Southern Ocean seabird population shifts over the Holocene revealed by peat sequestration of mercury from guano

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Abstract

Monitored seabird populations have declined by up to 70% worldwide since the 1950s, yet little is known about population sizes or long-term trends prior to anthropogenic impacts. This is particularly true for the Southern Ocean, where seabirds and many other species are currently facing multiple environmental threats. Here, we identify shifts in seabird populations over the last 8100 years by applying a mercury (Hg) flux and isotope signature technique as a novel tracer of population size via guano input into peatlands on sub-Antarctic Bird Island (South Georgia). Our results show that seabirds have colonized Bird Island between 6800 and 6100 years ago, which pre-dates evidence for colonization of other sub-Antarctic islands by more than 1000 years. There are five periods when seabird populations were at maxima during the mid- to late-Holocene, coeval with periods of lower Southern Hemisphere westerly wind intensity. Our study provides unprecedented insights into cyclicity in seabird population sizes as a consequence of regional to large-scale environmental change.

Keywords: seabird populations, climate change, Holocene, peat, mercury

Introduction

Monitored seabird populations have declined globally by ~70% between 1950 and 2010 [1] due to a range of human activities, such as overfishing of food sources, pollution, climate change, and incidental mortality (bycatch) in fishing gear, particularly in the Southern Hemisphere [2]. These rapid declines threaten wider ecosystem structure and function, because seabirds provide ecological services, including energy and nutrient transport and cycling [3]. Seabirds are also excellent indicators of spatiotemporal changes in marine ecosystem health since they are long-lived, wide-ranging, and forage at high trophic levels [4].

The Southern Ocean is an area of high conservation priority because it is the foraging area for very large seabird populations [5], including many threatened species [2]. Numerous Southern Ocean seabird species are projected to decline further in response to future climate change, such as increased sea surface temperature and decreased sea-ice extent [6] that reduce survival rates and breeding performance [6–9]. Current monitoring of seabird population sizes and trends largely relies on counts in the field, digital image analysis (from satellites, aircraft or drones) [10], or acoustic loggers for some burrowing species [11,12]. However, almost all monitoring programs started in the last few decades, and are therefore not able to determine longer-term impacts of natural and anthropogenic drivers. This limits our understanding of pre-industrial baselines and ability to develop longer-term (decadal scale) mitigation plans or assess the range of natural pressures on seabird populations.

Biogeochemical analysis of natural archives, such as lake sediments and peat cores, offers opportunities to fill this knowledge gap by providing long-term reconstructions of changing seabird populations [13]. Many Southern Ocean seabirds breed on islands where there are lakes, ponds, and peatlands. Seabirds feed on crustaceans (e.g., Antarctic krill, *Euphausia superba*), cephalopods, and fish[14–16], and when back at their breeding and roosting sites excrete guano that is enriched in nutrients and bio-elements (e.g., N, C, P, Fe, Cu, Se, Co, Ni, Zn, Mn); these can facilitate plant growth and peat formation [17]. Guano can also be transported through runoff and seepage into coastal waters, and lakes, where elements are preserved in sediments [18,19].

Several studies of lake sediment records from the Northern Hemisphere [13,20–25] and Antarctica [19,26,27] have shown seabird population changes in response to climate, ecosystem shifts, explosive volcanism, or anthropogenic influences. For example, geochemical and biomarker methods applied to an 8.5-ka lake sediment profile from Ardley Island revealed that a penguin colony was established following warm conditions on the northern Antarctic Peninsula c. 6.7 ka BP, which is the earliest known for the region [19]. Data on seabird population trends prior to the 1950s are limited, and information derived from peat deposits is even rarer, with only three relevant studies available to date [17,25,28]. Two studies that are largely based on permafrost cores show different timing of seabird presence at different coastal areas in northwest Greenland [25,28], including the first recorded arrival of the little auk (*Alle alle*) at c. 4.4 ka BP in the Annikitsoq area [25]. In the Southern Ocean, a peat core from the east coast of the Falkland Islands indicates colonization by seabirds c. 5 ka BP during a period of regional cooling [17]. The past seabird information from all three peat studies largely relies on bio-elements [17,25] and stable isotopes (C, N) [28], in addition to grass pollen and charcoal proxies [17]. However, some bio-elements might not be widely applicable as tracers for seabird presence in peatland deposits because of their role in metabolism. These bio-elements can be recycled by vegetation during peat decomposition, possibly obscuring the signals of guano deposition at the time of peat formation.

Mercury (Hg) is a non-essential trace element that can be a suitable tracer for the incorporation of guano into peat deposits. This element bioaccumulates in marine organisms, and biomagnifies through trophic levels, ultimately reaching high concentrations in top predators such as seabirds [29,30]. Seabird guano input enhances Hg concentrations in peatlands compared to unoccupied sites, leading to high Hg loads at breeding colonies [31–33]. For example, a mean total Hg (THg) concentration of 114 ± 50 ng g^{-1} (n = 43) was recorded in deposited guano from a colony of herring gulls *Larus argentatus* on a peatland surface in North America [33]. This is three times higher than the mean THg concentration in a remote, uncolonised peatland (37 ± 34 ng g^{-1}, n = 101) [34], which mainly receives Hg from atmospheric deposition. Vegetational sequestration of gaseous element Hg^0, the dominant form of Hg in the atmosphere, is the main deposition pathway of Hg to peatlands in the absence of avian influence [35]. Once taken up by vegetation, Hg^0 is oxidized to Hg^{II} via intra-cellular enzymatic reactions or by reactive oxygen species [36]. Rainfall also contributes Hg^{II} to peatlands, but at lower rates (e.g., 20 – 30% of total atmospheric Hg [34,35,37]). Deposited Hg^{II} from rainfall, or produced by oxidation of Hg^0 associated with plant uptake, forms thermodynamically stable complexes with thiol groups of decomposing organic matter in peat, potentially forming immobile nanoparticulate β-HgS [38]. The strong affinity of Hg^{II} to organic matter thiols makes it less susceptible to reduction back to Hg^0 [39], thus Hg in peatlands has the potential to reflect input from both the atmosphere and guano [40]. Additionally, the Hg stable isotope signatures of atmospheric Hg^0, rainfall $Hg^{II,}$ and guano Hg are distinct [27,34], enabling quantification of these input sources to peat.

