ECOLOGY

Seabird establishment during regional cooling drove a terrestrial ecosystem shift 5000 years ago

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The coastal tussac (*Poa flabellata*) grasslands of the Falkland Islands are a critical seabird breeding habitat but have been drastically reduced by grazing and erosion. Meanwhile, the sensitivity of seabirds and tussac to climate change is unknown because of a lack of long-term records in the South Atlantic. Our 14,000-year multiproxy record reveals an ecosystem state shift following seabird establishment 5000 years ago, as marine-derived nutrients from guano facilitated tussac establishment, peat productivity, and increased fire. Seabird arrival coincided with regional cooling, suggesting that the Falkland Islands are a cold-climate refugium. Conservation efforts focusing on tussac restoration should include this terrestrial-marine linkage, although a warming Southern Ocean calls into question the long-term viability of the Falkland Islands as habitat for low-latitude seabirds.

INTRODUCTION

Seabirds are sentinels of global change, bridging marine and terrestrial ecosystems as chemical and physical engineers (*1–3*). Seabird populations in the South Atlantic (i.e., south of 50°S) and Southern Ocean are facing direct and indirect impacts of climate change due to rising temperatures and ocean acidification (*2, 4*). However, long-term monitoring of seabird populations in the South Atlantic and Southern Ocean typically only began in the 1950s, posing a challenge to understanding the long-term responses of seabirds to global change (*5–7*). Seabirds there today are sensitive to broad-scale physical forcing like the Southern Hemisphere westerly winds (SWW) (*8–10*) and linked to the El Niño–Southern Oscillation (ENSO)–mediated sea surface temperatures (SSTs), which can alter the functioning of ecosystems, such as pulses of marine primary productivity leading to bottom-up food web changes (*11*). Availability of breeding habitat and oceanographic processes play a key role in the redistribution and shifting abundances of seabird species. During deglacial warming, Antarctic sea ice retreated; in response, circumpolar seabirds expanded poleward from sub-Antarctic glacial refugia, a process that may have been echoed by more recent range shifts (*12*). Limited evidence from a single species from the Falkland Islands suggests that seabirds did not use the Falkland Islands as refugia during the last glaciation (*12*). Thus, the baseline natural variability of seabird populations in the South Atlantic Ocean remains unknown because of a lack of long-term records from the region. Furthermore, it is difficult to disentangle the relative influence of recent climate change from the influence of over a century of threats from terrestrial habitat degradation, oil exploration, fishing, and whaling (*2, 13*). Paleoecological reconstructions offer a promising way forward, providing information about the response of seabirds and their terrestrial habitats to past climate change (*10, 14*). These natural experiments can inform conservation strategies, identifying populations or ecosystem processes at risk while contemporary threats may still be emerging (*15*).

Because seabirds breed on land, predicting their sensitivity to climate change requires an understanding of long-term trends in both marine and terrestrial habitats. Seabirds deposit high concentrations of guano in coastal plant communities (*16*), which enhances primary productivity across sub-Antarctic islands and drives terrestrial food webs (*1, 17*). In turn, many seabirds rely on the terrestrial plant communities their subsidies support by providing nest building material, soft peat for digging burrows, and shelter from the persistent SWW (*17*). Fecal subsidies also leave behind geochemical signatures, such as high concentrations of nitrogen enriched in the heavy nitrogen isotope (^{15}N) (*18*) and "bio-elements" (e.g., As, Cd, Cu, P, Se, and Zn), heavy metals that bioaccumulate in top marine predators such as seabirds (*19*). These bio-elements are preserved in sediment archives for millennia, providing long-term records of the response of seabirds to changing environments (*10, 18–20*). In the South Atlantic, many species of seabirds rely on grasslands that form a coastal fringe around ice-free sub-Antarctic islands (*21*). These coastal grasslands are composed primarily of a single species, *Poa flabellata*, or "tussac" grass. *P. flabellata* forms extensive peat deposits beneath tall, fibrous pedestals, reaching heights of >4 m (fig. S1). These provide shelter for burrowing and ground nesting seabirds and pinnipeds from the strong SWW, including endemic species and several with "near threatened" or "vulnerable" status. Globally important populations of seabirds, shorebirds, and passerines use *P. flabellata* grasslands for breeding, resting, and molting (table S1).

