

**Ornithogenic vegetation: how significant has the seabird influence been on the Aleutian Island vegetation during the Holocene?**

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## **Abstract:**

We have studied the long- and short-term periods of seabird influence on coastal vegetation. In the Aleutian Islands during the Holocene, terrestrial predators were virtually absent; as a result, large seabird colonies thrived along the coasts or across entire islands. Bird guano enriches the soil with nitrogen, which can lead to the formation of highly modified ornithogenic (bird-formed) ecosystems. The vegetation of several Aleutian Islands has been reconstructed; however, only the vegetation on Carlisle Island had noticeable impact from the seabird guano. For more detailed investigation of bird influence, we conducted pollen analysis to reconstruct the 9,300-year-old vegetation dynamics of the coast of Shemya Island. From earlier studies of nitrogen isotopes in peat, we discovered that a large seabird colony existed on Shemya from 4600 to 2400 years ago, and birds also influenced coastal ecosystems between 1470–1160 and 810–360 years ago. In these sequences, the tundra dominated by Ericaceae dwarf shrubs initially spread on the coast. During a period of at least 2200-years nitrogen enrichment led to the development of herb meadows with a high presence of Apiaceae. After a noticeable reduction in seabird colonies due to human hunting, grass-meadows spread. During the late Holocene several hundred years of seabird impact led to an increase in abundance of indicator taxa, ferns and umbelliferous species, as well as in total pollen concentration, but this did not result in a radical change of dominants. In recent decades, due to the extinction of the bird colonies, heather communities have begun to spread on the Shemya coast. Also large ash emissions in the Aleutian Islands can lead to a decrease in pollen concentration even in peat located far from an eruption.

Keywords: pollen analysis, islands ecosystems, vegetation dynamics, guano.

## **i. Introduction**

The Aleutian Islands are a volcanic origin archipelago extending almost 2000 km from Kamchatka to mainland Alaska. Regional flora and vegetation were formed mainly in the Holocene (Hulten, 1968; Garrouette et al., 2018). The fundamental climatic patterns of the Aleutian Islands are determined by the position of the Aleutian Low (Rodionov et al., 2005; 2007; Broadman et al., 2020). Mild winters, high humidity, cloudiness, fogs, frequent storms, and strong winds are the features that define the Aleutian landscape and vegetation (Hulten, 1968). According to modern vegetation studies, the plant communities also depend on altitude, drainage, and soil properties (Hulten, 1968; Byrd, 1984; Talbot, Talbot, 1994; Talbot et al., 2010a). Another important factor is the snow distribution in winter, which is determined by the wind strength and topography (Hulten, 1937; 1968). The proximity of Kamchatka to the west of the Aleutian arc and Alaska to the east also regulate the difference

in the flora and vegetation of islands (Hulten, 1937; Garrouette and Ickert-Bond, 2013; Garrouette et al., 2018). Among more than 200 Aleutian islands, the Holocene vegetation dynamics have been studied on Attu (Heusser, 1990), Shemya (Smyshlyaeva et al., 2021 in press), Atka (Heusser, 1990), Tanaga (Anderson, Bank, 1952), Adak (Heusser, 1978; Noguchi et al., 2018), Umnak (Heusser, 1973), Carlisle (Kuzmicheva et al., 2019), and Unalaska (Anderson, Bank, 1952). Previous studies show that climate influenced the vegetation, but it was difficult to identify the general pattern. Other important influences included local moisture, topography, and soil characteristics (Anderson, Bank, 1952; Heusser, 1973, 1978, 1990; Noguchi et al., 2018; Kuzmicheva et al., 2019). Volcanic activity has also strongly affected plants and landscapes (Heusser, 1990; Noguchi et al., 2018; Kuzmicheva et al., 2019). Huge seabird colonies and anthropogenic activity could be considerable driving forces as well (Kuzmicheva et al., 2019). Actually, we can only make assumptions about how exactly the above factors influenced the Aleutian vegetation during the Holocene.

In this study, we investigated the influence of seabird colonies on vegetation. The Aleutian Islands are remarkable because there were largely no terrestrial predators east of the Commander Islands and west of Umnak prior to Russian Contact in 1741 (West et al., 2007; Crockford, 2012). However, according to recent data, the mammalian predators could have lived in the Islands of Four Mountains before Russian colonization (Vasyukov et al., 2019). It is safe to say that only humans hunted on most of the islands from the beginning of their settlement in the Holocene (Laughlin, 1975). Due to this lack of terrestrial predators, billions of birds have formed large colonies on the Aleutian Islands over thousands of years, as evidenced by archaeological data (Crockford, 2012; Krylovich et al., 2019). On Buldir Island, which was not inhabited by any terrestrial predators excluding humans, seabird colonies numbered 1.8 million pairs between 1972 and 1984 (Byrd and Day, 1986). With this example, we can imagine how the small Shemya Island could have been densely populated by avian fauna throughout most of the Holocene. According to modern botanical research on other North Pacific Islands, even short-term impact of seabird colonies can cause changes in vegetation cover, and in the chemistry of soil or bedrock leading to the formation of ornithogenic ecosystems and vegetation (Ivanov, 2013). Plant communities near seabird colonies have lower species diversity, higher biomass, and few dominants of ruderal, annual, and cosmopolitan species (Anderson and Polis, 1999; Ellis, 2005; Mochalova, 2008; Mazei et al., 2018). In order to study past ornithogenic vegetation we can predict the impact of seabird colonies from bird bones recovered in archaeological sites (Lefevre et al., 2010; Crockford,

2012; Krylovich et al., 2019) or by stable isotope analysis in peat cores (Savinetsky et al., 2014; Kuzmicheva et al., 2019). Seabird guano enriches the substrate with a heavy nitrogen isotope ( $^{15}\text{N}$ ) (Croll et al., 2005; Maron et al., 2006; Szpak et al., 2012) and  $\delta^{15}\text{N}$  dynamics can reflect the degree of avian influence on soil and vegetation (Bergstrom et al., 2002; Kuzmicheva et al., 2019).

