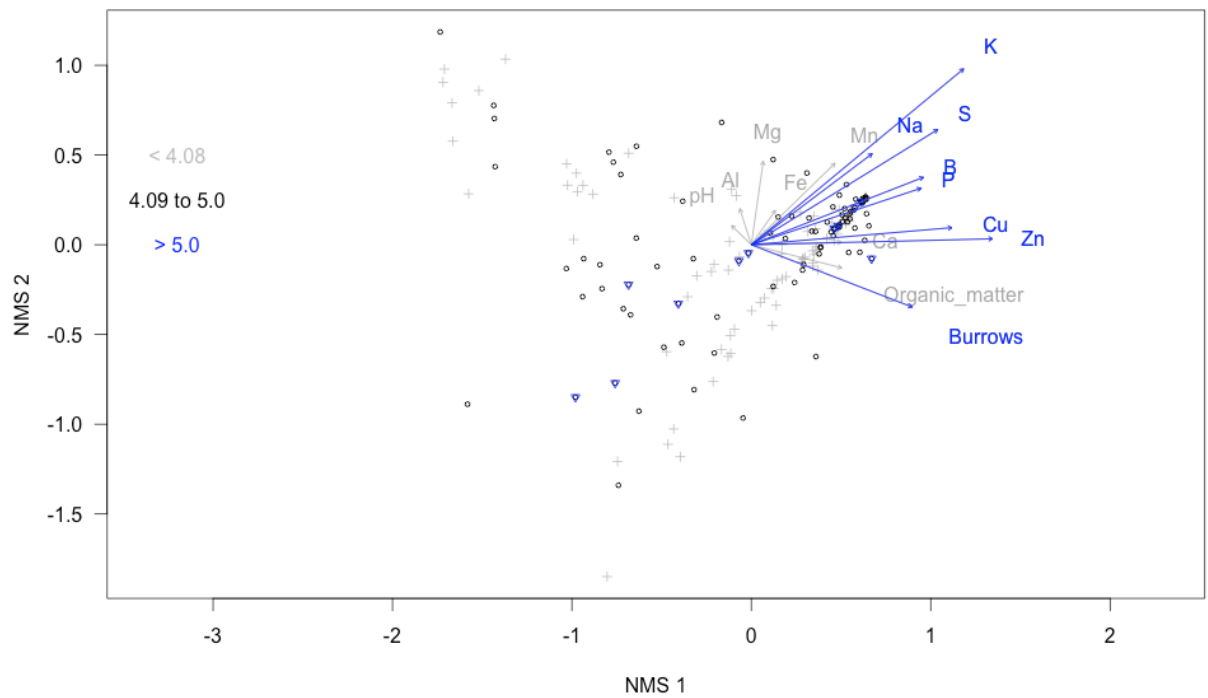


Figure 4.7. NMDS ordination of plots in peatland species space grouped by pH range.

Gray crosshair symbol (+) represents pH below the median, 4.08, black circle (O)

represents pH range between 4.09-5.0, and blue triangle represents pH ranges > 5.0 (▽).