To understand the long-term sensitivity of seabirds and their terrestrial habitats, we generated a 14,000-year multiproxy reconstruction from *P. flabellata* peatlands in the Falkland Islands, a region of high marine productivity positioned in the core of the SWW (51°S) and at the northern boundary of the sub-Antarctic front (Fig. 1A). This location is ideal for testing hypotheses about primary drivers and long-term seabird responses to global change, for two reasons: First, the Falkland Islands are located at the boundary of several potential climate drivers, and our record should thus be sensitive to changes in the SWW, Antarctic sea ice, and SST. Second, *P. flabellata* peatlands have the highest accumulation rates of any peatland in

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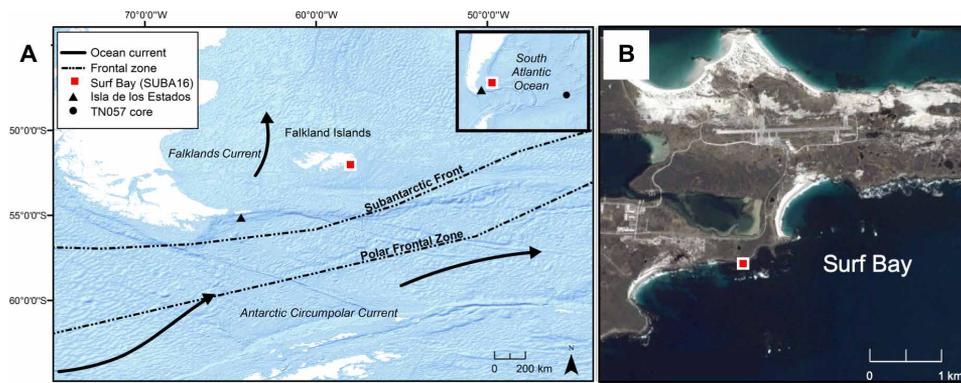†These authors contributed equally to this work.

Fig. 1. Maps of the study area in the Falkland Islands and coring locations important to this study in the South Atlantic Ocean region. (**A**) Geographic location of the Falkland Islands with regionally important oceanic currents and frontal zones. Coring site is demarcated by a red square at Surf Bay, East Falkland (SUBA16; this study); a triangle at Isla de los Estados, Tierra del Fuego, Argentina is the site of a wind reconstruction (*30*) and a solid black circle marks the site of the TN057 core from the eastern South Atlantic (map inset) (*36*, *37*). Location of peat collection site (**B**) Surf Bay, East Falkland (red square). Map data in (A) from NASA and in (B) from Google and Maxar Technologies, 2019.

the world, providing an unusually high-resolution record capable of recording abrupt changes (*22*). Our multiproxy approach to reconstruct the sensitivity of a terrestrial-marine linkage to global change combines several proxies: bio-elements as geochemical indicators for seabird presence, elevated $\delta^{15}N$ as an indicator for animal-derived nitrogen for vegetation, pollen accumulation rates and abundance (%) to reconstruct past coastal vegetation changes and tussac grass trends, accumulation rates of long-distance transported (LDT) pollen from southern South American trees (e.g., *Nothofagus*) as a proxy for changes in the latitudinal position and/or strength of the SWW (*23*), and macroscopic charcoal accumulation rates (CHAR; no. >125 μm particles cm^{-2} $year^{-1}$) to reconstruct past fire history, which, in grasslands, is typically controlled by fuel loads and productivity rather than aridity (*24*).