To study the seabird impact on Aleutian Islands plant communities, we reconstructed vegetation dynamics recovered from the coastal peat deposit (McDonald Point) on Shemya Island using pollen analysis. For at least 2,200 years, McDonald Point peat core has been markedly affected by seabird guano. The  $\delta^{15}\text{N}$  value increased by almost 10 ‰ and was high from 4,600 to 2,400 years ago (Savinetsky et al., 2014). The existence and subsequent significant reduction of the colony is also confirmed by zooarchaeological discoveries in archaeological sites (Lefevre et al., 2010). A similar increase in  $\delta^{15}\text{N}$  was observed in the peat core on Carlisle Island (the Islands of Four Mountains, the Aleutian Islands), but the exposure time did not exceed several hundred years. Such short-term events did not lead to a drastic change in vegetation dominants on Carlisle Island, but were reflected in the pollen spectra by the presence of indicator taxa (Kuzmicheva et al., 2019). We also compared the dynamics of coastal vegetation and vegetation in the Shemya island interior, where, according to the analysis of stable isotopes, there was no influence of seabird colonies (Smyshlyaeva et al., 2021 in press). We assumed that volcanism, an important factor for the Aleutian Islands plant communities, did not significantly affect the coastal vegetation of Shemya Island. Our hypothesis was based on the fact that there are no ash layers in the McDonald Point deposit (Kiseleva et al., 2002), and the nearest active volcanoes are located 100-200 km away (Miller et al., 1998; Corbett et al., 2010). In this paper, we answer two questions: How do long periods of seabird impact affect subarctic vegetation? And how do plant communities change after reduction of this influence?

## ii. Materials and Methods

### • Sampling

Shemya is a flat island, devoid of volcanoes, located at 52°43'27"N and 174°07'08"E; is approximately 4.5 km wide, and approximately 7 km long; its total area encompasses about 15 km<sup>2</sup> (Figure 1). The island relief is gently-hilly. The vegetation is represented by two types of communities – with herbs and dwarf shrub dominance (Kiseleva et al., 2002; Savinetsky et al., 2014). Grasses and sedges along with a noticeable abundance of forbs dominate the streams valleys, lowlands, and slopes of different exposures. These communities are more

diverse on well-drained southern slopes. Meadow vegetation dominated by *Elymus arenarius*, *Heracleum lanatum*, and *Senecio pseudo-arnica* occurs on hills near the sea coast (Savinetsky et al., 2010). Sedges often become dominant under waterlogged conditions (Kiseleva et al., 2002). The second type of community is dominated by dwarf shrubs (*Empetrum nigrum*, *Vaccinium vitis-idea*, *Linnea borealis*) (Kiseleva et al., 2002).

A peat deposit was sampled at McDonald point on the east coast of Shemya Island in 1999 (Figure 1). The land surface was flat, slightly sloping, with a steep ledge protruding into the sea. The ledge was cut during quarrying and exposed the bedrock and peat profile. The depth of the sampled core was 385 cm (Table 1).

### ● Radiocarbon dating

To determine the age and accumulation rate of the sediment, we selected plant remains from seven layers for radiocarbon dating (Table 2). Dating was carried out by the scintillation method in the Laboratory of Historical Ecology of A.N. Severtsov Institute of Ecology and Evolution of Russian Academy of Science. Radiocarbon dates were calibrated to determine calendar ages and to frame the age-depth model (Figure 2) by the “IntCal13” ground calibration curve (Reimer et al., 2013). We carried out calculations in the package “Bchron” 4.2.6 (Parnell, 2015) in the statistical environment R v. 3.6.2 (R Core Team, 2019). The details and math used in the package are presented in the work of Haslett and Parnell (2008). Calibrated dates are given in the text below.

### ● Pollen analysis

A total of 66 samples 2-4 cm<sup>3</sup> in size with an interval of 5-10 cm were selected for pollen analysis. We used boiling in 10% HCl, 10% KOH, washing through a sieve (250 μ), boiling in HF, acetolysis, according to the standard procedure with some modifications (Faegri and Iversen, 1975; Chambers et al., 2011) for chemical processing of samples. To determine the concentration of pollen and spores the special markers were added before chemical treatment (Stockmarr, 1973). We added two tablets of *Lycopodium clavatum* spores from batch #483216 to each sample. Pollen atlases and keys (Reille, 1998; 1999) and electronic databases (<https://globalpollenproject.org>) were used to determine pollen and spores taxa. Using an Axioskop ZEISS light microscope with a magnification of x400 we counted pollen up to at least 500 pollen grains in those samples, where possible. The percentage of pollen types was calculated from the total of all pollen in the sample, and the percentage of spores from the total of pollen and spores. Tilia software v.2.0.41 was used to construct pollen diagrams (Grimm, 2015). Percentage and concentration diagrams are

presented in abbreviated form; taxa that occur singly are excluded. Complete diagrams and spreadsheets are available in the Data Accessibility Statement. We identified pollen zones by stratigraphically constrained cluster analysis (CONISS) (Grimm, 2015).

### iii. Results

The McDonald Point deposit began formation prior to 9300 cal yr BP, as evidenced by the date for 363 cm (Figure 2, Table 2). There were two stages of material deposition. The first period from before 9300 cal yr BP to 3500 cal yr BP (372-224 cm), the average accumulation rate was 0.024 cm / year (Figure 2). In the second period, from 3500 cal yr BP to present, accumulation was relatively rapid - 0.064 cm / year (Figure 2). In the pollen spectra, we identified a total of 46 palynotypes: 7 arboreal taxa (trees and shrubs; we included Ericaceae in this group), 31 non-arboreal taxa, and 8 types of spores. The pollen concentration of arboreal taxa varied from 0 to 82450 grains / cm<sup>3</sup> (on average 14 600 grains / cm<sup>3</sup>), non-arboreal taxa - from 40 to 380240 grains / cm<sup>3</sup> (on average 87880 grains / cm<sup>3</sup>) and spore from 0 to 217250 grains / cm<sup>3</sup> ( 9260 on average). The main dominant taxa are Cyperaceae (0-94.4%), Apiaceae (from single pollen grains to 85.4%), Ericaceae (0-65.3%), Poaceae (0-50.7%), *Lycopodium annotinum* (0-66.1%) (Figure 3). The total pollen concentration (TPC) varied from 120 to 448520 pollen grains / cm<sup>3</sup> (Figure 4). Pollen was nearly absent in samples 318-310 cm (7330-6700 cal yr BP) and 100-95 cm (1048-992 cal yr BP). During periods 5880-4860 years ago (290-270 cm) and 560-420 years ago (60-50 cm) the TPC also decreased significantly.