In this study, we apply Hg flux and stable isotope analysis to peatland deposits found on sub-Antarctic Bird Island, a small island at the western end of the South Georgia island group (Fig. 1). South Georgia holds globally important breeding populations of seabirds, including several small but highly abundant burrowing petrel species, as well as threatened albatross, petrel and penguin species listed by the *International Union for the Conservation of Nature* because of steep population declines [2,41]. Our main study site at Bird Island, BI10, is a valley peatland that dates back c. 8.1 ka ago. The BI10 site receives water largely from surface drainage, with a high water table sustained through gravitational lateral seepage from adjacent slopes [42,43]. Guano from seabirds breeding on these slopes is transported from the catchment to the BI10 peatland site. For reference, we investigated changes in Hg at two control sites in the absence of large resident bird colonies: 1) POB4, a highly minerotrophic peatland profile was taken from the Prince Olav Harbour Bog on nearby mainland South Georgia, and 2) FIGG, a peat profile was taken 12 km east of Goose Green on the Falkland Islands. The POB4 profile includes a (lacustrine) sediment sequence at its base and is dated between c. 4.5 – 8.5 ka BP (Supplementary note 1; Supplementary Figs. S1, S2). All the peat profiles examined in this study were undisturbed and increased in thickness over time, providing a continuous record of the environmental conditions prevailing at the time of peat formation [44].

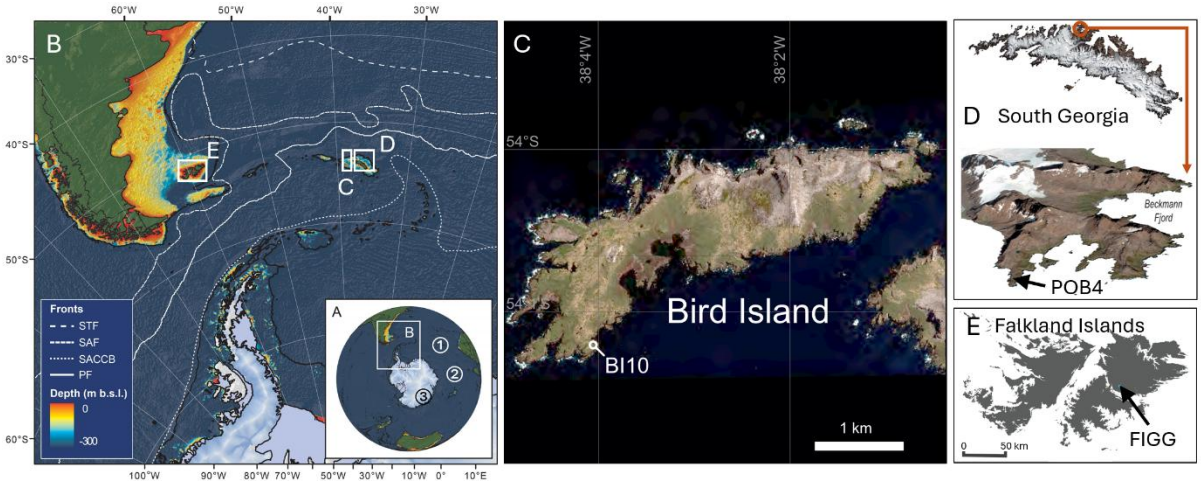

Fig. 1: (A) Map of the Southern Hemisphere, highlighting sub-Antarctic regions where peatlands were sampled for this study. ①, ②, ③ show sea-ice records from Nielsen et al., (2004) [45], Orme et al., (2020) [46], and Röthlisberger et al., (2002) [47], respectively. (B) Map of the southwest Atlantic sector of the Southern Ocean, showing the locations of our three peatland study sites: Bird Island, South Georgia (C, BI10 site), mainland South Georgia (D, POB4 site), and the Falkland Islands (E, FIGG site). Major oceanic fronts where seabirds can forage are shown in (B), including the Subtropical Front (STF), Subantarctic Front (SAF), Southern Antarctic Circumpolar Current Boundary (SACCB), and the Antarctic Polar Front (PF).

Results and Discussion

Holocene Hg accumulation rates at sub-Antarctic Islands

Over the past 8.1 ka, the mean Hg accumulation rates (HgAR) at Bird Island BI10 were 31.9 ± 18.3 µg m^{-2} yr^{-1} (1σ, n = 155, Supplementary Table S1; Fig. 2A), significantly higher than at the control sites at the Falkland Islands FIGG and mainland South Georgia POB4 ($p < 0.01$ for both). BI10 was characterized by prominent fluctuations with a maximum HgAR value of 97 µg m^{-2} yr^{-1}. The mean HgAR during the oldest peat formation period at BI10 of 8.1 to 6.8 ka BP was 9.2 ± 3.1 µg m^{-2} yr^{-1} (1σ, n = 4). This was followed by an approximately five-fold increase to a mean of 43.2 ± 19.0 µg m^{-2} yr^{-1} (1σ, n = 7) from c. 6.8 to 6.1 ka BP, and four other prominent HgAR peaks of up to a millennium in duration in more recent years; 5.2 – 3.5 ka BP, 2.7 – 2.1 ka BP, 1.4 – 1.2 ka BP and 0.5 – 0.1 ka BP, with HgAR of 48.3 ± 18.2 (1σ, n= 28), 45.8 ± 12.2 (1σ, n= 30), 50.0 ± 21.1 (1σ, n= 6) and 26.7 ± 6.1 µg m^{-2} yr^{-1} (1σ, n= 15), respectively (Fig. 2A).

In contrast, HgAR at the control site FIGG ranged from 1.1 to 5.9 µg m^{-2} yr^{-1}, with a mean of 2.2 ± 1.1 µg m^{-2} yr^{-1} (1σ, n = 33; Supplementary Table S2). This mean is lower than that in the mainland South Georgia POB4 profile, which was 6.0 ± 3.9 µg m^{-2} yr^{-1} (1σ, n= 74, $p < 0.01$, Supplementary Table S3; Fig. 2A). Both FIGG and POB4 receive Hg predominantly from the atmosphere by vegetation uptake of Hg^0 and rainfall supply of Hg^{II} [35]. The mean HgAR at both FIGG and POB4 are comparable to global natural background levels for peat (4.5 ± 3.2 µg m^{-2} yr^{-1}, 1σ, n = 17 peat cores) [48].

Holocene HgAR was significantly higher at BI10 than at FIGG and POB4, implying an additional, predominant source of Hg at the BI10 site (Fig. 2A). This was also reflected in the BI10 Hg/C profile (Fig. 2B), which normalizes Hg accumulation for changes in peat carbon accumulation. BI10 Hg/C shows a broadly increasing trend during the periods of high HgAR, suggesting excess Hg inputs compared to the FIGG and POB4 sites (Fig. 2B). BI10 Hg/C was at least three times higher than in the FIGG and POB4 peat cores (to c. 4.5 ka BP in POB4; Supplementary note 1), even though the mean percentage of carbon in the BI10 peat (39.0 ± 5.8 %, 1σ; n = 155) was not significantly different from

that of FIGG (43% ± 3.70 %, n = 65, $p > 0.05$) and POB4 (42.4 ± 6.7 %, n = 59, $p > 0.05$; Supplementary Table S1, S2, S3).