The climate of the Falkland Islands is primarily influenced by the SWW that drive upwelling of the cold, nutrient-rich waters of the Antarctic Circumpolar Current and the Falklands Current that support high primary productivity in seabird foraging grounds (*11*, *25*). In recent decades, the SWW has intensified and shifted poleward (*26*, *27*). Foraging success in penguins has been linked to windier conditions in the Falkland Islands (*9*), and the shift may lead to increased wind-driven upwelling and optimal foraging conditions for seabirds (*11*). Pelagic seabirds on sub-Antarctic islands of the Indian Ocean improved foraging performance by tracking the intensifying and shifting SWW (*8*); however, their response in the South Atlantic is unknown. Short-term monitoring of seabirds in the South Atlantic indicates provisioning rates, and the growth of chicks declined with increased SST (*9*, *11*), whereas colder than average winter SST provided optimal foraging conditions (*28*). Long-term declines in sea ice extent and warming SST in the South Atlantic are linked to the recruitment and dispersal of prey species and drive productivity of higher trophic level predators (*13*, *29*). The seabird response to regional climatic and local factors is unknown in the Falkland Islands, and their variability would also depend on other characteristics of a species (e.g., foraging ecology and trophic level) (*13*).

RESULTS
Surf Bay, East Falkland, Falkland Islands (51°42.012′S, 57°46.962′W) is a designated recreational open space near the town of Stanley,

East Falkland (Fig. 1B). Today, there are no established colonies of seabirds at Surf Bay, and the predominant vegetation includes a mix of grasses, including restored *P. flabellata*, and an ericaceous shrub, *Empetrum rubrum* (diddle-dee). The lack of seabirds today is likely due to the site's use as a common ground for grazing outside of the capital of Stanley. In 2016, we collected a 476-cm column of peat from an exposed bank (fig. S1). The peat column was uniformly organic with an abundance of compact, undecomposed *P. flabellata* leaves, terminating in gray inorganic silts at its base (fig. S2). Four tussac grass leaves were submitted for radiocarbon analysis (table S2), and the dates were used to construct a linear age model (fig. S3).

