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RESEARCH PAPER

Modern pollen–vegetation relationships on Onekotan Island (Northern Kuril Islands, NW Pacific): implications for paleoenvironmental reconstructions

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ABSTRACT

We analyze surface spore-pollen spectra (SPS) from Onekotan Island (Northern Kurils) in order to develop a modern analogue for paleogeographic reconstructions under conditions of high island isolation. Eighteen soil samples from shrub thickets, dwarf shrub–tundra-like communities, and meadows were processed using standard palynological techniques and analyzed by multivariate statistics. *Duschekia* pollen absolutely dominates (14.5–83.0 %), with *Pinus* subg. *Haploxylon* reaching 56.1 % in some samples. Fern spores reach up to 48.5 %. Despite a strong regional background from highly productive taxa, multivariate analyses (PCA and DCA) reveal broad compositional differences among the local vegetation communities. Long-distance transported pollen of *Betula*, *Picea*, *Abies*, and broadleaved taxa (maximum 8 % in open coastal meadows) indicates wind transport from Kamchatka, Sakhalin, Hokkaido, and continental areas. These first quantitative data on marker taxa and allochthonous pollen provide a reference framework for interpreting fossil pollen spectra and palaeogeographic changes in the Northern Kurils.

Keywords: pollen analysis, Kurils, paleogeographic reconstructions, long-distance pollen transport, local plant associations, wind-pollinated shrubs

РЕЗЮМЕ

Романова А.В., Петренко Т.И., Евстигнеева Т.А., Добридень С.П., Савинов И.А., Гвоздева И.Г. Взаимосвязи современного растительного покрова и пыльцевых данных на острове Онекотан (Северные Курильские острова, северо-западная Пацифика): значение для палеоэкологических реконструкций. Статья посвящена анализу поверхностных спорово-пыльцевых спектров (СПС) острова Онекотан (Северные Курилы). Актуальность исследования обусловлена необходимостью создания репрезентативной базы для палеогеографических реконструкций в регионе с высокой степенью островной изоляции и своеобразием растительного покрова. Проанализировано 18 почвенных образцов в стланиковых, кустарничковых и луговых сообществах с применением многомерного статистического анализа (кластерный анализ, PCA, DCA). Установлено абсолютное доминирование пыльцы *Duschekia* (от 14,5 до 83,0 %) при значительном участии *Pinus* subg. *Haploxylon* (15–25 %). Споры папоротников достигают 48,5 %. Несмотря на сильный региональный фон, формируемый таксонами с высокой пыльцевой продуктивностью, многомерный анализ (PCA и DCA) выявляет общие различия в составе СПС, связанных с локальными растительными сообществами. Выявлено присутствие заносной пыльцы березы, ели, пихты и широколиственных пород (максимум 8 % в открытых прибрежных лугах), что свидетельствует о дальнем ветровом переносе с Камчатки, Сахалина, Хоккайдо и континентальных территорий. Полученные результаты служат основой для корректной интерпретации ископаемых палинологических данных и палеогеографических реконструкций на Северных Курилах.

Ключевые слова: спорово-пыльцевой анализ, Курилы, палеогеографические реконструкции, дальний перенос пыльцы, локальные растительные ассоциации, ветроопыляемые кустарники

Palynological research has developed actively over recent decades and now plays a key role in reconstructing Late Quaternary vegetation and climate (Edwards et al. 2000, Tarasov et al. 2000). Pollen analysis remains one of the primary tools for Holocene palaeogeographic studies (Borisova 2014). A critical step in ensuring reliable palaeogeographic reconstructions is the study of surface spore-pollen spectra (palynological assemblages). Understanding how modern pollen assemblages form and how accurately they reflect vegetation structure provides the basis for correctly interpreting fossil data.

In the southern Russian Far East, extensive work on subfossil palynological assemblages has focused on continental areas (Korotky 2002, Mokhova et al. 2009, Petrenko et al.

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2009, Mokhova & Kudryavtseva 2022, Mikishin et al. 2025). For island territories, such studies have been conducted on Sakhalin Island (Mikishin & Gvozdeva, 2009) and several islands of the Greater Kuril Chain (Anderson & Lozhkin 2017, Mokhova & Eremenko 2020, Mokhova 2024).