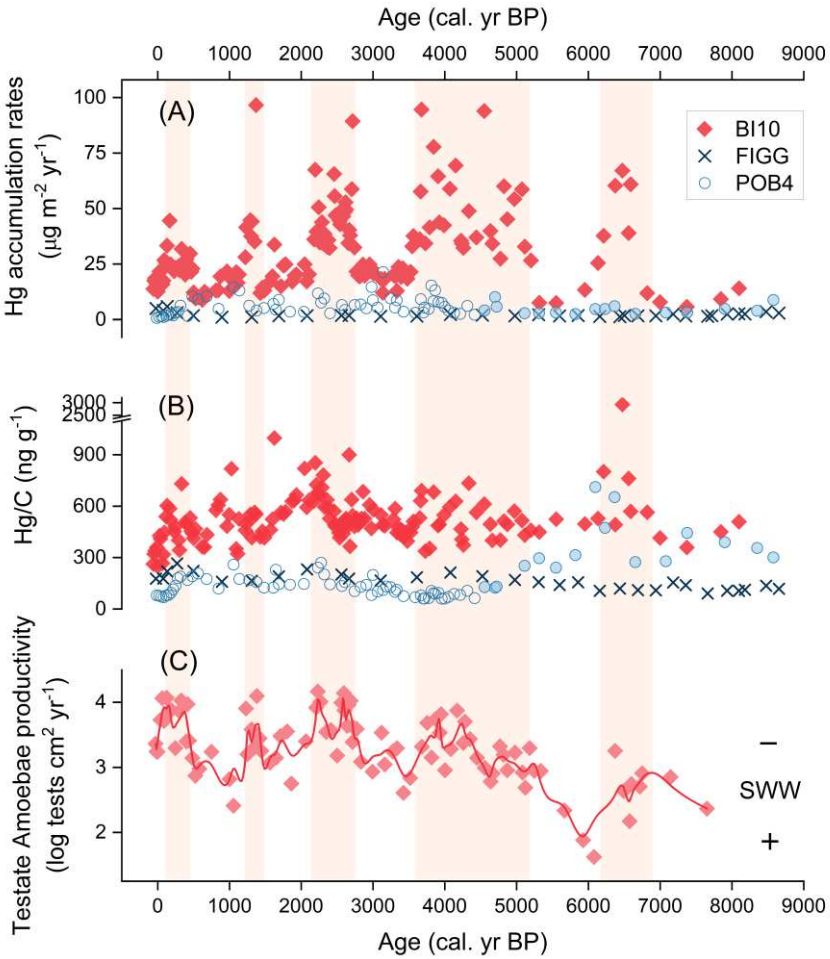

Fig. 2: (A) Hg accumulation rates in peat cores at Bird Island, South Georgia (BI10, diamonds), Falkland Islands (FIGG, crosses), and mainland South Georgia (POB4, peat section from 0 – 4.5 ka BP in open circles, sediment section from c. 4.5 – 9.0 ka BP in filled circles). (B) Hg/C profiles in BI10, FI, and POB4 cores. (C) The intensity of Southern Westerly Winds (SWW) reconstructed from BI10 *testate amoebae* productivity that is sensitive to wind-blown sea spray (Supplementary note 2) [49,50]. The red line represents the data smoothed using a 3-point moving average. Orange-shaded areas highlight five periods with high HgAR linked to enhanced guano input.

The most likely additional source of Hg at BI10 is the input of seabird guano, as this has a very high Hg content (1,200 to 21,600 ng g^{-1}, dry weight, Supplementary Table S4; Supplementary note 3). Seabirds currently breeding in the BI10 catchment at Bird Island include white-chinned petrel *Procellaria aequinoctialis*, wandering albatross *Diomedea exulans*, northern giant petrel *Macronectes halli*, southern giant petrel *Macronectes giganteus*, Antarctic prion *Pachyptila desolata,* and brown skua *Stercorarius antarcticus,* of which the first four species are likely the main sources of guano given their large body sizes and, for white-chinned petrels, also high nesting densities. Seabird guano is known to increase Hg levels in adjacent terrestrial environments [51].

Human activities can be excluded as an important long-term Hg source at BI10, because Bird Island was first discovered in 1775 CE [41], and apart from occasional sealing activities, was occupied intermittently by small numbers of researchers from 1957 until a small permanent research station operated year-round from 1982 onwards. Additionally, the substantial difference in HgAR between

BI10 and the two control sites cannot be explained by differences in plant species composition [40]. All these sites were influenced predominantly by an oceanic cold climate with a vegetation of graminoids, dwarf shrubs, and mosses. The atmospheric Hg pool is also unlikely to be the predominant source for BI10 during the mid to late Holocene because similarly elevated Hg deposition would then have been expected at our control sites, POB4 and FIGG, as the atmospheric Hg pool is relatively well-mixed at hemispheric scales [52]. Furthermore, the climate has been comparatively stable over the last c. 8.1 ka, with no dramatic glacial-interglacial scale shifts that could substantially increase (or decrease) regional atmospheric Hg deposition [53]. Nor were there periods of very high dust deposition with substantial oxidized Hg, as was the case during the last glacial period [53].

During periods of high Hg flux, the principal climate signal reconstructed from the BI10 peatland site indicated lower wind intensities (reconstructed from *testate amoebae* productivity that is sensitive to wind-blown sea spray [49,50], Supplementary Note 2, Fig. 2C). This suggests a potential link between high guano Hg accumulation and a more favorable climate regime for nesting seabirds at Bird Island. Additionally, this link indicates that wind-regulated rainfall may not play a significant role in guano deposition at the peatland site over the long term (i.e., catchment hydrological influence). Lower wind intensity is accompanied by lower humidity and rainfall [34], which could have led to lower guano runoff and Hg deposition in BI10 peat, contrary to the observations. Next, we discuss how Hg stable isotopes can fingerprint seabird guano as the dominant source of Hg in BI10.

Seabird guano Hg contribution constrained by Hg stable isotopes

Mercury has seven stable isotopes with masses ranging from ^{196}Hg to ^{204}Hg that can undergo mixing or fractionation via transformation processes [54]. Unlike δ^{202}Hg, which represents a typical mass-dependent fractionation (MDF) of Hg isotopes, the odd-mass Hg isotopes can undergo mass-independent fractionation (MIF, Δ^{199}Hg or Δ^{201}Hg) in specific processes, such as photochemical reactions [54]. In contemporary seabird guano collected at Bird Island, Δ^{199}Hg was 1.32 ± 0.05‰ (1σ, n = 5, Supplementary table S4), comparable with penguin guano from the Antarctic Peninsula (0.96 ± 0.03‰, 1σ, n = 2) [27]. Guano Hg acquires its distinct positive Δ^{199}Hg from the marine methylmercury (MeHg, organic form of Hg) when marine MeHg is partly degraded by sunlight in ocean surface waters [55]. The pool of residual marine MeHg with positive Δ^{199}Hg subsequently bioaccumulates and biomagnifies in the marine foodweb, leaving its signature in guano, whose Hg is composed of up to 100% of MeHg [33]. Guano Hg inputs to peat, therefore, carry distinctly more positive Δ^{199}Hg than atmospheric Hg inputs to peat (Hg^0 Δ^{199}Hg = −0.28 ± 0.05‰, 1σ, n = 23; and Hg^{II} Δ^{199}Hg = 0.21 ± 0.42‰, 1σ, n = 21) [34].