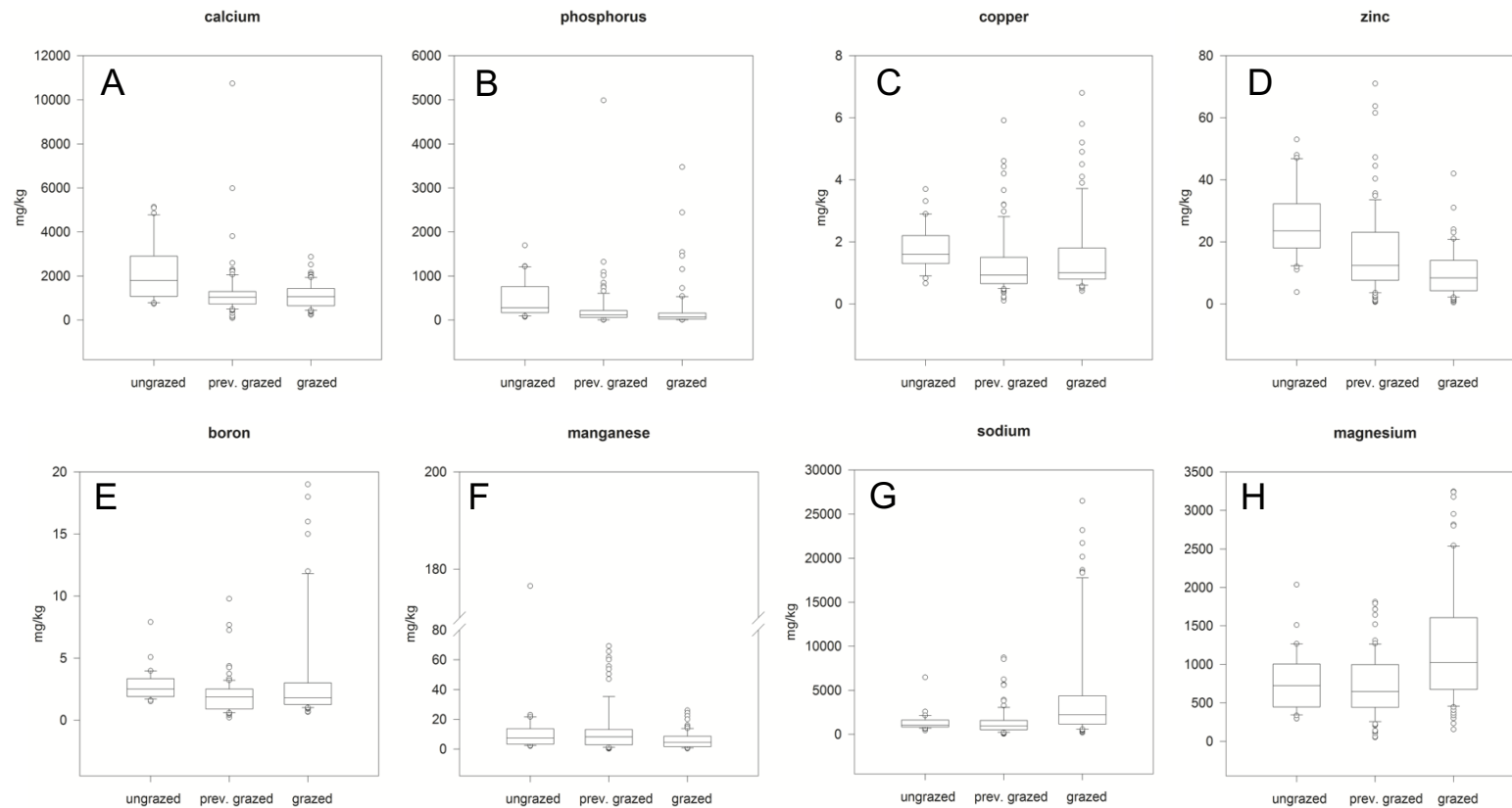


Figure 4.8. Box plots of nutrient concentrations (mg/kg) for Ca, P, Cu, Zn, B, Mn, Na, and Mg in soils by grazing treatment. Median values are horizontal lines between the interquartile range (boxes = 50% of the distribution). Whiskers extend to the minimum and maximum values. Analysis of variance based on ranks significance level of $p < 0.05$ and included ungrazed plots ($n = 30$), previously grazed plots ($n = 87$), grazed plots ($n = 71$).