According to the CONISS of pollen abundance, we recognized 3 pollen zones: McDP-Z1 (385-265 cm, 9300-4600 cal yr BP), McDP-Z2 (265- 175 cm, 4600-2400 cal yr BP), McDP-Z3 (175-0 cm, 2400-0 cal yr BP) (Figure 3). The CONISS of pollen concentration demonstrates the same zonation (Figure 4). The most remarkable changes in pollen composition occurred at 4600 and 2400 cal yr BP (Figure 3).

#### **McDonald Point-1 (385-265 cm, 9300-4600 cal yr BP).**

The Ericaceae and Cyperaceae pollen dominated at these depths; their abundance reached values up to 65.3 and 55.0%, respectively. The Asteraceae pollen peak was about 9300 cal yr BP - up to 21.0%, and then gradually decreased. The percentage of *Lycopodium annotinum* spores was the highest in this zone (up to 66.1%). TPC was on average 104094 grains / cm<sup>3</sup> (from 970 to 231270 grains / cm<sup>3</sup>).

In the deepest samples (385-365 cm) TPC ranged from 76840 to 448520 grains / cm<sup>3</sup> with no obvious trend. At a depth of 372-385 cm, the pollen spectra contained a few taxa; TPC was 76840 grains / cm<sup>3</sup> and the spectra are dominated by spores of *Lycopodium annotinum* (66.1%) and pollen of Ericaceae (44.3%). Cyperaceae, Poaceae, and Asteraceae pollen abundance were 11.4% each; Apiaceae pollen also had a noticeable value – 9.1%. The deepest sample also contained 3.9% *Huperzia* spores. At 369-372 cm TPC increased to 448520 grains / cm<sup>3</sup>. *Lycopodium annotinum* spores continued to dominate (45.5%). The Cyperaceae pollen increased to 38.5% and Asteraceae – to 20.8%. Single pollen grains of *Typha*, *Alnus*, Boraginaceae, Polygonaceae, and spores of Ophioglossaceae also occurred. At 365-369 cm TPC decreased to 237740 grains / cm<sup>3</sup>. The percentage of *Lycopodium annotinum* declined to 3.6% and Cyperaceae increased to 49.5%. Along with sedges, Ericaceae dominated, their abundance increased to 34.4%. The Apiaceae amounts decreased to 2.3%, while Asteraceae markedly dropped to 4.9%. At this depth, there were single pollen grains of *Typha*, *Fritillaria*, Ranunculaceae, *Cornus*, as well as *Huperzia* and *Equisetum* spores.

At 9300-9100 cal yr BP (365-360 cm), TPC decreased to 82150 grains / cm<sup>3</sup>. The dominants changed from Cyperaceae (17.5%) to Ericaceae (56.3%). The Asteraceae pollen percentage again slightly increased to 10.6%, *Lycopodium annotinum* spores – to 9.3%, Apiaceae pollen – to 4.5%.

Approximately 6400 years ago Apiaceae pollen abundance started to increase gradually (from 2.9 to 5.6% and further above). Poaceae pollen abundance began to rise circa 6200 years ago. At the period 5880-4860 cal yr BP (290-265 cm), TPC decreased to 2030-5470 grains / cm<sup>3</sup>, and by 4600 cal yr BP increased again to 1467000 grains / cm<sup>3</sup>. The Ericaceae abundance significantly decreased by 4600 cal yr BP (from 40.0 to 19.8%), while the Cyperaceae, on the contrary, significantly increased from 7.5 to 50.6%. The *Lycopodium annotinum* percentage increased from 21.6% (5880 cal yr BP) to 32.0% (5100 cal yr BP), and by 4600 cal yr BP it decreased to 11.0%.

#### **McDonald Point-2 (265- 175 cm, 4600-2400 cal yr BP).**

Apiaceae pollen dominated in this zone. Its percentage was maximum during the entire period of deposition formation - up to 85.4%. Poaceae pollen reached its maximum in the upper part of this zone, the concentration was also consistently high. On the contrary, Cyperaceae pollen abundance was minimal. Ericaceae pollen percentage and concentration



also dropped dramatically. TPC peaked at this time and reached, on average, 156160 grains / cm<sup>3</sup> (from 59050 to 300430 grains / cm<sup>3</sup>).

For the time period 4600-3080 years ago (265-205 cm), TPC markedly increased from 75820 to 241880 grains / cm<sup>3</sup> (147730 grains / cm<sup>3</sup> on average). Apiaceae pollen was significantly dominant – from 44.7 to 85.4% (71.6% on average). The percentage of Poaceae pollen was the lowest (7.3% on average) compared to higher and lower depths. The Cyperaceae abundance also decreased from 21.6 to 4.6%, with significant fluctuations. Ericaceae pollen had practically disappeared from the peat core. The concentration of Polypodiaceae ranged from single spores to 3720 grains / cm<sup>3</sup>.

In the interval 3080-2430 cal yr BP (205-175 cm), TPC increased to 301970 grains / cm<sup>3</sup> by 2870 years ago, and then began to decline. The average TPC value for the entire period was 168480 grains / cm<sup>3</sup>. Poaceae pollen together with Apiaceae dominated, and the grass pollen abundance increased from 29.2 to 50.7% (37.7% on average). The Poaceae pollen concentration peaked at 152280 grains/cm<sup>3</sup> also by 2870 cal yr BP. The Apiaceae pollen concentration, on the contrary, decreased to 32720 grains / cm<sup>3</sup> by 2650 cal yr BP. The Apiaceae abundance also gradually decreased to 30.7% (it was 45.5% on average at this depth).