The Kuril Islands are a unique area for palaeogeographic research (Razjigaeva et al. 2009, 2011, 2013, 2014, 2018, Ganzey 2010, Lyashchevskaya et al. 2018, Lozhkin et al. 2010, 2017, 2020, 2022). Located at the boundary between the Circumboreal and East Asian floristic regions (Barkalov 2002), they combine several natural and climatic factors within a relatively small area, resulting in high biodiversity and regional distinctiveness: diverse landscape and coenotic conditions, high humidity, and active volcanism. However, many islands of the central and northern Kuril Chain remain poorly studied in terms of palaeogeography, primarily due to their remoteness, harsh climate, and logistical difficulties in organizing fieldwork.

Among the Northern Kuril Islands, Onekotan is of particular interest. Unlike the southern islands (Kunashir, Iturup) and northern islands (Paramushir, Shumshu), Onekotan had no direct land connections with the continent (Kamchatka) or Hokkaido during the Late Pleistocene and Holocene, which led to the depauperate composition of its biota (Bezverkhny et al. 2002). At the same time, possible historical connections with more northern territories through ice bridges explain the occurrence of some Siberian and Kamchatkan elements, while unique isolation conditions favored the preservation of relict plant groups, such as high-mountain plants (Barkalov 2009). Palaeoecological studies further demonstrate that the vegetation history of Onekotan differed from that of the southern and central Kuril Islands. Pollen and stratigraphic records indicate that tundra and heath communities dominated the island during the Early Holocene, with scattered graminoid communities and shrubs, whereas later Holocene vegetation included more extensive *Pinus pumila–Duschekia* shrub communities, forb meadows, and wetland vegetation (Razjigaeva et al. 2011, 2013). These reconstructions also emphasize the strong influence of local volcanism on vegetation development, particularly following major tephra-forming eruptions, and demonstrate that vegetation changes on the Kuril Islands were spatially heterogeneous and not always synchronous even among neighbouring islands (Razjigaeva et al. 2011, 2013, 2014, 2019). This biogeographic and palaeoecological specificity makes the island particularly attractive for studying vegetation history under conditions of island isolation.

Despite growing research interest in the Kuril Archipelago, modern surface pollen spectra from Onekotan linked to well-characterized vegetation communities remain poorly documented. Previous palaeoecological studies have provided pollen and stratigraphic records from Holocene peat sections on the island (Razjigaeva et al. 2011, 2013), but a modern pollen–vegetation dataset suitable for comparison with these fossil records is still lacking. Here, we analyze modern surface spore-pollen spectra from Onekotan Island and compare them with the associated vegetation communities. The uniqueness of our material lies in the difficulty of collecting samples in remote areas of the island and the limited availability of modern surface pollen data linked to well-characterized vegetation communities on Onekotan. These data provide an important modern reference for interpreting fossil pollen records and for future palaeoclimatic and palaeogeographic reconstructions in the region.

MATERIAL AND METHODS

Study area

Onekotan Island (425 km²) is located in the northern part of the Greater Kuril Chain (Fig. 1). Onekotan Island is of volcanic origin and forms part of the Pacific Ring of Fire (Melekestsev et al. 1974). Its topography is dominated by two stratovolcanoes, Krenitsyn (1325 m a.s.l.) and Nemo (1019 m a.s.l.), whose steep slopes are composed of lavas, tuffs, and pyroclastic deposits and dissected by ravines (barrancos) that often retain snowbeds until mid-summer. It extends approximately 45 km from north to south and 8–18 km from west to east. The island has an oceanic climate, with relatively warm winters (-5°C) and cool summers (+11°C; Komedchikov 2009). Oceanic influence determines an even precipitation distribution, averaging 1500 mm per year (100–200 mm per month). A characteristic feature of the island is the high frequency of strong winds (exceeding 15 m/s) occurring on 150 days per year. At the Vasilyeva Cape weather station (southern Paramushir Island), the maximum wind speeds for the archipelago were recorded, reaching up to 230 km/h (Grishin et al. 2005).