Mean Δ^{199}Hg at BI10 was 0.61 ± 0.19‰ (1σ, n = 36, Fig. 3A), and showed a significant negative relationship with 1/Hg (r = −0.49, $p < 0.01$, Fig. 3B). This indicates that higher Δ^{199}Hg is concomitant with higher Hg concentrations at BI10, which is in line with guano Δ^{199}Hg and Hg concentration signatures. In contrast, the Δ^{199}Hg at FIGG was negative overall, with a mean of −0.63 ± 0.06 ‰ (1σ, n = 18) and no significant relationship with 1/Hg ($p > 0.05$). The binary source mixing diagram, Fig. 3B, showing linearized 1/Hg vs Δ^{199}Hg, indicates that the high Hg concentrations in BI10 can be explained by simple source mixing of guano Hg inputs and atmospheric Hg (manifested as predominant source at FIGG). The Δ^{199}Hg determined in peatlands worldwide without identified avian influences [34,37,56,57] is generally negative due to the inherently negative Δ^{199}Hg (−0.28 ‰) of atmospheric Hg^0 that accumulates in peat. Post-depositional negative shifts in peat soil Δ^{199}Hg occur due to predominant sulfur-ligand bound peat Hg^{II} photoreduction [58] or dark abiotic reduction [59], which leaves more negative Δ^{199}Hg in the peat residue, as observed for FIGG (Fig. 3A; Supplementary note 4). These reduction processes, if they occur, will not cause such a positive Δ^{199}Hg as recorded at the BI10 site

(0.61 ± 0.19‰). Furthermore, as evidenced by the slope of $\Delta^{199}Hg/\Delta^{201}Hg$ as a process indicator, the BI10 peat signature (1.10 ± 0.12, 1σ, Fig. 3C) is comparable to that of MeHg in marine biota (~1.20) [60,61]. Overall, contrasting values of $\Delta^{199}Hg$ between BI10 and peatlands largely free from seabird colony influence confirm the influence of guano input to the BI10 site.

Similar to $\Delta^{199}Hg$, $\delta^{202}Hg$ in BI10 (−0.79 ± 0.31‰, 1σ, n = 36, Fig. 3D), was also significantly higher than in FIGG, which ranged from −2.04‰ to −1.63‰ ($p < 0.01$). Fractionation of $\delta^{202}Hg$ occurs during all physical, chemical, and biological processes [54]. At our reference site, the FIGG peat $\delta^{202}Hg$ values show a mean shift of −2.25 ‰ from the dominant atmospheric Hg^0 sources to peat (Hg^0 $\delta^{202}Hg$ = 0.51 ± 0.16‰, 1σ, n = 23) [34]. Low $\delta^{202}Hg$ in FIGG is a result of preferential foliar uptake of light Hg isotopes from the atmospheric gaseous Hg^0 pool [35] (Fig. 3A), which is in good agreement with global peatlands [34,37,56,57]. Significantly higher $\delta^{202}Hg$ in BI10 than FIGG is most likely due to the input of guano with a high Hg concentration and a mean $\delta^{202}Hg$ value of −0.49 ± 0.39‰ (1σ, n = 5). This is further evidenced in the significant negative correlation between BI10 $\delta^{202}Hg$ and 1/Hg (r = −0.53, $p < 0.01$, Fig. 3D). Additionally, BI10 $\Delta^{199}Hg$ and $\delta^{202}Hg$ were positively and significantly correlated (r = 0.67, p < 0.01, Fig. 3A), implying that the variability of these two isotope signatures in peat is more driven by Hg sources, rather than post-depositional processes. The important Hg post-depositional processes, such as sulfur-ligand bound peat Hg^{II} photoreduction or dark abiotic reduction [58,59,62], generally lead to more negative $\Delta^{199}Hg$ and more positive $\delta^{202}Hg$ signatures in peat residue, which is contrary to their positive correlation in BI10. Taken together, the peat $\delta^{202}Hg$ signature further confirms a dominant guano contribution to the BI10 site.