### **McDonald Point-3 (175-0 cm, 2400-0 cal yr BP)**

The Cyperaceae pollen dominated in this zone, its abundance varied from 43.3 to 95.4%. Poaceae and Apiaceae pollen percentages were significantly reduced in comparison with the previous zone. TPC was the lowest compared to the other two zones and varied from 120 to 204040 grains / cm<sup>3</sup>, with an average of 51120 grains / cm<sup>3</sup>. But there was also a separate peak of TPC around 2000-1900 cal yr BP of up to 392390 grains / cm<sup>3</sup>.

About 2430-90 years ago (175-11 cm), TPC varied from 120 to 397390 grains / cm<sup>3</sup> (71080 grains / cm<sup>3</sup> on average). We identified a period up to 1160 years ago when the TPC was relatively high (from 7080 to 397390 grains / cm<sup>3</sup>, 106190 grains / cm<sup>3</sup> on average), and later the concentration significantly decreased (from 120 to 93770 grains / cm<sup>3</sup>, 32450 grains / cm<sup>3</sup> on average). Cyperaceae pollen clearly dominated and increased from 43.3 to 94.4% (72.7% on average) until the last decades. The Apiaceae abundance significantly decreased compared to the lower layers – on average 10.0%, with small fluctuations and maximums circa 1590 and 740 years ago. The Poaceae percentage was low – from 0 to 19.1% (8.4% on



average). Asteraceae pollen abundance was also small – from 0 to 8.8% (2.7% on average). Single pollen grains of *Geranium* and Caryophyllaceae were stably found in the peat.

Between 2430-90 years ago, we observed two waves of increased Polypodiaceae spore abundance: 1470-1160 cal yr BP (130-110 cm) – from 4.4 to 8.9% (7.3% on average) and 810-360 cal yr BP (80-45 cm) – from 0.7 to 16.2% (9.1% on average). The Poaceae and Asteraceae pollen percentages also increased during these periods.

About 90-0 years ago (11-0 cm), TPC ranged from 1810 to 67740 grains / cm<sup>3</sup>, on average 36200 grains / cm<sup>3</sup>. Cyperaceae pollen abundance varied from 50.6 to 74.4% (65.5% on average). The Poaceae pollen percentage fluctuated from 1 to 18.8% (8.2% on average), Apiaceae - from 1.0 to 18.0% (10% on average). Ericaceae pollen and *Lycopodium annotinum* spores reappeared in the peat - their percentage increased up to 7.7% and 3.4%, respectively. Cichorioideae pollen also appeared and reached 2.1%.

#### iv. Discussion

Herein, we studied the impact of the seabird colonies on the Shemya Island coastal vegetation. To reconstruct plant community dynamics, we conducted pollen analysis of the McDonald Point peat deposit. We will briefly outline the vegetation changes that we identified. The peat began to accumulate before 9300 cal yr BP. During the initial development stages, the peatland was surrounded by sedge-heather tundra with some Asteraceae. The species which dominated in vegetation cover replaced each other during several centuries. Heather tundra with a noticeable abundance of sedges occupied the main area of the island coast 9100 years ago and then dwarf shrubs gradually decreased. Between 6400 and 4600 cal yr BP, hearth-grass-sedge tundra with lycopodiums dominated along the coast. Probably patches of ornithogenic vegetation also grew in the vicinity. These comprised plant communities with high abundance of Apiaceae and Poaceae formed as a result of the mechanical and chemical effects of seabird colonies. The pollen spectra changed dramatically 4600 cal yr BP, when sedge-grass meadows with high levels of Apiaceae spread. About 3000 cal yr BP, the abundance and size of ornithogenic vegetation patches began to decrease and sedge tundra changed to meadows by 2400 cal yr BP. Ornithogenic vegetation still remained, although the seabird colonies had already significantly decreased. In recent decades, tundra with the heather dwarf shrubs has spread again on the coast of Shemya Island. Below, we discuss multiple factors that influenced the vegetation dynamics.

During the early stages of coastal vegetation formation, dwarf shrub communities were widespread near the McDonald Point peat deposit. Dwarf shrub communities dominated

286 by crowberry occurred on well-drained slopes up to the vegetation border and in the lowlands  
287 open to winds in the Aleutian Islands and on the Alaska Peninsula (Heusser, 1978, 1983;  
288 Jordan, Krumhardt, 2003). Heusser (1990) assumed that in the pollen spectra, heathers are an  
289 important indicator of habitats which are exposed to strong wind, which has been noted for  
290 Ericaceae in other regions (Vital, 2002; Breslina, 1987). The predominance of herbaceous  
291 taxa in pollen spectra may indicate more protected habitats (Heusser, 1990). In general,  
292 heathers are a common component of a subarctic island's vegetation in an oceanic climate  
293 (Charman, 1994; Kutenkov and Stoykina, 2010). In the Alpine lands, grasses and sedges  
294 dominate together with crowberry, and *Lycopodium* dominates with *Empetrum* in the open  
295 lowlands (Heusser, 1978). We attribute the change in dominant species in the first samples of  
296 the McDonald Point peat core (Figure 3) and significant fluctuations in pollen concentration  
297 during this period (Figure 4) with high climate variability at the beginning of the Holocene  
298 (Kaufman et al., 2016).

299         The presence of Apiaceae pollen and Polypodiaceae spores in the pollen spectra  
300 (Figures 3, 4) indicates that, even during the earliest stages of peat deposit development,  
301 surrounding vegetation could be influenced by the guano associated with seabird colonies  
302 (Savinetsky et al., 2014; Kuzmicheva et al., 2019). Studies of extant bird activity provide  
303 strong evidence that birds form colonies of up to several thousand individuals on the Aleutian  
304 Islands devoid of terrestrial predators during the Holocene (Byrd et al., 2005). Increase in the  
305  $\delta^{15}\text{N}$  value reflects the introduction of additional heavy nitrogen from guano into the substrate  
306 (Croll et al., 2005; Maron et al., 2006; Szpak et al., 2012). On Shemya Island this nitrogen  
307 value was low during early stages of peat formation (Figure 5), suggesting that the colony did  
308 not directly alter the vegetation at that time (Savinetsky et al., 2014). Either the coastline was  
309 farther away than the modern (Black, 1980) or seabird colonies were small and did not have a  
310 crucial impact on coastal ecosystems. In general, a high mosaicity and change of dominants  
311 are indicative of the vegetation formed under the influence of guano (Breslina, 1987; Ivanov,  
312 2013; Garrouette et al., 2018). Apiaceae and Asteraceae in pollen spectra can also reflect the  
313 presence of tall grass meadows similar to those on the Kamchatka Peninsula (Zubkova, 1948;  
314 Hulten, 1937). These two taxa are present in the contemporary pollen spectra of the Alcan  
315 Creek peat deposit located in the interior of Shemya Island (Smyshlyaeva et al., 2021 in  
316 press). Apiaceae and Asteraceae pollen was also found in the lower peat layers of  
317 neighboring Attu Island (Heusser, 1990) and have been noted in this particular island's  
318 modern vegetation (Talbot et al., 1994).