The island lies north of the deep-water Bussol Strait, a critical biogeographic boundary of the Kurils. Territories north of the strait are characterized by a predominance of boreal and arctoalpine floristic and faunal elements, whereas East Asian species dominate to the south (Barkalov 2002). During the Late Pleistocene (18–15 ka), Onekotan formed part of a single land block together with Ekarma, Shiashkotan, and Kharimkotan Islands; final isolation occurred in the Early Holocene due to sea-level rise (Bezverkhny et al. 2002).

The vegetation of the island has a dwarf, low-growing appearance, which markedly distinguishes Onekotan from neighbouring Paramushir (Grishin et al. 2005). The Kira thermal coefficient here is 12.6°C, whereas tree growth requires at least 15°C (Grishin et al. 2005). The flora includes approximately 315 species of vascular plants (Grishin & Barkalov 2009, Volkova et al. 2019). Endemism does not exceed 2 %, indicating recent isolation and the possibility of gene exchange with the continent during the Late Pleistocene–Holocene (Barkalov 2009).

Shrub thickets form the basis of the vegetation cover (Fig. 2). The absolute dominant is alder shrub (*Duschekia fruticosa* (Rupr.) Pouzar and *D. maximowiczii* (Callier) Pouzar). *Pinus pumila* (Pall.) Regel plays a subordinate role, occupying no more than one-third of rocky or steep slopes and not forming closed canopies (Grishin & Barkalov 2005). *Duschekia fruticosa* forms both pure stands and mixed thickets with *Pinus pumila*. Siberian dwarf pine occurs not only on steep rocky slopes but also in mixed communities with alder shrub, particularly on wind-exposed surfaces (Grishin et al. 2005). Altitudinal zonation is reduced to a hypertrophically expanded alder belt, rising to 900–1000 m, and on the largest volcanoes up to 1200 m (Grishin & Bar-