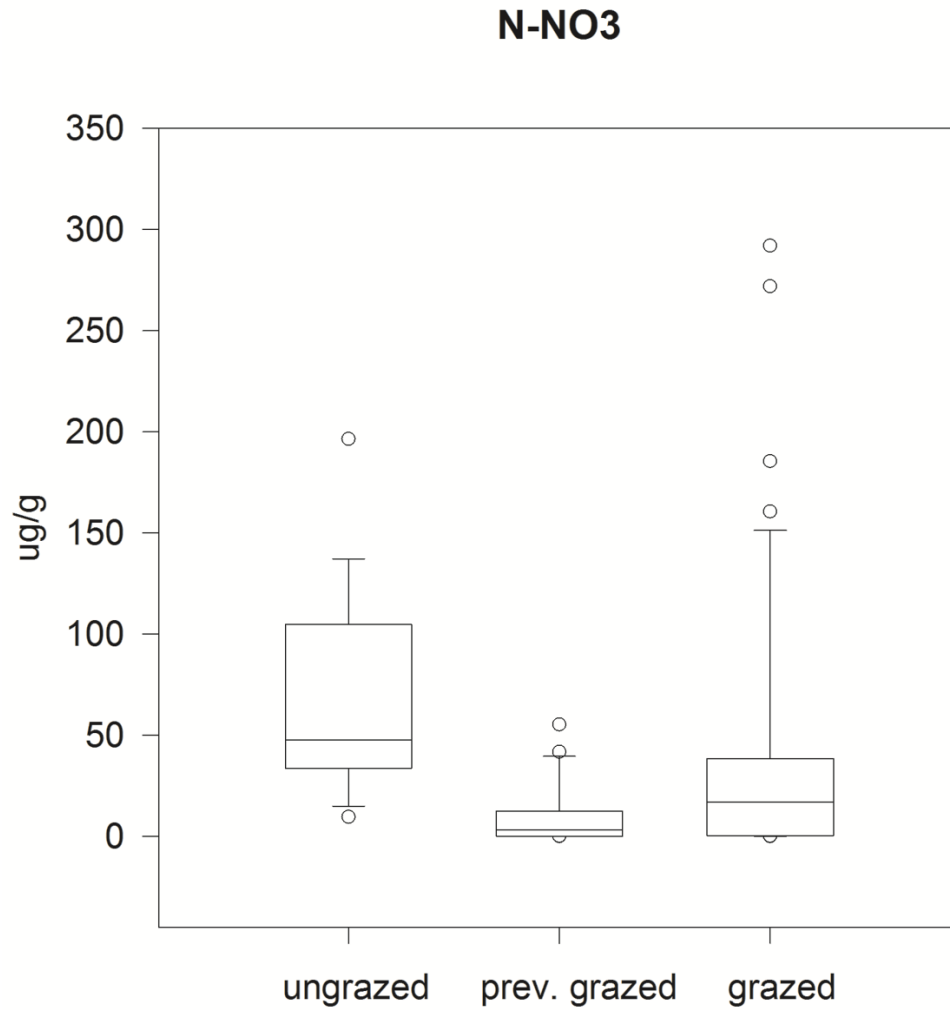


Figure 4.9. Box plots of median concentration of exchangeable nitrogen-NO₃⁻ (ppm) in plots by grazing treatment. The median concentration of ungrazed plots (47.586 ppm) is significantly higher ($H = 20.845$; $p < 0.001$) than previously grazed (3.055 ppm) or grazed plots (16.908 ppm).