Diatom analysis indicates relatively deep fresh water existed around McDonald Point during the initial stages of peat formation (Neplukhina et al., 2018). However, we only found single *Typha* pollen and *Equisetum* spores in the lowest pollen assemblies (Figures 3, 4).

These taxa are indicators of open water bodies (Galka et al., 2018), but their presence was too insignificant to indicate waterlogged vegetation in the McDonald Point pollen spectra.

The discovery of *Betula*, *Alnus*, *Pinus* pollen can be attributed to the long-distance air mass transport from Kamchatka (Heusser, 1990; Noguchi et al., 2018). In this regard, we did not consider their variation in the reconstruction of the Aleutian Islands vegetation.

Between 9100-6300 years ago, the  $\delta^{15}\text{N}$  value in the McDonald Point peat deposit was relatively low (Figure 5). Coastal vegetation was relatively stable, as was the climate in the region (Kaufman et al., 2016). In general, heather tundra dominated (Figure 3). The combination of Poaceae, Cyperaceae, and *Empetrum* in the vegetation composition is typical for the coastal tundra of Alaska (Jordan, Krumhardt, 2003) and the other oceanic islands including Shetland, Faroe, Iceland, and the White Sea Islands (Breslina, 1987; Hulme and Shirriffs, 1994; Lawson et al., 2008). Single pollen grains of miscellaneous herbs also correspond to tundra vegetation during this period of time (Figure 3). The high sedge abundance is partly explained by the formation of sedge mire in the interior between 7000-4700 years ago (Smyshlyaeva et al., 2021 in press). Holocene warming 7000-5000 years ago (Kaufman et al., 2016) was not reflected on the coastal vegetation of Shemya Island. Ornithogenic vegetation or tall grass meadows were distributed considerably distant from the peat core (Figure 3), their existence on the coast is evidenced by the relatively high percentages of Apiaceae and Asteraceae pollen in the Attu Island pollen spectra up until 5700 years ago (Heusser, 1990).

The input of additional organic matter from the seabird guano led to the gradual formation of meadow vegetation on the coast of Shemya Island (Figure 3). The  $\delta^{15}\text{N}$  value began to increase noticeably circa 6300 years ago (Figure 5, Savinetsky et al., 2014), but this was not clearly reflected in the pollen spectra. Plant communities commenced gradual change around 6400 cal yr BP (Figure 3). Alpine meadows with an undulating increase in lycopods became abundant instead of dwarf shrub tundra. This type of meadow is common in the Aleutian Islands, but occupies small areas (Zubkova, 1948). To the west of the Aleutians, in the Commander Islands, crowberry also gradually decreased following the appearance of bird colonies (Mochalova, 2008). A study of seabird colonies on the Pacific coast shows that even a short exposure of guano can lead to changes in the soil, plant communities, as well as chemical alterations in bedrock (Ivanov, 2013). In the absence of human and terrestrial

predators, birds can inhabit the entire island and form special ornithogenic ecosystems. Under the bird colonies pressure, dry peat soils are formed; they have an acid reaction, low ash content of peat and are enriched with nitrogen and phosphorus (Pleshchenko, 1992). Additional mineralization of peat, which does not have time to decompose in a northern oceanic climate, occurs due to extra input of shells, bones and nesting material. Similar processes and soil types have been noted for the islands of the White Sea (Breslina, 1987), the North Pacific (Ivanov, 2013), and Antarctica (Abakumov, 2010). In general, studies point out a high mosaicity of vegetation and a noticeable change in the dominant species under the influence of bird colonies (Breslina, 1987; Ivanov, 2013; Garrouette et al., 2018).

With bird colony influence the  $\delta^{15}\text{N}$  value increased to 4.7‰, which corresponds to the median  $\delta^{15}\text{N}$  value at CR-03 core on Carlisle Island in the Islands of Four Mountains of the Aleutian Islands (Kuzmicheva et al., 2019). Interestingly, at the earliest stages of the CR-03 peatland development, despite the high  $\delta^{15}\text{N}$  values (up to 11.0 ‰), heather tundra predominated. We associate this phenomenon with the formation of CR-03 peat deposition in more drained conditions, confirmed by the difference in  $\delta^{13}\text{C}$  (Figure 5) (McClymont et al., 2010; Loisel et al., 2010). Ericaceae also dominated due to their ability to resist wind. The dwarf shrub communities were also stable because of their ericoid mycorrhiza. In an oceanic climate, there is strong soil leaching, which can lead to nutrient deficiency (Hulme and Shirriffs, 1994; Lawson et al., 2008). With a lack of available nitrogen compounds, ericoid mycorrhiza allows shrubs to be more competitive than herbaceous plants (Makarov, 2019). A similar trend has been observed on other oceanic islands, in example Shetland and Faroe (Hulme and Shirriffs, 1994; Lawson et al., 2008). At the same time, the ericoid mycorrhiza fungi are able to regulate the activity of enzymes if the availability of nitrogen compounds increases. This allows the heathers to remain in the vegetation cover for some time following changes in soil conditions (Makarov, 2019).