Our 14,000-year record captures the development of a terrestrial-marine linkage that supports some of the most important breeding colonies of seabirds in the Southern Ocean today. Our record of marine animal–derived $\delta^{15}N$ signature of +20 per mil (‰) indicates the presence of high trophic level species similar to modern seabirds (see Supplementary Text for examples). At Surf Bay, bio-elements indicate that seabirds were absent or in low abundance from 14 to 5.0 thousand years before present (ka BP; all dates are calibrated years before 1950; Fig. 2, A to F). At ~5.0 ka BP, multiple proxies indicate an abrupt transition. First, bio-element concentrations increased, indicating the establishment of seabird breeding colonies at Surf Bay (Fig. 2, A to D); a second shift in bio-elements at 2.0 ka BP (an assemblage transition from As, Cd, Cu, and Se to P and Zn) may indicate a change in the seabird communities at this site (Fig. 2, E and F). Second, grass pollen accumulations rates, which had been low since the beginning of the record, increased to their highest values, indicating the establishment of a *P. flabellata* grassland within 200 years or less following the establishment of seabird colonies (Fig. 2H). Because *P. flabellata* is the main peat forming coastal grassland, we assume that it is the main contributor to the Poaceae pollen accumulation record; although other grass species [e.g., coastal bluegrass (*Poa alopecurus*) and white grass (*Cortaderia pilosa*), an acid grassland species] may have contributed, their pollen is indistinguishable (fig. S4). Third, the $\delta^{15}N$ signature of the peat increased from ~0 to ~20‰ (Fig. 2G) at the same time as the increase in bio-elements and before the Poaceae pollen accumulation rate increase, representing a state shift in the baseline nutrient cycling at this site. Last, charcoal accumulation rates increased above background levels after 5 ka BP and exceeded previous rates ~4 ka BP, indicating either a change
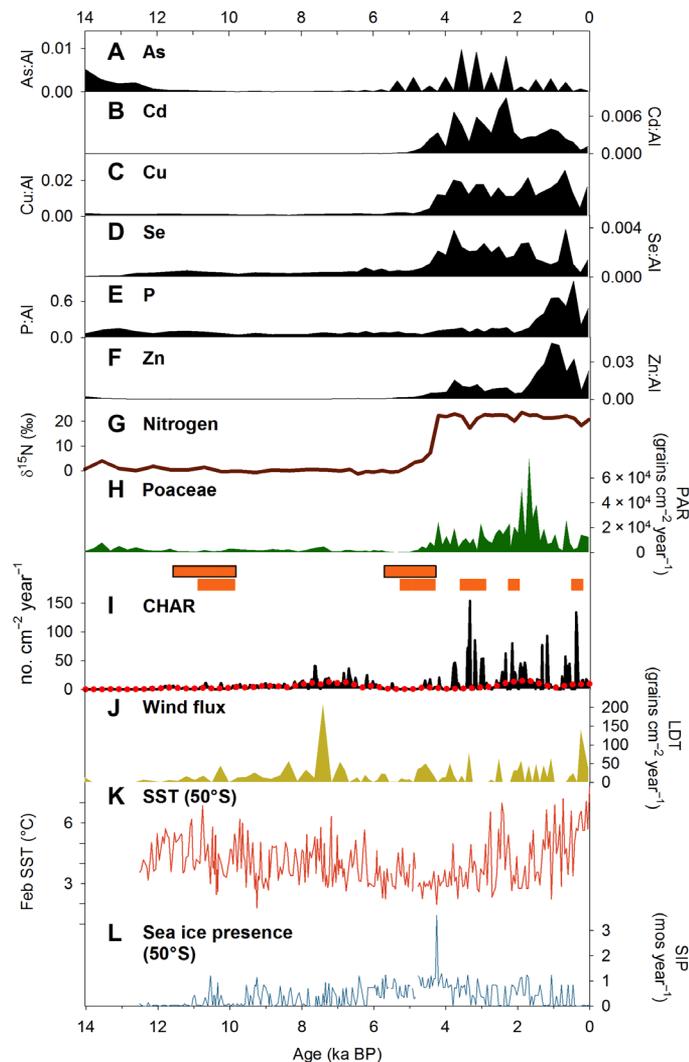
Fig. 2. Development of a terrestrial-marine linkage in the Falkland Islands over 14,000 years from a peat record (SUBA16) and other regional proxies. (**A** to **F**) Seabird-derived bio-element influx (ratio of bio-element to aluminum, a lithogenic component not influenced by guano; fig. S4). (**G**) δ15N of bulk sediment from SUBA16. (**H**) Grass pollen accumulation rate (PAR) from SUBA16 (grains cm−2 year−1); orange bars indicate >10% abundance of shrub (*E. rubrum*, outlined in black) and fern (*Blechnum* spp., orange bars) pollen, suggesting drier conditions from SUBA16. (**I**) Charcoal record (CHAR no. cm−2 year−1) in black; the red dotted line indicates charcoal background levels (low frequency) calculated using a robust 500-year Lowess smoothing window from SUBA16. (**J**) LDT pollen accumulation rate from SUBA16. (**K**) February SST (°C) at 50°S South Atlantic Ocean (*37*). (**L**) Sea ice presence (SIP; months year−1) at 50°S South Atlantic Ocean (*37*).

in ignition conditions or an increase in fuel loads (i.e., *P. flabellata* and other grasses; Fig. 2I). Fire in grassland systems is typically fuel limited (*24*), so we interpret this increase as a result of seabird-derived nutrient inputs enhancing *P. flabellata* grasslands via increased pollen accumulation rates.

DISCUSSION

Our multiproxy, high-resolution approach allows us to establish a precise order of events: For 9000 years before the arrival of seabirds

(14 to 5.0 ka BP), the region around Surf Bay was dominated by low levels of grasses and a heathland of ferns (*Blechnum* species) and dwarf Ericaceous shrubs like *Empetrum* (diddle-dee; fig. S5). An abrupt change occurred after 5.0 ka BP, with the establishment of coastal *P. flabellata* grasslands immediately following the establishment of seabird colonies, recorded by guano bio-elements and δ15N (fig. S6). These marine-derived subsidies drove changes in terrestrial plant community structure, composition, and function and facilitated an increase in fire activity and nutrient cycling. Rates of peat accumulation were lower (0.021 cm year−1) in the earlier part of the record and accumulated linearly (0.05 cm year−1) after 6.8 ka BP (fig. S3). The total pollen accumulation rate increased after ~4.6 ka BP and is similar to the record of grass pollen accumulation rate (fig. S5). This is consistent with contemporary work demonstrating that primary productivity on low-productivity islands is enhanced by marine-derived subsidies (*1*, *17*).