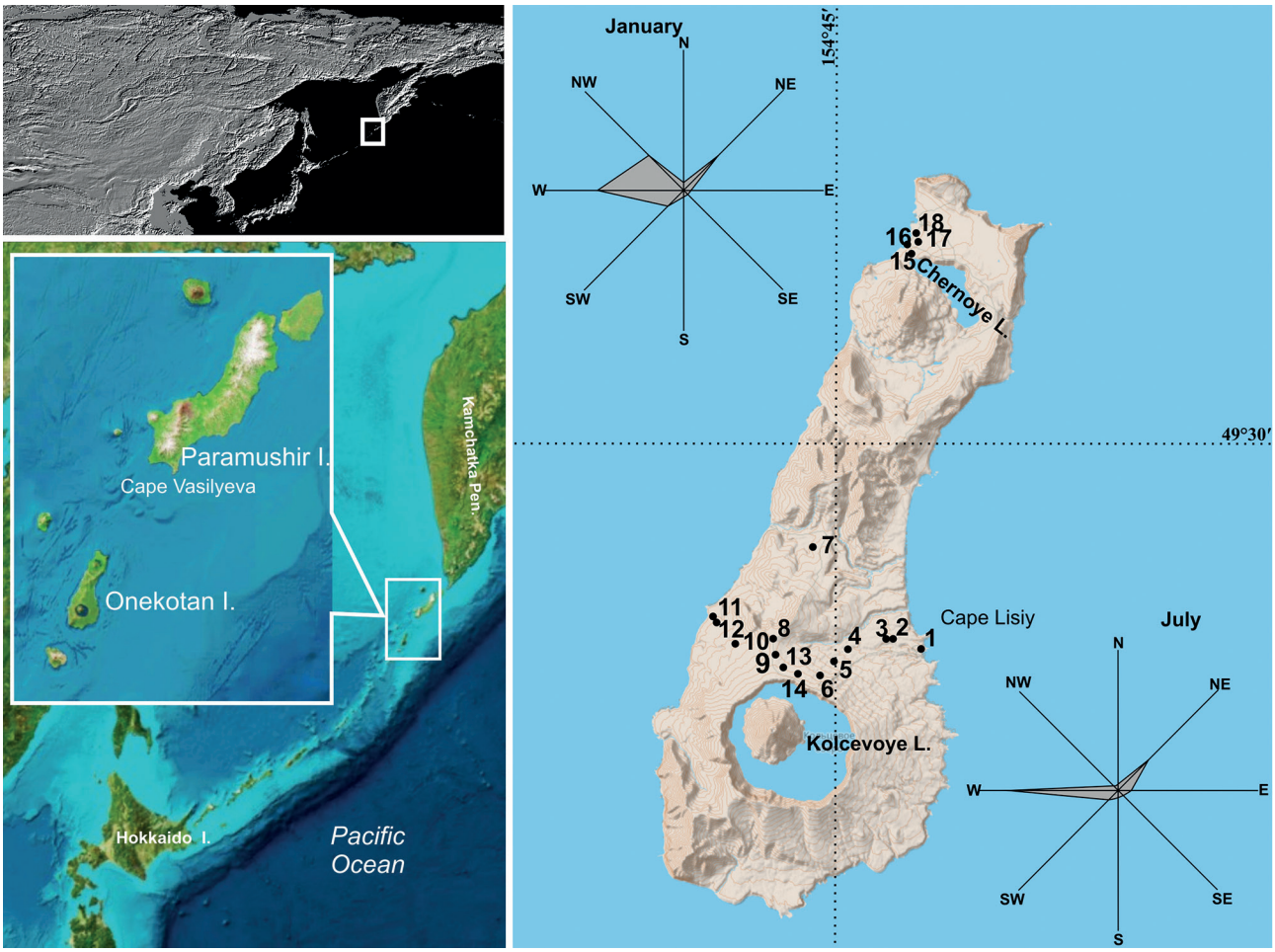


Figure 1 Location map of sampling sites for modern sediment samples analyzed by pollen analysis on Onekotan Island. Base map from www.ru-topographic-map.com. Wind rose constructed from data of the nearest weather station (Vasilyeva Cape)

kalov 2005). Above this belt, vegetation is interrupted by rock outcrops, talus slopes, and volcanic deposits. Forest vegetation is absent, a characteristic feature of the entire northern Kuril group.

Meadow communities are widespread. On areas with thick soil cover and adequate moisture, tall-herb and forb meadows develop with large herbs, including *Senecio cannabifolius* Less., *Parasenecio kamtschatica* (Maxim.) Kadota, and *Angelica gmelinii* (DC.) M. Pimen.), among others. Reed grass meadows (*Calamagrostis langsdorffii* (Link.) Trin.) with tall herbs, as well as forb, tall-herb, and sedge wet meadows predominate along river and lake shores, in the coastal zone, and on slopes.

On open dry sites, grass-forb and sedge meadows form, along with dwarf shrub communities with *Rhododendron camtschaticum* Pall., *Empetrum sibiricum* V. Vassil. and *Vaccinium uliginosum* L. Heathlands are represented by crowberry heaths and ericaceous tundra, confined to the most wind-exposed habitats, the coastal zone, and mountain tops.

On upper slopes and volcanic substrates, vegetation is sparse, represented by moss-lichen and dwarf shrub tundra communities. On volcanic deposits (especially on Krenitsyn Volcano), vegetation is at initial stages of succession (crustose lichens). Mountain tundra occurs on ridges and slopes above 400 m a.s.l., and snowbed communities occur on slopes of marine terraces and in mountains. Wetland complexes are confined to the valley between Kryzhanovsky and Zavaritsky mountains, as well as to local depressions on coastal terraces (Savinov 2025).

Thus, the modern vegetation cover of Onekotan represents a combination of alder and Siberian dwarf pine thickets, tall-herb and forb meadows, and dwarf shrub–tundra communities, whose formation is determined by climatic conditions, topography, and volcanic activity.

Data collection and analysis

We collected 18 surface soil samples on Onekotan Island in 2024 during a joint expedition of the Russian Geographical Society and the Expedition Center of the Ministry of Defense of the Russian Federation "Eastern Bastion – Kuril Ridge". Our sampling points are located on a transect from the eastern coast westwards along Koltsevoye Lake (southern volcanic massif) and in the area of Chernoye Lake (northern Nemo volcanic complex). All samples were taken from the surface soil layer (Fig. 1).