Circa 5000 years ago the sea coast reached the McDonald Point peat deposit and the impact of the seabird colony became more evident (Black, 1980; Kiseleva et al, 2002; Savinetsky et al., 2014). By 4700 cal yr BP, in the interior of Shemya Island sedge mire began to be overgrown by herb-sedge-grass meadow as a result of the cooling that followed the Holocene maximum (Smyshlyaeva et al., 2021 in press). Probably at that time, sedge-grass meadows dominated on the entire island (Figure 3). About 4600 years ago,  $\delta^{15}\text{N}$  increased significantly in the coastal peat core and the pollen spectra dramatically changed (Figures 3, 4, 5). Over 1400 years (up to 3200 cal yr BP),  $\delta^{15}\text{N}$  increased from 8.2 to 16.0 ‰

(Figure 5; Savinetsky et al., 2014). Plant community productivity, including pollen productivity, increased, along with Apiaceae pollen abundance. We also found single pollen grains of Boraginaceae, Gentianaceae, Scrophulariaceae, *Epilobium*, Ranunculaceae, *Ranunculus*-type, *Geranium*, Saxifragaceae, Rosaceae, Caryophyllaceae, Liliaceae, and *Fritillaria* in the spectrum (see Data Availability Statement). According to Breslina (1987), these taxa are typical in the vicinity of bird colonies in the White Sea Islands. In the Commander Islands, Poaceae species are also significant members of ornithogenic communities (Mochalova, 2008). *Calamagrostis purpurea* and *Leymus mollis* are typical for coastal meadows, but due to avian influence, they grow higher on the slopes and occupy greater areas (Mochalova, 2008). During 1500 years (up to 3100 cal yr BP), ornithogenic vegetation predominated on the coast of Shemya Island (Figures 3, 4), possibly representing an analogue of the Kamchatka tall-grass meadows. Cooling after the Holocene temperature maximum (Kaufman et al., 2016) may have led to a noticeable increase in the productivity of the Bering Sea (Anderson et al., 2005) and, as a consequence, an expansion of seabird colonies. Associated intensive input of organic matter also caused a noticeable decrease in ash content and the  $\delta^{13}\text{C}$  value in the peat core (Figure 5, Savinetsky et al., 2010; 2014; Kiseleva et al., 2002). TPC, an indicator of pollen productivity, in the McDonald Point also increased markedly (Figure 4).

The decline of  $\delta^{15}\text{N}$  began about 3000 years ago. For nearly 600 years, the value decreased from 14.0 to 9.0 ‰ (Figure 5). However, this was several times higher than the  $\delta^{15}\text{N}$  median value of the entire peatland (Savinetsky et al., 2014). Grass meadows with forbs dominated on the Shemya coast between 3000 and 2400 cal yr BP and, at that time, the abundance of ornithogenic vegetation gradually decreased (Figure 3). TPC remained relatively high (Figure 4). Savinetsky et al. (2014) explained that the migration of humans to Shemya reduced the number of colonial birds which resulted in a decline in guano and  $\delta^{15}\text{N}$ . Circa 3000 years ago, at least one settlement existed on the island, and by 2000 years ago, there were three additional sites, according to archaeological evidence (Lefevre et al., 2010). The hypothesis of hunting is supported by numerous bird remains identified in these archaeological sites (Lefevre et al., 2010). The flat and low topography of Shemya Island, provided no sufficiently protected habitats from human predation which could allow a large seabird colony to survive (Savinetsky et al., 2014). The gradual decline in the colony population as a result of hunting led to a decrease in avian influence on vegetation over time. In this case, we argue that, despite the absence of grazing or agriculture in the Aleutian Islands, humans could significantly alter ecosystems during the Holocene. Anthropogenic

settlement notably influenced the vegetation of other oceanic islands (Bennett et al., 1997; Hannon and Bradshaw, 2000; Roy et al., 2018).

The climate could also directly affect vegetation changes, especially during ecologically unstable periods (Bunting, 1994). Between 4000 and 3000 years ago, the Neoglacial commenced gradually without a pronounced pattern in the region (Kaufman et al., 2016). This climatic event was associated with a decrease in temperatures, high ice cover in the Bering Sea, and an intensification of winter-spring storms (Majewski et al., 2004; Harada et al., 2014; Kaufman et al., 2016; Bailey et al., 2018). More severe conditions could have resulted in the gradual spread of grass-meadows in the place of herb-meadows with high pollen productivity on Shemya Island (Figures 3, 4). Changes in plant communities are also associated with climate in Ireland (Birks and Peglar, 1979; Molloy and O'Connell, 2004), the Kuril Islands (Razjigaeva et al., 2013), the Shetland Islands (Hulme and Shirriffs, 1994), and the Faroe Islands (Lawson et al., 2008).

An alternative hypothesis is that the climate influenced colonial seabird population dynamics, which subsequently led to changes in vegetation. Similar impacts have been observed in different regions, including the Atlantic coast of Canada (Diamond and Devlin, 2003), the Bering (Springer et al., 2007), and the Okhotsk seas (Andreev et al., 2002). Avian reproductive success can depend on the oceanic climate on the decadal scale (Bond, 2011). Additionally, avian reproductive success is influenced by the temperature in the winter-spring period, which was altered during the Neoglacial (Harada et al., 2014; Sydeman et al., 2017).

Forb-grass meadows were replaced by sedge tundra with fragments of ornithogenic vegetation circa 2400 cal yr BP (Figure 3). Long-term impact (for more than 2200 years from 4600 to 2400 years ago) of bird colonies on coastal vegetation is visible in the pollen spectra (Figures 3, 4). The similarity in intensity and time effect was not observed in any of the studied Aleutian Islands (Heusser, 1973; 1978; 1990; Noguchi et al., 2018; Kuzmicheva et al., 2019; Smyshlyaeva et al., 2021 in press). Birds played an important role in the coastal vegetation history of Carlisle Island. There were periods of significant increase in  $\delta^{15}\text{N}$ , these periods did not exceed 600 years and did not strongly alter ornithogenic vegetation (Kuzmicheva et al., 2019).

Circa 1470-1160 and 810-360 cal yr BP,  $\delta^{15}\text{N}$  slightly increased (Savinetsky et al., 2014). Polypodiaceae spores, Asteraceae, and Poaceae pollen relatively increased during these periods (Figure 3). The beginning of the second period overlapped with the early stage of Little Ice Age and a consequent decrease in precipitation in the central part of the Aleutian ridge (Vaillencourt, 2013). This could also be the reason for the increase in the Bering Sea



productivity and the subsequent restoration of seabird colonies. The end of both periods is associated with the Aleutian Low (AL) rapid intensification and westward transition (Rodionov et al., 2007), which led to an increase in the frequency of mild winters due to the warm air mass influx into the Bering Sea (Anderson et al., 2005). The resulting decrease in sea productivity may have led to a reduction in bird populations. Thus, short periods of bird impact, 300-600 years, lead to fluctuations in the indicator-taxa abundance, but not to a noticeable change in the dominants of the vegetation cover (Figure 3).