What drove the abrupt ecosystem state shift at Surf Bay at 5.0 ka BP? Causality can be difficult to establish in paleoecological records, but the order of events allows us to rule out and explore several proposed mechanisms. First, our record indicates that coastal tussac grasslands established immediately following the arrival of seabird colonies at the site, which rules out the possibility that seabirds were responding to terrestrial habitat changes (although we cannot rule out that each acted independently). Second, on the basis of the hypothesis that greater wind strength increases travel speeds (i.e., lower energy expenditure) of flying seabirds and the foraging success of flightless seabirds in modern systems (*8*, *9*), we expected seabird populations to coincide with windiness. Although our record indicates a decline in long-distance pollen from South America before the establishment of seabirds or grasses (Fig. 2J), we cannot rule out the hypothesis that *P. flabellata*, seabirds, or both were responding to enhanced SWW driving greater marine productivity or foraging success. Wind speed peaked between 8.0 and 7.0 ka BP (Fig. 2J) and then decreased as a result of a latitudinal shift and/or general weakening of the winds. This observation is partially consistent with evidence from Tierra del Fuego where winds increased at 7.2 ka BP for ~250 years; winds increased again between 4.5 and 3.5 ka BP over longer millennial-scale durations (*30*). Other paleoclimate records agree with the pattern of increased SWW strength from the middle to the late Holocene from southern South America (*31*), the sub-Antarctic (*32*), New Zealand (*33*), and Tasmania (*34*). Thus, seabirds established at Surf Bay when the SWW were in a stronger phase across the Falkland Islands. The change in depositional environment could have influenced the decline in LDT pollen (Fig. 2J). Tall tussac pedestals may be more effective at intercepting LDT pollen than a low-profile heathland. Because of a lack of actualistic studies, it is unknown whether LDT pollen is a reliable indicator of the SWW in Falkland Islands peat records. Pollen data from South America show that the precipitation-sensitive *Nothofagus* forest-steppe ecotone was at its maximum (easternmost) extent by 4.5 ka BP (*35*), suggesting that the depositional environment may be the primary influence with the tussac grasslands somehow "masking" the LDT pollen signal.

Multiple terrestrial and marine records indicate that the intense SWW during the middle to late Holocene coincided with a period of regional cooling from ~6.0 to ~4.0 ka BP, when cooler ocean temperatures supported sea ice presence over longer durations (*36*, *37*). In periods of cooler SSTs and higher wind stress, increased nutrient upwelling drives an increase in primary productivity (*12*), which, in turn, supports more resources for predators like seabirds (*9*). Extensive

glacier advances occurred at a similar latitude in Patagonia between 6.0 to 4.0 ka BP (*38–40*). These recent well-dated chronologies revise the timing of neoglacial cooling in the region to 6.0 ka BP, approximately 1000 years before previous interpretations (*41*). Before this marked cooling, the South Atlantic was warm and ice-free from 10.0 to 6.0 ka BP (*37*). The absence of seabirds at this site before 5.0 ka BP suggests that seabirds may be sensitive to warmer SSTs in the future. Periods of cooler SST can have impacts such as increases in seabird prey as a result of marine ecosystem restructuring (e.g., Humboldt Current) (*11*) and nonlinear effects on Gentoo penguin (*Pygoscelis papua*) populations in the Falkland Islands associated with ENSO (*42*).