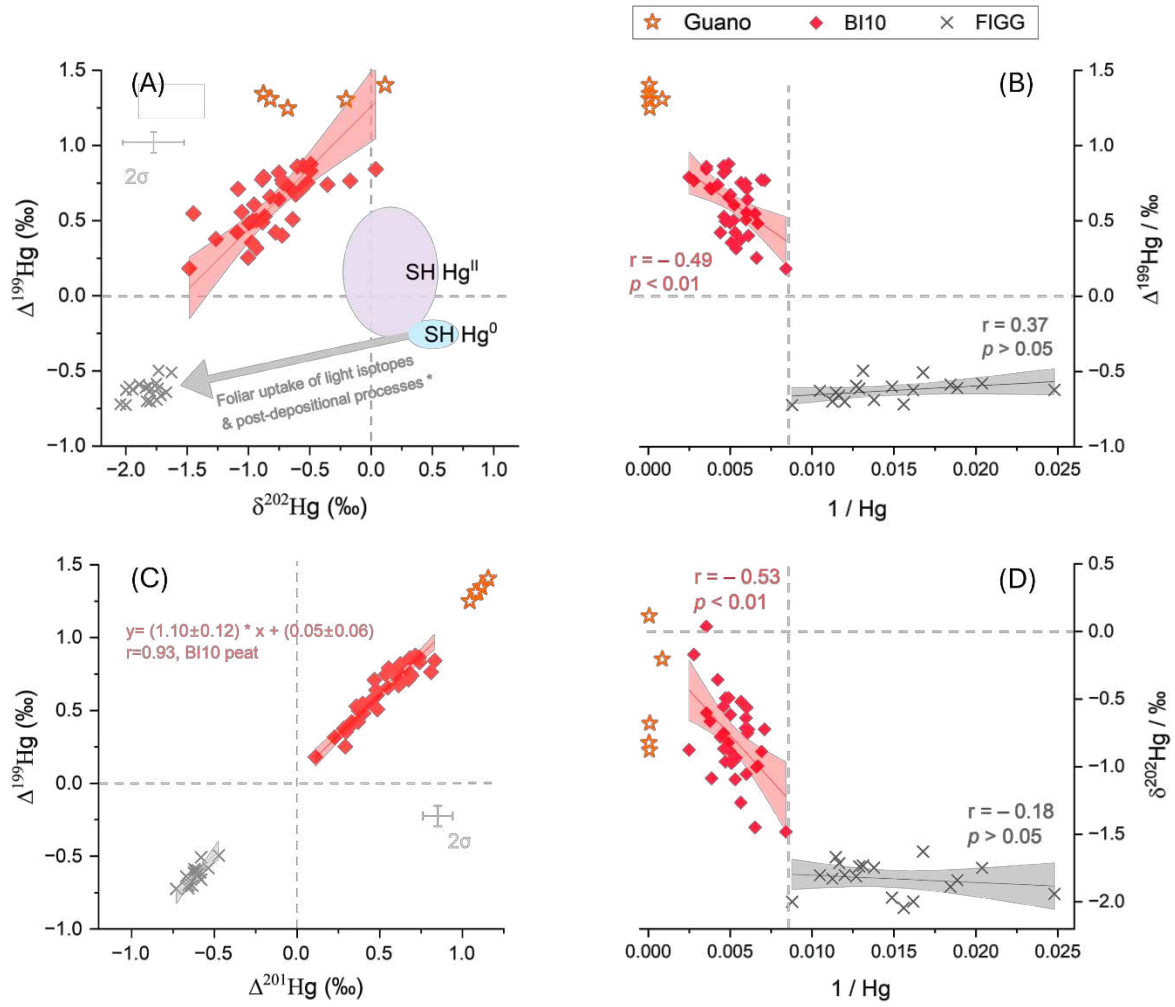

Fig. 3: (A) Δ^{199}Hg vs δ^{202}Hg, (B) Δ^{199}Hg vs 1/Hg, (C) Δ^{199}Hg vs Δ^{201}Hg , and (D) δ^{202}Hg vs 1/Hg in BI10 (red solid diamonds) in comparison to FIGG peat profile (grey crosses) and Bird Island guano (orange open stars). Grey arrow in (A) indicates preferential foliar uptake of light isotopes from the Southern Hemisphere atmospheric Hg^0 pool (SH Hg^0, blue filled ellipse), and peat Hg isotope signatures after post-depositional processes on deposited Hg^0 and rainfall Hg^{II} (SH Hg^{II}, purple filled ellipse) [34]. The vertical dashed lines in (B) and (D) operationally separate 1/Hg above 0.0087 (FIGG data) and below (BI10 data). The red and grey lines in A-D indicate the linear fit to data from BI10 and FIGG, respectively, and the shaded areas indicate the 95% confidence band.

Guano nutrient-fueled Hg sequestration by peat vegetation

In addition to Hg, guano contributes a substantial amount of nutrients (e.g., N, P) to peatland ecosystems, promoting vegetation growth [63]. This could be the reason why during c. 8.1 – 0.2 ka BP, carbon accumulation rates in BI10 were 62 ± 33 g C m^{-2} yr^{-1} (1σ, n = 143, below water table level), which is 4 times higher than at the FIGG site (12 ± 4 g C m^{-2} yr^{-1}, 1σ, n = 54; Supplementary Fig. S4; Supplementary Table S1, S2) [64]. Without significant avian influence via guano fertilization, long-term carbon accumulation rates on sub-Antarctic Islands are generally low due to the cold climate [65], with multi-millennial mean values typically below 20 g C m^{-2} yr^{-1} [66]. Despite being affected by fire activities [64], FIGG carbon accumulation is comparable to the accumulation rates in some Falkland Islands peat profiles spanning a similar timescale (e.g., mean 19 g C m^{-2} yr^{-1} from Whalebone Cove since c. 8.0 ka BP, with 18.73 – 19.34 m^{-2} yr^{-1} for 5th to 95th percentile) [66]. Peat carbon accumulation rates result from

the mass balance between primary production and decomposition loss. Significantly higher carbon accumulation rates at BI10 compared to FIGG could be explained by enhanced primary productivity fueled by guano nutrient input, instead of a lower decomposition rate at BI10. Although nutrient inputs through guano can also facilitate the rates of peat decomposition [66] due to enhanced microbial activities, nutrient-fueled primary productivity at BI10 appears to outweigh higher decomposition rates, ultimately leading to high carbon accumulation rates at the BI10 site. This phenomenon has also been documented in Beauchene Island, the southernmost of the Falkland Islands, where the long-term apparent carbon accumulation rates are also very high (139 g C m^{-2} yr^{-1}) [66,67]. N and P fluxes from seabird populations globally are estimated to be 591 Gg N yr^{-1} and 99 Gg P yr^{-1}, with the highest input in Antarctica and Southern Ocean regions [68]. Overall, guano nutrient input promotes peat vegetation growth and carbon sequestration. Enhanced peat vegetation growth presumably leads to increased Hg^0 uptake, hence higher HgAR.

Increased Hg^0 uptake can be examined by the relatively conservative Hg source tracer, even-Hg MIF (represented by $\Delta^{200}Hg$), although it generally has very small variations among sources [54,69]. During high HgAR periods, BI10 peat $\Delta^{200}Hg$ is −0.04 ± 0.03 ‰ (1σ, n = 20, Supplementary Fig. S4). These BI10 periods were characterized by lower $\Delta^{200}Hg$ values than BI guano $\Delta^{200}Hg$ signatures (0.01 ± 0.01 ‰, n = 5). In contrast, BI10 $\Delta^{200}Hg$ values appear to be more commonly associated with atmospheric Hg^0 composition (−0.06 ± 0.02 ‰, 1σ, n = 23) [34], indicating higher atmospheric Hg^0 sequestration by peat vegetation. Evidences from peat carbon accumulation rates and $\Delta^{200}Hg$ suggest two important sources of Hg to the BI10 record, particularly during peak HgAR phases (Fig. 4A): elevated Hg directly from guano, and enhanced plant uptake of Hg^0 associated with greater primary production fueled by guano nutrients.

Besides the peak HgAR phases in the BI10 profile, there are five periods with lower HgAR (i.e. c. 8.1 – 6.8, 6.1 – 5.2, 3.5 – 2.7, 2.1 – 1.4, 1.2 – 0.5 ka BP, Fig. 4A). A likely explanation for the periods of lower Hg accumulation in BI10 is less guano input linked to lower seabird breeding densities in the peatland catchment. In contrast, photochemical Hg loss from peatlands, which is identified as the main Hg loss pathway [57], is not a primary cause for low Hg accumulation periods at BI10. Because these periods reflect higher wind intensity (Fig. 4B) and accompanying increased humidity and cloud cover, which are associated with lower insolation in the study site.