tussac cover vs. seabird burrows

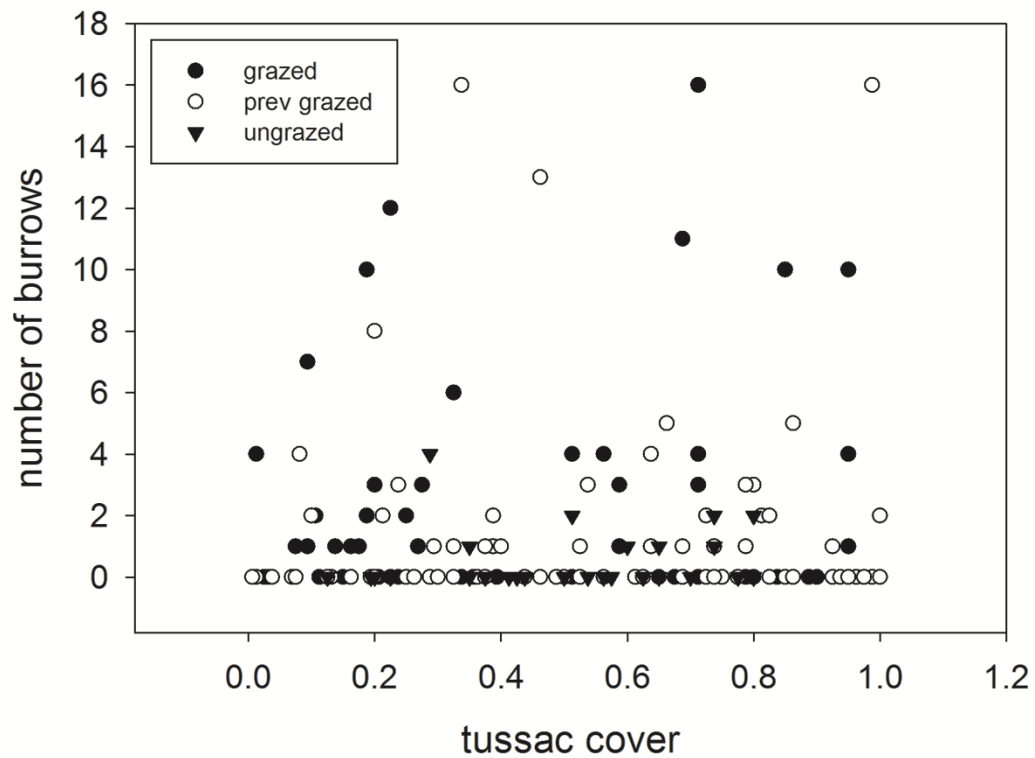


Figure 4.10. Scatter plot of tussac cover ($n = 191$) and the number of seabird burrows categorized by grazing treatment. Grazed plots are filled circles, previously grazed plots are open circles, and ungrazed plots are symbolized by solid triangles. There is no significant correlation between the number of seabird burrows and tussac cover ($r^2 = -0.034$; $p > 0.05$).

Table 4.1. Locations of surveys and time since last grazed in years. Sites surveyed in 2018 are labeled with * and all other sites were surveyed in 2016. ** Kidney Island site was never grazed by livestock, and was classified as >200 years time since last grazed. Historically, tussac grass leaves were cut by hand, harvested and shipped to feed livestock elsewhere.

Location name	Site name	Last grazed (years)	Lithology
Albemarle	Reindeer stand*	0	Quartzite
Albemarle	Cattle stand*	0	Quartzite
Bleaker Island	Cobb's stand*	~100	Sandstone and mudstone
Bleaker Island	North stand	15	Sandstone and mudstone
Bleaker Island	South stand	0.42	Sandstone and mudstone
Cape Dolphin	Peninsula	0.42	Quartzite and sandstone
Ear Island	Ear Island*	6	Quartzite
Kidney Island	Kidney Island	Never**	Quartzite
New Island	Precipice Hill*	14	Quartzite
New Island	Rabbit's Ear*	14	Quartzite
New Island	Settlement Rookery*	40	Quartzite
New Island	South End*	40	Quartzite
Port Harriet	Port Harriet*	16	Quartzite
Sea Lion Island	Northeast End*	10	Sandstone and mudstone
Sea Lion Island	Southwest End*	10	Sandstone and mudstone
Surf Bay	Surf Bay	44	Quartzite and sandstone
West Point Island	West Point Island	0.42	sandstone

Table 4.2. Vascular plant taxa in surveys from 2016 and 2018. Species statuses use the following abbreviations: n = native; i= introduced; u = species of uncertain status; * = endemic; C = common; F = frequent; O = occasional; S = scarce; R = rare; V = very rare;