We processed samples for spore-pollen analysis using standard palynological techniques (Pokrovskaya 1966). For each sample, we counted more than 300 pollen grains and spores. We used a pollen sum (100 %) that included arboreal and nonarboreal pollen. We calculated spore percentages relative to this sum.



Figure 2 Landscapes of Onekotan Island:a – general view of the northern part of the island with *Pinus pumila* in the foreground and Duschekia thickets in the background; b – dwarf shrub–tundra plant community at station 8; c – *Pinus pumila* thickets, with the Pacific coast in the distance; d– meadow vegetation at the northern part of the island

To identify allochthonous taxa in the spore-pollen spectra, we compared our data with existing floristic lists for Onekotan Island (Barkalov 2009, Volkova et al. 2019). According to modern taxonomy (POWO 2026; WFO 2026), *Duschekia fruticosa* (Rupr.) Pouzar and *Duschekia maximowiczii* (Callier) Pouzar, recorded in modern vegetation descriptions, are considered synonyms of *Alnus alnobetula* subsp. *fruticosa* (Rupr.) Raus and *Alnus maximowiczii* Callier, respectively. In this paper, we retain the traditional name *Duschekia*. The monolete spores found in the palynological assemblages most likely belong to the fern *Dryopteris expansa* (C. Presl) Fraser-Jenk. & Jermy, which is widespread on the island. Pollen grains of Ericaceae belong to different species of crowberry (*Empetrum* L.), bilberry (*Vaccinium* L.), rhododendron (*Rhododendron* L.), and *Phyllodoce aleutica*. Following the palynological practice established for the Kuril Islands (Anderson & Lozhkin 2017, Mokhova 2024), we distinguish between *Pinus* subg. *Haploxylon* and *Pinus* subg. *Diploxylon*. We assign the *Haploxylon* type to *Pinus pumila* (Pall.) Regel, whereas the *Diploxylon* type is considered allochthonous pollen. The plant scientific names allow to modern international taxonomic databases – Plants of the World Online (POWO), World Flora Online (WFO).

The circumscription of plant taxa adopted here follows APG IV (Chase et al. 2016) for angiosperms, PPG I (Schuettpelz et al. 2016) for lycophytes and ferns, and GPG (Christenhusz et al. 2011) for gymnosperms.

We constructed percentage pollen and spore diagrams using Tilia software (version 2.0.41; Grimm, 1991). We performed principal component analysis (PCA), detrended correspondence analysis (DCA), cluster analysis, and diversity index calculations using PAST software (version 5.3; Hammer et al. 2001).

To identify the structure of palynological data, group samples by similarity of pollen spectra, assess ecological gradients, and test the response type of taxa (linear vs. unimodal) while minimizing the influence of regional highly productive pollen taxa and rare taxa, we conducted cluster analysis and multivariate ordinations (PCA and DCA). We used log-transformed data as the input matrix. For cluster analysis, we employed Euclidean distance as the similarity measure and Ward's method as the clustering algorithm. Cluster stability was assessed using a non-parametric bootstrap procedure with 2 000 replicates. Taxa retained in the original dataset were resampled with replacement, and the clustering was recalculated using the same log-transformation, Euclidean distance and Ward's method. Bootstrap support was calculated as the proportion of bootstrap replicates in which the corresponding sample group was recovered as a clade. In addition, an independent k-means analysis with four groups was performed using the same transformed dataset, and agreement between the Ward and k-means classifications was assessed using the adjusted Rand index (ARI). To minimize the influence of rare taxa and statistical noise, we included only taxa with an abundance exceeding 2 %. To quantify the structure of the palynological assemblages, we also calculated palynological richness (S), defined as the total number of taxa per sample.