Considerations of other local environmental drivers of the ecosystem changes in our record are worthy of discussion, although the evidence is less substantiated. It is possible that the ecosystem changes in our record may not reflect true seabird establishment at Surf Bay and are instead an artifact of changing sea levels driving the migration of coastal plant communities inland to our core site. However, we argue that this was likely not the case, for two reasons: First, a recent Falkland Islands sea-level reconstruction found that isostatic sea levels have only fluctuated from +0.3 m above to 1 m below present levels since 7 ka BP (*43*). When sea level was 1 m below present levels, the shoreline would have been <500 m away from our study site, so we interpret the observed changes to represent the establishment of *P. flabellata* grasslands and not the inland migration of coastal plant communities (fig. S7). Given that in the absence of grazing, *P. flabellata* can cover small islands (e.g., nearby Kidney Island is ~33 ha) and grow inland ~300 m, our study site has likely remained close enough to the ocean to support coastal communities over the period in which the study covered. Another conceivable local driver of the seabird and plant community shift is the arrival of an extinct predator, the endemic Falkland Islands wolf or "warrah" (*Dusicyon australis*) (*44*). The introduction of predators on islands can cause abandonment and redistribution of ground nesting seabirds and have an indirect effect on plant productivity and composition (*45*). The timing of the warrah's arrival remains disputed, with the earliest dated fossil evidence suggesting that it was present at least since ~3.5 ka BP (table S2) and genetic data suggesting a Last Glacial Maximum or Late Glacial presence (*46*). We cannot disentangle the warrah from other drivers of the seabird shift, and we do not rule it out as a potential driver for causing the redistribution of seabird populations within the Falkland Islands.

Our seabird-derived bio-element data suggest a compositional turnover of seabirds at ~2.0 ka BP. We consider the shift of the two bio-element assemblages to represent a community shift in either seabird species (Supplementary Text and fig. S4) (*47*) or pinniped species (e.g., Southern sea lion *Otaria flavescens*) (*48*). This coincides with a shift from cool and wet conditions in the Falkland Islands from 5.0 until 2.5 ka BP, when the Amundsen Sea low strengthened (deepened) (*49*) and the climate became warmer and drier at a similar latitude (51°S) in South America (*31*). The Surf Bay charcoal record also supports a shift to warm/dry conditions at ~3 ka BP, when charcoal influx was the highest in the 14,000-year record (Fig. 2I). The potential faunal shift indicated by the change in the bio-element assemblage at ~2.0 ka BP (Fig. 2, A to F) occurred after a 2°C warming of February SSTs at 50°S in the South Atlantic Ocean (*37*) and enhanced SWW over Tierra Del Fuego at 1.75 ka BP (*30*). It also coincides with west Antarctic Peninsula SST warming (*50*), a highly variable ENSO state, a longer duration of sea ice presence in the eastern South Atlantic (*37*), and regional cooling (*38*, *51*). Without knowing species compositions, it is difficult to identify a causal mechanism for the apparent turnover, but it may reflect poleward range shifts in seabird species as ocean temperatures warmed. Additional paleontological data, compound-specific stable isotope analyses, and contemporary genetic data may help resolve this question and shed light on the future of nearshore food webs in the Falkland Islands. Regardless of a causal mechanism, the nitrogen isotope remained high during the turnover, indicating that some degree of functional replacement as marine predators were present before and after grasses reached peak productivity (Fig. 2G). Whether the shift is representative of a regional, versus a local, shift should be determined by analyzing additional seabird locations. The ultimate disruption of these coastal communities came with the widespread establishment of grazing, which reduced tussac coverage by ~80% (*52*), although the possible impact of sealing and whaling on marine food webs, and thus the terrestrial-marine linkage, remains unknown.

A warming South Atlantic casts doubt over the future of the Falkland Islands as a long-term seabird breeding hot spot. Warm SST can affect seabirds by limiting food resources (*13*), as warmer SSTs and reduced wind stress lead to shallow mixing and less nutrients available for primary productivity (*53*). Seabirds of the South Atlantic forage across great distances and are some of the most well studied in the world (*11*). Our work suggests that as the Southern Ocean continues to warm in the coming decades, the Falkland Islands seabird communities may undergo abrupt turnover or collapse, which could happen on the order of decades.