Seabird establishment and population dynamics

High peat HgAR implies more guano input, which we interpret as higher seabird densities in the catchment of BI10 (and vice versa). The peatland formation at BI10 was initiated c. 8.1 ka, likely associated with gradual warming during the early Holocene in the Southern Ocean region (45–60°S) [70]. At the onset of peat initiation, BI10 was characterized by guano-like positive $\Delta^{199}Hg$ and high Hg/C (Supplementary Fig. S4). This suggests the first colonization of Bird Island by seabirds was around 8.1 ka, but possibly before, and associated with the retreat of glaciers and perennial snow cover. The first period of sustained growth of the seabird colony at BI10 was during c. 6.8 – 6.1 ka, reflected in a pronounced increase in HgAR (Fig. 4A). This is in line with the timing of colonization of Antarctic Ardley Island (South Shetland Islands) by penguins [19], but pre-dates other sub-fossil and geochemical evidence of occupation of the eastern coast of the sub-Antarctic Falkland Islands by at least 1000 years [17].

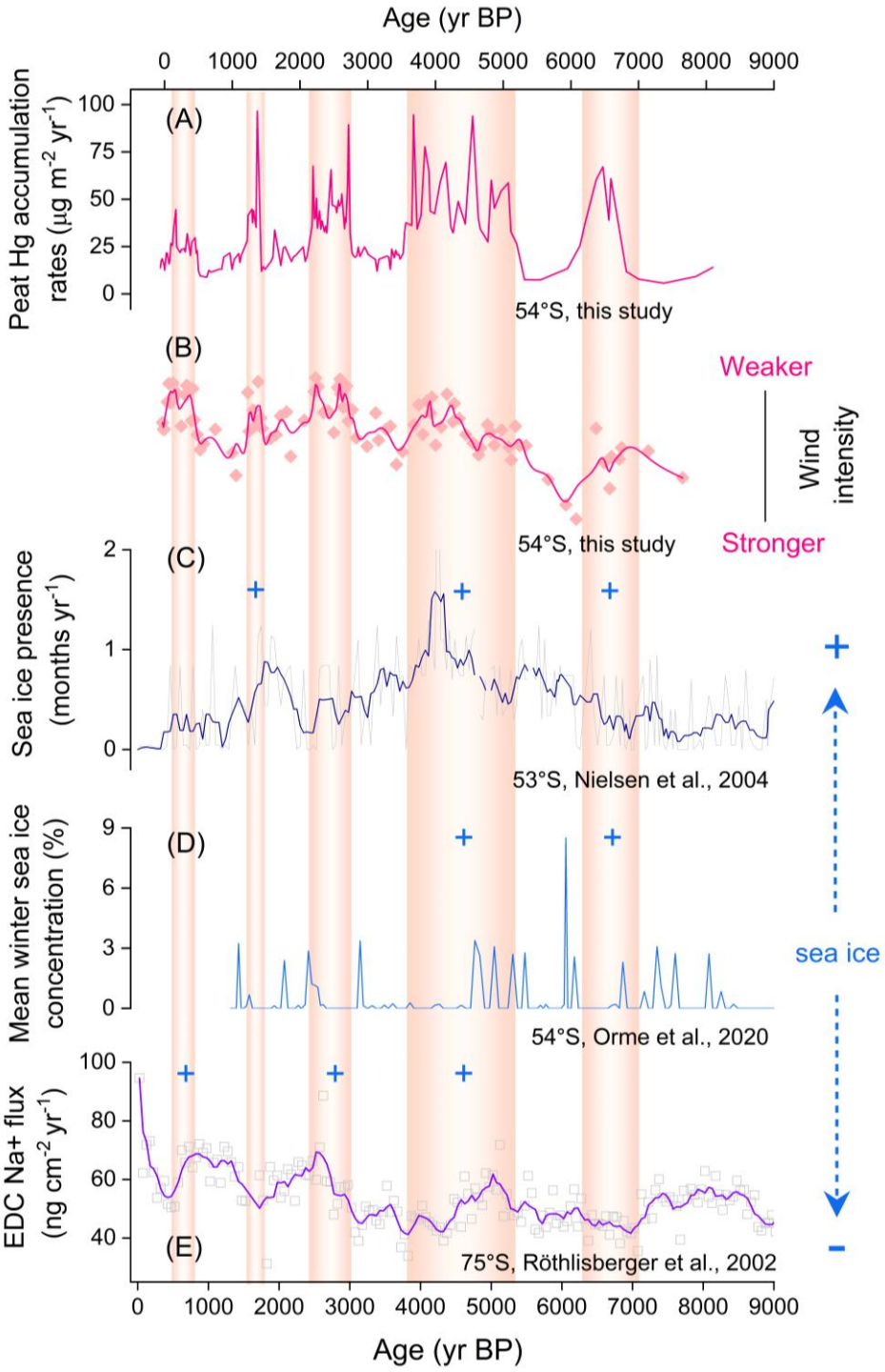

Fig. 4: (A) Hg accumulation rates at BI10 (HgAR, 54°S, this study). (B) SWW intensity reconstructed by *testate amoebae* productivity at the BI10 site [49,50]. (C) Sea-ice presence from the Antarctic Polar Front in the east Atlantic Ocean (53°S, Fig. 1A) [45]. The dark blue line depicts the results of 3-point smoothing. (D) Mean winter (September) sea-ice concentrations for core COR1GC (54°S, Fig. 1A) [46]. The modern winter sea-ice concentration is marked as 0 as the sea-ice limit is at 59°S. (E) DOME C sea-salt sodium as a proxy for sea salt (75°S, Fig. 1A) [47]. Sea-salt concentrations are thought to be influenced by the sea-ice extent and wind speed in the potential source region, as well as the transport from there to the ice core site. The purple line depicts the results of 3-point smoothing. Blue crosses indicate enhanced sea-ice cover. Orange-shaded areas highlight five periods with high Hg flux linked to enhanced guano input.

Including the colonization at c. 6.8 – 6.1 ka, there were five periods of high Hg fluxes, associated with locally higher seabird abundance (the others were at c. 5.2 – 3.5, 2.7 – 2.1, 1.4 – 1.2, and 0.5 – 0.1 ka; Fig. 4). All five periods are aligned with periods of weaker Southern Westerly Wind (SWW) intensity reconstructed from *testate amoebae* productivity (Figs. 4A, 4B). Wind regimes affect seabird energy budgets and flight costs, influencing foraging trip durations, chick provisioning rates, breeding success and hence population dynamics [71]. Weaker SWW, therefore, potentially promoted seabird breeding in the BI10 catchment areas. Conversely, during sustained periods of high winds, the slopes above BI10 became less suitable for nesting because of increased risk of crash landing, flooding, thermal exposure or, in surface-nesting species, of adults or chicks being blown off their nests, any of which can lead to breeding failure [71].