Family	Latin	Common	n / i	Rarity	Abbrev
Apiaceae	<i>Apium australe</i>	wild celery	n	F	apiaus
Apiaceae	<i>Bolax gummifera</i>	balsam bog	n	F	bolgum
Asteraceae	<i>Baccharis magellanica</i>	Christmas bush	n	C	bacmag
Asteraceae	<i>Bellis perennis</i>	daisy	i	F	belper
Asteraceae	<i>Cirsium vulgare</i>	spear thistle	i	R	cirvul
Asteraceae	<i>Hieracium antarcticum</i>	Antarctic hawkweed	n	S	hiepat
Asteraceae	<i>Leptinella scariosa</i>	buttonweed	n	F	lepsca
Asteraceae	<i>Nassauvia gaudichaudii</i>	coastal nassauvia	n*	F	nasgau
Asteraceae	<i>Senecio vaginatus</i>	smooth Falkland daisy	n	O	senvag
Asteraceae	<i>Senecio vulgaris</i>	groundsel	i	F	senvul
Blechnaceae	<i>Blechnum magellanicum</i>	tall fern	n	F	blemag
Blechnaceae	<i>Blechnum penna-marina</i>	small fern	n	C	blepen
Brassicaceae	<i>Lepidium didymum</i>	lesser swine watercress	n	O	lepdid
Callitrichaceae	<i>Callitriche antarcticum</i>	water starwort	n	F	calant
Calyceae	<i>Lobelia pratiana</i>	berry lobelia	n	F	lobpra
Caryophyllaceae	<i>Cerastium arvense</i>	field mouse ear	u	F	cerarv
Caryophyllaceae	<i>Sagina filicaulis</i>	annual pearlwort	i	V	sagfil
Caryophyllaceae	<i>Spergularia marina</i>	lesser sea-spurrey	n	O	spemar
Caryophyllaceae	<i>Stellaria graminea</i>	lesser stitchwort	u	-	stegra
Caryophyllaceae	<i>Stellaria media</i>	chickweed	i	O	stemed
Crassulaceae	<i>Crassula moschata</i>	stonecrop	n	F	cramos
Ericaceae	<i>Empetrum rubrum</i>	diddle dee	n	C	emprub
Ericaceae	<i>Gaultheria pumila</i>	mountain berry	n	C	gaupum
Gunneraceae	<i>Gunnera magellanica</i>	pigvine	n	C	gunmag
Juncaceae	<i>Juncus scheuchzerioides</i>	Native rush	n	F	
Juncaceae	<i>Luzula alopecurus</i>	native woodrush	n	F	luzalo
Juncaceae	<i>Marsippospermum grandiflorum</i>	tall rush	n	F	margra
Juncaceae	<i>Rostkovia magellanica</i>	short rush/brown rush	n	F	rosmag
Myrtaceae	<i>Myrteola nummularia</i>	teaberry	n	F	myrnum
Oxalidaceae	<i>Oxalis enneaphylla</i>	scurvygrass	n	F	oxaenn
Poaceae	<i>Agrostis magellanica</i>	Magellanic bent	n	O	agrmag
Poaceae	<i>Aira caryophyllea</i>	silvery hair grass	i	F	aircar
Poaceae	<i>Ammophila arenaria</i>	marram grass	i	O	ammare
Poaceae	<i>Deschampsia flexuosa</i>	wavy hair grass	n	F	desfle
Poaceae	<i>Elymus magellanicus</i>	Fuegian couch	n	O	elymag
Poaceae	<i>Festuca contracta</i>	land tussac	n	O	fescon
Poaceae	<i>Festuca magellanica</i>	Magellanic fescue	n	F	fesmag
Poaceae	<i>Hierochloe redolens</i>	cinnamon grass	n	F	hiered
Poaceae	<i>Holcus lanatus</i>	Yorkshire fog	i	F	hollan
Poaceae	<i>Poa alopecurus</i>	blue grass	n	F	poaalo
Poaceae	<i>Poa annua</i>	annual meadow grass	i	F	poaann
Poaceae	<i>Poa flabellata</i>	tussac grass	n	F	poafla
Poaceae	<i>Poa pratensis</i>	smooth stalked meadow grass	i	F	poapra
Polygonaceae	<i>Rumex spp.</i>	dock / sheeps sorrel	i	F	rumace
Rosaceae	<i>Rubus geoides</i>	Falkland strawberry	n	F	rubeo
Rubiaceae	<i>Galium antarcticum</i>	Antarctic bedstraw	n	F	galant
Urticaceae	<i>Urtica urens</i>	annual stinging nettle	i	S	urture