CONCLUSION

Our 14,000-year record provides evidence of a direct linkage between marine top predators and island plant communities and a terrestrial ecosystem state shift associated with regional neoglacial cooling. Our results show that seabirds have largely used the Falkland Islands as refugia during climate cooling in the Holocene; however, the question of where seabirds were during warmer conditions remains open. This knowledge is troubling, as contemporary seabirds face a warming southern South Atlantic and Southern Ocean compounded by other anthropogenic threats such as fisheries bycatch and invasive species (*4*); contemporary reserve designs may not be robust to range shifts, especially as they cross international boundaries. Our work does offer hope for coastal restoration efforts, highlighting the importance of incorporating seabird-derived nutrients or their analogs in efforts to restore coastal grasslands. These habitats can establish within decades of a state shift and persist for millennia, providing critical ecosystem services. How will seabirds adapt in a warmer world? Our results suggest that as they shift their ranges to track suitable habitats, we may see coastal ecosystem changes as a result of changing nutrient subsidies, which may, in turn, have impacts on other biodiversity, as tussac grasslands are highly productive but relatively species poor. Our work highlights the utility of paleoecological information to reveal the response of sensitive cross-ecosystem linkages to abrupt climate change and to inform restoration efforts as seabirds face unprecedented global changes.

MATERIALS AND METHODS
Peat profiles
We excavated a 476-cm column from Surf Bay on East Falkland, Falkland Islands (51°42.012′S, 57°46.962′W) in 2016 (SUBA16) (fig. S1),

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 (fig. S2).

Chronology
Grass leaf macrofossils were selected from each peat profile and submitted to the Keck Laboratory (University of California, Irvine) for accelerator mass spectrometry radiocarbon dating. Radiocarbon dates were calibrated to calendar years with the Southern Hemisphere calibration curve SHCal13 (table S2) (54), and age-depth models were constructed using a linear interpolated age-depth model in clam software (clam v. 2.2; fig. S3) (55).

Loss on ignition and ash-free bulk density calculation
Subsamples (2 cm^3) were analyzed for loss on ignition (LOI) by weighing after heating in a muffle furnace at 100°C for 24 hours (dry weight), 550°C for 4 hours (to remove organic carbon), and 1000°C for 2 hours (to remove carbonates), following Heiri et al. (56); post-LOI residue weights were also recorded to quantify the mineral fraction (fig. S3). We used the dry bulk density, which is calculated as the ratio of dry weight (g) to volume (cm^3) of each LOI subsample. The ash-free bulk density (g cm^{-3}; fig. S3) is the product of the dry bulk density and LOI at 550°C (57).

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 (58) at the University of Maine. Each sample was processed with 10% potassium hydroxide (KOH) to remove humic acids, processed with 10% hydrochloric acid (HCl) to remove carbonates, sieved through a 250-μm mesh to remove large particles, processed with hydrofluoric acid to remove silicates, and processed with 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-centistoke silicone oil. Samples were spiked with a 0.5-cm^3 solution containing a known number of microspheres (2.5 × 10^4 ± 8% SD; LacCore) to calculate pollen concentrations (no. grains cm^{-3}), which is the ratio of the number of pollen grains counted to number of microspheres counted multiplied by the ratio of known concentration of microspheres and sample volume. Terrestrial and aquatic pollen, fern spores, and algae were identified using a Nikon microscope at ×40 magnification. We counted at least 300 total pollen and spores for each subsample. To estimate time and effort to encounter a previously unidentified or rare pollen type for these samples, we used PolyCounter 3.1.4 by T. Nakagawa to tally and create a rarefaction curve of the ratio of the number of species to total count of pollen and spores. We quantified pollen accumulation rates and abundance (%) to reconstruct past coastal vegetation changes. Pollen accumulation rates were calculated using the sedimentation rate and pollen concentration for each horizon. The sedimentation rate (cm year^{-1}) used is the average sedimentation rate from clam results of the linearly interpolated age-depth model (ranging from 0.25 to 0.5 cm year^{-1}). The pollen accumulation rate (grains cm^{-2} year^{-1}) is the product of the