In recent decades (since about 90 cal yr BP), grass-sedge tundra with some patches of ornithogenic vegetation were widespread. Heather pollen returned to the spectra in the upper samples. On Attu, Atka (Heusser, 1990), and Adak (Heusser, 1983; Noguchi et al., 2018), as well as the interior of Shemya Island (Smyshlyaeva et al. 2021 in press), heather dwarf shrubs also gradually began to dominate in plant communities (Figure 3). We assume that 300 years after the significant reduction of the seabird colonies, heather returned and became the dominant vegetation cover around McDonald Point peat deposit. In the Faroe Islands, the emergence of heather communities was associated with intense soil leaching (Lawson et al., 2005). We also assume that the intensive leaching of soils contributed to the gradual return of heathers to Shemya Island coastal vegetation. On treeless islands, dwarf shrub communities are the final stages of the ecological succession series (Breslina, 1965). Similar communities have been noted on the Kamchatka and Sakhalin Peninsulas (Breslina, 1965). On North Pacific islands, near areas abandoned by seabird colonies more than 10 years ago, tundra with the *Empetrum* dominance was formed, thus completing the cycle of vegetation restoration (Ivanov, 2013). The same tendency was recognized on the White Sea Islands: after a year or several years, eider nesting sites were overgrown with the same vegetation seen prior to nesting (Breslina, 1987). On the Kola Subarctic islands, heather communities are also the final stage of vegetation succession at puffin colony sites (Breslina, 1987).

Volcanic eruptions also played a significant role in the Aleutian Islands vegetation history (Heusser, 1990; Talbot et al., 2010b; Kuzmicheva et al., 2019). Ash falls of various intensity could lead to the complete destruction of island landscape, a change in vegetation dominants, various disturbances of whole plants or their parts, a change in productivity or biomass, or have no effect (Heusser, 1990; Talbot et al., 2010; Kuzmicheva et al., 2019). However, there are no volcanoes on Shemya Island and Kiseleva *et al.* (2002) found that the mineral layers in the peat deposits from Shemya Island are sand, and not ash. Thus, we previously assumed that volcanic activity had no noticeable effect on Shemya Island coastal vegetation. However, about 7300-6900 years ago there was a significant and sharp decrease



in pollen concentration in the McDonald Point peat deposit (Figure 4). The TPC was also very low around 1900 years ago (Figures 3, 4), which appears to correspond to the Okmok II volcanic eruption (Okuno et al., 2017; Kuzmicheva et al., 2019). The eruption of the Okmok volcano (Umnak Island) was so massive that it led to significant climatic and ecological effects as far away as the Mediterranean (McConnell et al., 2020). Moreover, a comparatively sharp drop in the pollen concentration was recognized circa 1050-990 years ago, which temporally correlates with the Cleveland volcano eruption on Chuginadak Island (the Islands of Four Mountains). The eruptions noted above formed visible ash layers in the peat core on Carlisle Island (the Islands of Four Mountains) (Okuno et al., 2017; Kuzmicheva et al., 2019), but not in McDonald Point peatland (Table 1; Kiseleva et al., 2002). We also do not exclude that the noted reductions in pollen productivity could be due to numerous eruptions of Kamchatka volcanoes (Kyle et al., 2011). We propose that massive eruptions could lead to decreased plant pollen productivity on Aleutian islands located a significant distance from eruption epicenters.

## **v. Conclusions**

In order to study the influence of seabird colonies on Aleutian Islands vegetation, we carried out a pollen analysis of a peat deposit from Shemya Island. The primary communities on the Shemya Island seashores were a mosaic; the dominants often changed. About 9100 years ago, coastal vegetation was more or less stable. Sedge-heather tundra with patches of ornithogenic vegetation or tall-grass meadows spread. Plant communities began to gradually change in response to nitrogen enrichment around 6400 years ago. The noticeable influence of seabird colonies was enhanced 4600 years ago, when the role of ornithogenic indicator taxa in the pollen spectra dramatically increased. Meadows, instead of tundra, spread out on the coast. Circa 3000 years ago, the bird colonies and their influence on the plant communities declined, due either to the settlement of the island by people who hunted birds or to climate change in the region, including a decrease in average temperatures and increased storminess in spring and winter. Shifts in atmospheric patterns could affect vegetation both directly and indirectly through their impact on bird populations. In recent decades, as a result of a noticeable reduction in bird colonies, heather dwarf shrubs have started to spread again on the Shemya coast. The seabird colonies development between 1470-1160 and between 810-360 years ago are reflected in the pollen spectra by an increase in TPC and the indicator taxa abundance, but not by shifts in the vegetation dominants.

We assumed that ash eruptions did not significantly affect this flat island devoid of volcanoes. Most Aleutian volcanoes are concentrated in the eastern and central parts of the arc where their activity was more intense. However, we found the TPC significantly decreased in the McDonald Point peat deposit corresponding to at least three large eruptions. Although ash layers were not identified in peat, on other islands, ash layers are documented that include an unknown volcanic eruption about 7300-6900 years ago, the Okmok volcanic eruption about 1900 years ago, and the Cleveland volcanic eruption about 1000 years ago. Although such drops in concentration did not lead to noticeable vegetation changes on Shemya Island.

We believe that the complexity of factors affecting Aleutian vegetation can be determined by consistently studying each influence separately. Detailed knowledge about the local depositional formation will allow a better assessment of the impact of individual formation factors. When we compare vegetation shifts throughout time and space under different conditions, we will be able to gain a clearer picture of prehistoric interactions and driving forces on the Aleutian landscape.