Table 4.3. Diversity measures for all plots and each of the 17 sites sampled.

Diversity measures							
Sites	No. plots	A	B	Shannon index	Evenness index	No. Evenness plots	Simpson index
All Sites	191	3.6	0.52	0.60	0.51	151	0.31
Albemarle -cattle	12	4.3	0.40	0.91	0.78	8	0.45
Albemarle- reideer	12	3.6	0.45	0.79	0.76	9	0.43
Bleaker Is.-5 yr	11	2.4	0.26	0.43	0.47	8	0.23
Bleaker Is.-15 yr	9	4.9	0.29	0.93	0.59	9	0.50
Cape Dolphin	20	4.8	0.41	0.92	0.60	19	0.48
Cobb's stand (Bleaker Is.)	12	4.4	0.23	0.69	0.45	12	0.35
Ear	11	2.4	0.14	0.37	0.46	8	0.20
Kidney	20	3.4	0.22	0.47	0.38	17	0.23
North End	6	2.2	0.21	0.30	0.60	2	0.15
North West	7	2.3	0.23	0.37	0.54	4	0.20
Port Harriet	12	3.4	0.19	0.45	0.39	11	0.24
Precipice Hill	9	7.9	0.28	1.22	0.59	9	0.53
Rabbits ear	6	3.8	0.39	0.77	0.54	6	0.39
Sett. Rookery	4	4.5	0.28	0.93	0.72	3	0.49
South End	12	3.0	0.20	0.37	0.35	9	0.18
Surf Bay	12	3.3	0.45	0.63	0.53	12	0.36
West Point	16	1.4	0.06	0.04	0.14	5	0.01

Table 4.4. Pearson product correlations ≥ 0.5 between nutrients plant variables, tussac cover and non-native cover (%), and number of non-native species by treatment. Symbols for significant levels: p-value $<0.001 = ***$, p-value $<0.01 = **$, p-value $<0.05 = *$; Grazed n=71; Ungrazed n=30; Prev. grazed n=87;

nutrient s	tussac cover			Non-native % cover			Non-native species count		
	Grazed	Ungrazed	Prev. grazed	Grazed	Ungrazed	Prev. grazed	Grazed	Ungrazed	Prev. grazed
Ca	-	-	-	-	0.475	-	-	-	-
K	0.663** *	-	-	-	0.596** *	-	-	-	-
Mg	-	-	-	-	-	-	-	-	-
P	-	-	-	-	0.542**	-	-	-	-
Al	-	-	-	-	-	-	-	0.629** *	-
B	0.548** *	-	-	-	-	-	-	-	-
Cu	0.572*	-	-	-	-	-	-	-	-
Fe	-	-	-	-	-	-	-	0.688** *	-
Mn	-	-	-	-	-	-	-	-	-
Na	0.576** *	-	-	-	-	-	-	-	-
S	0.586** *	-	-	-	-	-	-	-	-
Zn	0.580** *	-	-	-	-	-	-	-	-

Table 4.5. Analysis of variance results for tussac cover (%), number of seabird burrows, and median nutrient concentrations (ppm) by treatment in 188 plots, except for exchangeable nitrogen (ppm) analyses where different sample sizes are noted. Dunn's posthoc results of statistically significant values for all pairwise comparisons are marked by asterisks when $p < 0.05$. Symbol “-” represents not statistically significant and “*” are statistically significant.