The main driver of population growth rates in seabirds in natural situations is the availability of prey [72]. The four seabird species most likely to be the sources of most of the guano at BI10 are the white-chinned petrel, wandering albatross, northern giant petrel and southern giant petrel, which exploit prey over very large areas [73–76] . These areas include the Patagonian Shelf and slope, Scotia Arc (including the South Georgia, South Sandwich and South Orkney Islands) and the southern water mass boundary of the Antarctic Circumpolar Current, the Subtropical Front, and the Subantarctic Front (Fig. 1B). Although these species have diverse diets that may include fish, squid, crustaceans and carrion, they all exploit the seasonal sea-ice zone at some stage in the breeding season, typically with a lag of several weeks presumably corresponding to the time taken for the spring plankton bloom to transfer energy to mid-trophic-level prey such as squid, fish or zooplankton [76]. For white-chinned petrels and giant petrels, a major component of their diets during chick rearing is Antarctic krill [14,77]; this feeds on sea-ice algae and is a key species within Southern Ocean food webs [78–80].

All five elevated Hg flux phases in BI10 peat occurred during periods of decreased SWW (Fig. 4B) and increased sea-ice extent in the Southern Ocean (Fig. 4C–E), so it seems reasonable to conclude that climate and environmental conditions in the Southern Ocean 5000 years ago favored seabirds breeding at Bird Island and elsewhere at South Georgia. Between c. 5 – 3.5 ka, seabird densities at BI10 were presumably high for a period of ~1500 years when sea ice extended to as far north as the Antarctic Polar Front (Fig. 4C–E). At this time, higher prey abundance in the Southern Ocean possibly contributed to the establishment of seabirds or seals breeding at Surf Bay site on the east coast of the Falkland Islands, as evidenced by marine-derived nutrients from guano facilitating tussac grass establishment and increased peat-forming plant productivity, and increased peat accumulation [17].

Implications

South Georgia is a globally important breeding site for seabirds, including several threatened species. Currently, knowledge of seabird population response to climate change and anthropogenic pressures is limited largely to the period since the 1950s, i.e., recent, decadal timescales. By extending the record of population change back thousands of years, our study has advanced our understanding of how seabird populations have varied on centennial to millennial timescales and how they respond to long-term natural variability in climate and marine ecosystems. This is particularly important because populations of pelagic seabirds have declined dramatically since the 1950s, which must be interpreted both in the context of direct anthropogenic impacts, and indirect anthropogenic impacts on climate [1,2]. The former includes resource exploitation (fisheries) [81], pollution (e.g., plastics) [82], and ecosystem impacts of invasive species (predation by mice and rats) [83], while the latter includes intensification and southward displacement of the SWW [84] and retreat of sea ice in the South Atlantic sector of the Southern Ocean [85]. For the climate impacts, this study provides a long-term perspective on which to base more accurate predictions of future changes in seabird populations. These include impacts on breeding success on individual islands as the core belt of the SWW intensifies and moves southward,

and on prey availability in the foraging zone as the sea ice retreats.

To summarize, our study has shown that: 1) Hg can be used as a reliable tracer of guano influx into peatlands because Hg cannot be recycled by peat vegetation as an essential element; 2) seabirds on Bird Island created substantial volumes of Hg-rich guano, with distinct Hg isotope signatures that were archived in peat, providing a long-term record of changes in nesting densities; 3) The Bird Island BI10 site (colony) experienced five Hg-reconstructed population maxima from the mid to late Holocene, all of which correspond with lower prevailing westerly wind intensity over the catchment, that likely resulted in more favorable foraging and breeding conditions in the region.

Methods

Study sites and sampling

Bird Island

Situated south of the Antarctic Polar Front (Fig. 1A), Bird Island is exposed directly to Antarctic storms from the southwest. Gale-force winds can occur all year round. It is cold, cloudy, and wet all year round. The annual temperature is 1.2 °C, and the annual rainfall is ~850 mm with an average humidity of 84% [86]. Temperatures vary from -10°C to 10°C, ~0°C in winter and ~4°C in summer, which is characterized by damp, misty, low cloud conditions [86]. In winter, the snow cover lasts from July to October, but there is no permanent ice cap, ice, or glaciers on the island, in contrast to mainland South Georgia.

The peat coring site, BI10 (54°01'04.9"S, 38°04'13.7"W) is from a valley floor mire located between the headland at Morris Point and Gony Ridge, surrounded by slopes that are primarily vegetated with tussock grass (*Poa flabelleta*) with mosses, including *Chorisodontium aciphyllum* and *Polytrichum alpestre*. The site is approximately 30 m above sea level on the western side of the island and therefore directly exposed to the westerly winds. It receives water largely from surface drainage, with a high water table sustained through gravitational lateral seepage from adjacent slopes [42]. The sampled valley mire can, therefore, record guano input through runoff from the surrounding catchment where there are nesting seabirds. The water table level is at 10 – 15 cm below the peat surface.

A 5 m–long peat sequence was collected from the BI10 site in Feb 2017 using a 50 × 6 cm Russian corer. Peat cores were described and wrapped in plastic film before placement in PVC tubes and transported to the British Antarctic Survey for frozen storage. Five samples of fresh guano from albatrosses were also collected on Bird Island and stored frozen in plastic tubes.

South Georgia

Located approximately 1,400 km south-east of the Falkland Islands, South Georgia lies between latitudes 54°S and 55°S, and longitudes 36°W and 38°W (Fig. 1B). Its climate is typical of the maritime subantarctic, with annual mean temperatures of 2.0°C, precipitation of 1,590 mm per year recorded at the research station, King Edward Point [87]. Temperatures range from -15°C to +20°C (with higher temperatures on the lee side of the mountains enhanced by foehn winds) [87], with snow covering from May to October. Situated in the northwest of South Georgia, Prince Olav Bog (POB4, 54°04'06"S, 37°06'40"W) is a Sphagnum-dominated peat bog with only 1-2 pairs of giant petrels nesting in the catchment (Fig. 1). *Sphagnum fimbriatum* forms dry hummock-like patches, surrounded

by wet hollows that are dominated by monocots and brown mosses. A 3.6 m–long peat profile was collected at one of the Sphagnum patches in 2008 using a 50 × 8 cm long Russian peat corer.

Falkland Islands

The Falkland Islands are located between 51°S and 52°30'S and 57° 45'W and 61°30'W. They consist of two large islands (East Falkland, about 6700 km^2, and West Falkland, about 5300 km^2), with approximately 700 smaller islands. The archipelago is about 700 km north-east of Cape Horn and 500 km east of the nearest part of the South American continent (Fig. 1). The coring site is ~12 km east of the settlement of Goose Green (FIGG) in an open basin, lying slightly lower than the surrounding hills. The climate is cool maritime, with annual mean temperatures of ~6°C, precipitation of ~600 mm per year, and a mean wind speed of ~30 km h^{-1} [88].

The coring site, FIGG, is characterized by a typical acid 'whitegrass' (*Cotaderia egmontia*) peatland, with *Blechnum penna-marina*, *Baccharis magellanica*, *Empetrum rubrum*, *Oreobolus obtusangulus*, *Gaultheria pumila* and *Myrteola nummularia*. This coring site is also not currently a nesting ground for seabirds. A 3.6 m-long peat sequence was collected in 2022 using a stainless-steel box of 10 × 10 cm for the top 50 cm of the peat profile, with the remainder sampled using a Russian peat corer with a 50 × 8 cm chamber.