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719 [istry\\_in\\_peat\\_Tools\\_to\\_investigate\\_past\\_hydrology\\_temperature\\_and\\_biogeochemistry](https://www.researchgate.net/publication/287097072_Stable_isotopes_and_organic_geochemistry_in_peat_Tools_to_investigate_past_hydrology_temperature_and_biogeochemistry)

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Table 1. Field description of peat deposit McDonald Point.

Depth, cm	Description
0–6	Brown to dark brown sod with plant roots penetration. The border with the underlying layer is clear, wavy.
6–11	Light gray horizon, sandy, structureless, penetrated by roots. Humus-peaty material alternates with tiny mineral accumulations. The border with the underlying layer is clear.
11–16(18)	Horizon from light brown to rusty brown, ferruginous, sandy, loose, moist, penetrated by roots; the color is irregular. The border with the underlying horizon is sharp, but irregular in color.
16(18)–46	Light brown horizon, dense, viscous, structureless, moist, sandy, ferruginous. The roots number is sharply reduced. Peat is found along the roots. The border with the underlying horizon is clear.
46–85(90)	Horizon from light brown to light maroon, very dense, viscous, moist, penetrated by roots; well decomposed peat with mineral sediments. The border with the underlying layer is clear.
85(90)–110	Light gray horizon, structureless, sandy, wet, irregular in texture; modern roots are rare; a lot of undecomposed plant remains. The transition to the underlying horizon is sharp, the boundary is flat.
110–144	Dense peat, homogeneous, wet, light yellow, well decomposed, very plastic, with thin mineral layers. The border with the underlying horizon is flat.
144–168	Peat is similar to the overlying layer, maroon, wet, plastic; enriched with fine-grained sandy sediments. The boundary with the underlying horizon is gradual and is distinguished by the disappearance of sand deposits.
168–270	Dense peat, homogeneous, light brown, well decomposed, wet, plastic, penetrated with old roots. The border with the underlying horizon is sharp.
270–296	Sandy horizon, dirty gray, structureless. Layer 270–280 cm has a more brown shade. The border with the underlying horizon is smooth and clear.

296–300	Dark maroon peat, very dense, well decomposed, wet, ferruginous. The border with the underlying horizon is wavy and clear.
300–310	Peat-mineral horizon, irregular color, implicitly layered, wet. The border with the underlying horizon is smooth and clear.
310–318	Structureless horizon, wet, roots are rare. Consists of two layers: 310-315 cm - fine-grained, well-sorted sand, 315-318 cm - coarse-grained sand. The border with the underlying horizon is smooth and clear.
318–372	Peat from dark brown to maroon color, homogeneous, viscous, well decomposed, saturated with fine mineral sediments, ferruginous. The border with the underlying horizon is flat, sharp.
372–386	Light loam, waterlogged, viscous, structureless. The bedrock lies at a depth of 385 cm.

826

827    Table 2. <sup>14</sup>C ages of McDonald Point peat deposit.

Depth (cm)	<sup>14</sup> C age (year BP)	Age range (cal. yr BP)	Mean age (cal. yr BP)	Lab ID
50-55	400 ± 100	560-370	470	IEMAE-1243
80-85	875 ± 65	960-760	860	IEMAE-1285
125-130	1405 ± 100	1670-1280	1420	IEMAE-1280
225-230	3295 ± 90	3820-3480	3620	IEMAE-1279
265-270	4060 ± 80	5110-4550	4760	IEMAE-1262
318-320	6430 ± 155	7600-7170	7390	IEMAE-1286
363-372	9550 ± 130	10840-8600	9330	IEMAE-1261

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829



830 **Figure legends:**

831 Figure 1. The study area map. The inset shows Shemya Island and the McDonald Point peat  
832 deposit (mark).

833 Figure 2. McDonald Point age-depth model. Dark gray - calibrated dates, gray - 95%  
834 chronology confidence interval.

835 Figure 3. Abbreviated pollen percentage diagram for McDonald Point peat deposit. Gray  
836 curves exaggerated x 4. McDP-Z1, McDP-Z2, McDP-Z3 pollen zones identified on the basis  
837 of CONISS are shown by dashed lines. The dotted line marks the beginning of vegetation  
838 change as a result of seabird colony impact. Signs + and ++ mark single pollen grains. The  
839 full diagram is presented in the Data Accessibility Statement.

840 Figure 4. Abbreviated pollen concentration diagram for the McDonald Point peat deposit  
841 (grains / cm<sup>3</sup>). Gray curves exaggerated x 4. McDP-Z1, McDP-Z2, McDP-Z3 pollen zones  
842 identified on the basis of CONISS are shown by dashed lines. The dotted line marks the  
843 beginning of vegetation change as a result of seabird colony impact. The full diagram is  
844 presented in the Data Accessibility Statement.

845 Figure 5. McDonald Point stable isotope analysis results are presented according to the data  
846 of Savinetsky et al., 2014. The changes in the Apiaceae percentage and the total pollen  
847 concentration are shown for comparison. The point colors represent the pollen zones  
848 identified by CONISS. The bands indicate important events in the Shemya Island vegetation  
849 history: red - the Holocene warming 7000-5000 years ago (Kaufman et al., 2016), green - the  
850 first archaeological evidence of the human presence on Shemya Island (Lefevre et al., 2010),  
851 blue - the Little Ice Age (Vaillencourt, 2013).

852 **DATA ACCESSIBILITY STATEMENT:** we will use Dryad data repository for complete  
853 pollen tables and diagrams.

854 **COMPETING INTERESTS STATMENT.** None declared.

855 **AUTHOR CONTRIBUTION:**

Olesya I. Smyshlyaeva: data curation (lead); formal analysis (equal), visualization (lead), writing - original draft preparation (lead), writing - review & editing (equal)

Elena E. Severova: investigation (lead), writing - review & editing (equal)

Olga A. Krylovich: visualization (supporting), writing - review & editing (equal)

Evgenya A. Kuzmicheva: writing - review & editing (equal), formal analysis (equal)

Arkady B. Savinetsky: conceptualization (lead), supervision (lead), funding acquisition (equal), writing - review & editing (equal)

Dixie L. West: conceptualization (equal), funding acquisition (equal), writing - review & editing (equal)

Virginia L. Hatfield: conceptualization (equal), funding acquisition (equal), writing - review & editing (equal)

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