	<i>Ungrazed</i> <i>n=30</i>	<i>Prev grazed</i> <i>n=87</i>	<i>Grazed</i> <i>n=71</i>	<i>p-value</i>	<i>H</i>
tussac cover	0.525	0.563*	0.325*	0.012	8.859
# burrows	0	0	0	-	-
Ca	1797.0*	1033.0	1061.0	<0.001	20.534
K	475.7	401.7	469.0	-	-
Mg	724.5	648.5	1022.0*	<0.001	23.171
P	278.5*	117.8	71	<0.001	28.272
B	2.502*	1.868	1.800	0.002	12.874
Cu	1.599*	0.932	1.000	<0.001	14.453
Mn	7.463	8.217	4.500*	0.0002	12.787
Na	1051.5	954.2	2218.0*	<0.001	32.430
S	122.51	65.790	105.0	-	-
Zn	23.50*	12.370*	8.400*	<0.001	38.680
Al	173.0	308.0	359.0	-	-
Fe	163.0	195.2	210.0	-	-
	<i>n = 18</i>	<i>n = 21</i>	<i>n = 47</i>	<i>p-value</i>	<i>H</i>
N-NO ₃ ⁻	47.586	3.055	16.908	<0.001	20.845
N-NH ₄ ⁺	18.344	40.369	24.453	-	-

Supplemental information:

Appendix A. Plant families, number of species, and percent (%) of taxa.

Family	Number of species	% of Taxa
Apiaceae	2	4.3
Asteraceae	8	17.4
Blechnaceae	2	4.3
Brassicaceae	1	2.2
Callitrichaceae	1	2.2
Calyceraceae	1	2.2
Caryophyllaceae	5	10.9
Crassulaceae	1	2.2
Ericaceae	2	4.3
Gunneraceae	1	2.2
Juncaceae	3	6.5
Myrtaceae	1	2.2
Oxalidaceae	1	2.2
Poaceae	13	28.3
Polygonaceae	1	2.2
Rosaceae	1	2.2
Rubiaceae	1	2.2
Urticaceae	1	2.2
Total	46	100.0

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BIOGRAPHY OF THE AUTHOR

Dulcinea V. Groff was born in Arkansas in 1983 to the parents of Robert and Julia Groff. D. Groff was raised on a farm in Quitman, Arkansas where she spent her summers learning how to grow plants for sustenance, building houses with her father, living with family friends in foreign countries, and playing the piano. After graduating from Conway Senior High School in 2001 in Conway, Arkansas, D. Groff attended Lisa-Meitner Gymnasium in Geldern, Germany for one year as a U.S. Ambassador in the Congress-Bundestag exchange program. After learning German, D. Groff attended intensive Spanish language classes at the school Carpe Diem in Madrid, Spain for six months. From 2003 to 2007, D. Groff earned a B.Sc. in Biology from the University of Central Arkansas (UCA) in Conway, Arkansas. While an undergraduate student at UCA, D. Groff contributed to the research of Dr. Richard Noyes, and subsequently began a M.Sc. in Biology with a focus on plant evolutionary biology. After defending her Master's degree, D. Groff worked as a research assistant for Dr. Noyes, followed by fieldwork on high mountain stream ecosystems in Yosemite National Park, California until 2013. In 2012, D. Groff instructed online courses in Biology at American Inter-Continental University Online. In August 2013, D. Groff began working on her PhD at the University of Maine, Orono. During her graduate studies at the University of Maine, D. Groff taught biology labs, lectured for courses in the Ecology and Environmental Sciences program, and completed a three-month internship at the World Wildlife Fund in Washington DC in 2016. She is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Sciences from the University of Maine in December 2018.