pollen concentration (no. grains cm^{-3}) and sedimentation rate (cm year^{-1}). Because no trees occur naturally on the Falkland Islands (59, 60), LDT pollen from southern South American trees (e.g., Nothofagus) is used as a proxy for the latitudinal position and/ or strength of the SWW (23, 61). The accumulation rate of exotic pollen grains has been used in the region (61) and Falkland Islands (23) as a proxy to reconstruct wind flux. LDT pollen may track the expansion of arboreal taxa in South America in the early Holocene (62). However, at 53°S, these South American arboreal taxa reached their current extent by 11.0 ka (31).

Geochemical analysis—Bio-elements and nitrogen
To reconstruct seabird populations, we analyzed 48 peat samples from SUBA16 for bio-elements associated with guano (19, 20, 47, 63–66). Bio-element subsamples were selected from the same horizons as pollen samples, but at 10-cm intervals instead of 5-cm intervals. 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 inductively coupled plasma mass spectrometry (ICP-MS) (Sawyer Water Research Laboratory, University of Maine) using internal standards and blanks (International Soil-Analytical Exchange: ISE921 7-31-11 2000, Riverclay-91, Netherlands) for concentration (parts per million) of Al, As, Ba, Be, Cd, Co, Cr, Cu, Fe, Mn, P, Pb, Se, Ti, U, V, and Zn. The bio-elements (As, Cd, Cu, P, Se, and Zn) were normalized by aluminum (Al) and are represented as the ratio of the bio-element to Al. Aluminum was presumed to be an indicator of mineral (non-guano) input; normalizing metal concentrations with an element that is less mobile and not influenced by guano provides a way to cope with the variations in mineral fractions. A principal components analysis of all non-normalized elemental concentrations in SUBA16 grouped assemblages of bio-elements and other elements corresponding to local lithology (e.g., Al and Ti) (67). Aluminum represents a lithologic component of the peat record influenced by mineral input because it is similar to other common lithologic components that are less likely to be remobilized because of postdepositional processes (fig. S4). The maximum concentrations of bio-elements in SUBA16 were compared to bio-elements from modern surface soils (top, 5 cm) collected opportunistically within and outside of seabird colonies in the Falkland Islands. Samples were treated and analyzed identical to peat samples prepared for ICP-MS (fig. S4).

We used analysis of nitrogen stable isotopes of peat to determine δ^{15}N of the vegetation and nitrogen sources at Surf Bay. Bulk samples were dried at 100°C for 12 hours and pulverized using an agate mortar and pestle. Ground samples were loaded into tin capsules for δ^{15}N stable isotope analysis at the University of Wyoming Stable Isotope Facility (Laramie, WY) using a Carlo Erba 1110 Elemental Analyzer coupled to a Thermo Delta V isotope ratio mass spectrometer. Values were normalized to the δ^{15}N of air using quality control standard reference material UWSIF-05 (alfalfa) for nitrogen isotopic composition. δ^{15}N values are reported with respect to air in parts per thousand (‰). Analytical precision was SD ± 0.06‰ for δ^{15}N based on repeated analysis of internal standards.

Charcoal analysis
Charcoal processing followed protocols modified from (68) using contiguous sampling of 1-cm^3 sediment volumes of peat. We placed the subsamples in ~25 ml of 7% hydrogen peroxide at 50°C for

24 hours and then wet-sieved them with deionized water through a 125-μm 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 (no. >125 μm particles cm^{-3}) and then converted to charcoal accumulation rates (CHAR; no. >125 μm particles cm^{-2} year^{-1}) using CharAnalysis version 1.1 for Windows OS (69, 70). CharAnalysis was used to calculate the low-frequency background component, CHARBACK, using a robust 500-year Lowess smoothing window (69).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/6/43/eabb2788/DC1

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