Peat subsampling

Cores were frozen and subsequently sliced at ~1 cm resolution for the whole core. Each new slice was cleaned with MilliQ water, edges removed, and subsampled for further analysis following established protocols [89]. The dimension of the largest subsample of each slice was measured using a Vernier caliper to obtain the volume for calculating the dry bulk density and to estimate the cut loss between each slice. Subsequently, the largest sub-samples from BI10 and POB4 were dried for geochemical analysis using the freeze-dryers at the University of Toulouse, while those from FIGG were oven-dried at 40 – 50°C at the University of Aberdeen.

Radiocarbon dating and age models

In total, ×14 plant macrofossil samples from Bird Island BI10, ×8 from South Georgia POB4, and ×9 from the Falkland Islands FIGG, were selected for radiocarbon analyses following established protocols [90]. All the selected samples were prepared and analyzed for radiocarbon analysis at the University of Aberdeen and the ^{14}CHRONO Centre at Queen's University Belfast, respectively. The age models for BI10 peat profiles, POB4 and FIGG were generated from ^{14}C results using the Bacon model (calibration curve SH Cal20) with the 'rbacon' package in R software (https://CRAN.R-project.org/package=rbacon) [91]. Details on the dated material and radiocarbon ages from BI10 and FIGG are detailed in refs [50,64], while POB4 is shown in the Supplementary Table S5.

BI10 has a chronology of 8.1 ka (Supplementary Fig. S3). The entire POB4 core is 380-cm long with a chronology of 8.5 ka constrained by eight radiocarbon dates (Supplementary Fig. S2). This Bog was formed from a dried lake approximately c. 4.5 ka ago, with a sediment section during c. 8.5-4.5 ka BP followed by a peat section from c. 4.5 ka BP onwards (Supplementary note 1).

Carbon measurements

Carbon content in BI10 and POB4 was estimated from Loss of Ignition (LOI) at 550°C, with carbon content estimated as approximately half of LOI [92]. Dried peat samples are combusted to ash and carbon dioxide at 550°C [93]. The LOI is then calculated using the following equations:

LOI550 = ((DW105–DW550)/DW)*100 (1)

Carbon content in FIGG was analyzed using a Flash Combustion Elemental Analyser (CE Instruments NA 2500 Flash Combustion EA) [64].

Hg concentration measurements and Hg accumulation rate calculation

Dried peat samples from BI10, POB4 and, FIGG were analyzed for total Hg (THg) concentration on a combustion cold vapor atomic absorption spectrometer (CV-AAS, Milestone DMA-80) at the University of Bern, Switzerland. The analytical performance of the DMA-80 was assessed by multiple measurements on reference material, NIST 1515 (Apple leaves). Results were not statistically different from the certified values, with Hg concentrations of 43.3 ± 2.1 ng g^{-1} (1σ, n = 78, certified 43.2 ± 2.3 ng g^{-1}) for NIST 1515.

Hg flux (μg m^{-2} yr^{-1}, Eq. 2) in sample *i* was obtained by Hg concentration (ng g^{-1}), density (g cm^{-3}), thickness (cm), and age interval (yr).

Hg flux = Hg concentration × density × thickness/age interval (2)

Hg isotope measurements

Due to sample availability, only BI guano, BI10 peat, and FIGG peat were extracted for Hg isotope analysis using a combustion method adapted from Enrico et al. [94]. Hg released from the combustion procedure was collected with 40% inverse *aqua regia* solutions. Following extraction, the Hg stable isotope compositions of guano (5 samples) and peat samples from Bird Island (36) and Falkland Islands (18) were determined from 20% (v/v, diluted from 40%) inverse *aqua regia* solutions using cold-vapor multi-collector inductively coupled mass spectrometry (CV-MC-ICP-MS, Neptune Plus, University of Bern). Sample isotopic ratios were corrected for mass bias by sample-standard bracketing using NIST 3133 [95]. Results are reported as δ-values in per mil (‰) representing Hg mass dependent fractionation by reference to NIST 3133 (Eq. 3).

$$\delta^{XXX}Hg=\{(^{XXX}Hg/^{198}Hg)sample(^{XXX}Hg/^{198}Hg)NIST3133-1\}\times1000 \quad (3)$$

MIF is calculated based on the deviations of δ-values from the theoretical MDF (Eq. 4).

$$\Delta^{XXX}Hg=\delta^{XXX}Hg-\beta\times\delta^{202}Hg \quad (4)$$

where XXX stands for 199, 200, 201 and 204. Symbol β is 0.2520, 0.5024, 0.7520, and 1.493 for ^{199}Hg, ^{200}Hg, ^{201}Hg, and ^{204}Hg, respectively.

The quality control of Hg isotope measurements is assessed by analyzing Almaden, ETH-Fluka and procedural standards (Apple leaves, NIST 1515, *n* = 35, Supplementary Table S6). Almaden showed $\delta^{202}Hg$ and $\Delta^{199}Hg$ of −0.56 ± 0.13‰ and −0.03 ± 0.07‰ (2σ, *n* = 70), respectively. ETH-Fluka displayed $\delta^{202}Hg$ and $\Delta^{199}Hg$ of −1.47 ± 0.16‰ and 0.08 ± 0.07‰ (2σ, *n* = 9), respectively. Hg isotopic signatures in procedural standards are reported for $\delta^{202}Hg$ (maximum 2σ = 0.25‰), $\Delta^{199}Hg$ (maximum 2σ = 0.07‰), $\Delta^{200}Hg$ (maximum 2σ = 0.05‰), $\Delta^{201}Hg$ (maximum 2σ = 0.09‰) and $\Delta^{204}Hg$ (maximum 2σ = 0.17‰). Hg isotope signatures of all three standards are comparable to other published Hg isotope data [57,96,97] (Supplementary Table S6).

Author Contributions:

C.L. designed the project and acquired funding. S.J.R., M.G., A.M., K.B., N.B., C.J., D.H. offered great mentorship. S.J.R., R.P., D.Ma., C.v.S., T.T., D.Mu., A.W., A.G-S., D.H. carried out field work. C.L., S.J.R., M.W., M.E., J.S., F.V., N.V.P., S.O., N.B., E.A., A. C-H. prepared/performed lab work and data analysis. C.L. wrote the original draft. S.J.R., M.G., A.M., M.W., R.P., M.E., K.B., U.S., D.M., C.S., T.T., A.W., A.G-S., J.S., F.V., N.V.P., P.B., O.M., S.O., N.B., T.F., E.A., A. C-H., P.Z., C.J., K.S., S.Y.K., D.W., R.B., L.S., D.H. contributed to the discussion, interpretations, and commented on the manuscript.

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