Because pollen of highly productive pollen taxa (*Duschekia* and *Pinus* subg. *Haploxylon*) creates a strong regional background that masks local differences, we excluded these taxa from the input matrix prior to ordination for PCA and DCA. To evaluate data structure and the quantitative contribution of axes, we used PCA, which assumes linear relationships among taxa. To verify the adequacy of the linear approximation and detect possible unimodal responses of taxa, we performed DCA. The gradient length of the first DCA axis was approximately 2.5–3 standard deviations (SD), exceeding the threshold of 2 SD recommended for choosing between linear and unimodal methods. Nevertheless, after

excluding *Duschekia* and *Pinus* subg. *Haploxylon*, the remaining taxa show predominantly linear responses across the limited elevational range (39–599 m), making PCA interpretable and informative. We used both methods as complementary: PCA for quantitative assessment of variance and visualization of data structure, and DCA for confirming ecological gradients and assessing taxon turnover.

RESULTS

Sample locations and vegetation communities

We placed surface sample points in the northern and central parts of Onekotan Island (Fig. 1), primarily within two main orographic structures: a transect from the eastern coast (Lisiy Cape) westwards along Koltsevoye Lake, and in the area of Chernoye Lake (northern part of the island). The sampling points cover an elevational range from 39 to 599 m a.s.l. and represent three vegetation types: shrub thickets, dwarf shrub–tundra-like communities, and meadow vegetation (Table 1).

Samples 1–6 were collected from shrub thickets developed at elevations between 109 and 599 m a.s.l. These sample points are located in the eastern part of the island. *Duschekia fruticosa* forms the basis of these communities, in places with an admixture of *Pinus pumila* (sample 5) and *D. maximowiczii* (sample 6). Under the canopy, ferns (*Dryopteris expansa*), grasses, and tall herbs (*Parasenecio kamtschatica*, *Veratrum oxysepalum*) are common.

We collected samples 7–10 from dwarf shrub–tundra-like communities occurring at elevations from 180 to 442 m a.s.l. These communities are confined to levelled watershed areas and gentle slopes of northern and western aspects, where conditions favour snowbed formation and prolonged snow cover. *Empetrum sibiricum*, *Vaccinium uliginosum*, *Rhododendron camtschaticum*, and other members of the Ericaceae dominate these communities. We also recorded willow (*Salix arctica* Pall. subsp. *crassijulis* (Trautv.) A. Skvorts., *Salix kurilensis* Koidz.,), alder shrub (*Duschekia fruticosa*), forbs (*Geranium erianthum* DC., *Saussurea riederi* Herd., *Aruncus dioicus* (Walter) Fernald), and lichens in these communities.

We collected samples 11–18 from meadow communities occupying coastal lowlands and lower slopes at elevations ranging from 39 to 534 m a.s.l. Sample points below 100 m (samples 15–18) are located near the seacoast, which results in an increased influence of marine aerosols and wind exposure on vegetation formation. Grasses (Poaceae), sedges (Cyperaceae), and tall herbs characterize the vegetation: *Angelica gmelinii* (DC.) M. Pimen., *Geranium erianthum* DC., *Heracleum lanatum* Michx., *Cirsium kamtschaticum* Ledeb., and *Senecio cannabifolius*. In some meadow sites, we also recorded dwarf shrubs (*Empetrum sibiricum*) and dwarf pine (*Pinus pumila*).

Table 1. Location of surface sample points and modern vegetation characteristics on Onekotan Island (Northern Kurils)

No.	Coordinates	Elevation (m a.s.l.)	Vegetation type	Dominant and associated taxa
1	49°23.367'N 154°49.248'E	134	shrub thicket	*Duschekia fruticosa* (Rupr.) Pouzar, *Parasenecio kamtschatica* (Maxim.) Kadota
2	49°23.690'N 154°47.912'E	109	shrub thicket	*Duschekia fruticosa*, *Dryopteris expansa* (C. Presl) Fraser-Jenk. et Jermy, Poaceae
3	49°23.642'N 154°47.619'E	109	shrub thicket	*Duschekia fruticosa*, *Dryopteris expansa*, *Veratrum oxysepalum* Turcz., Poaceae
4	49°23.448'N 154°46.634'E	153	shrub thicket	*Duschekia fruticosa*, Poaceae
5	49°22.927'N 154°45.600'E	286	shrub thicket	*Pinus pumila* (Pall.) Regel, *Duschekia fruticosa*, *Dryopteris expansa*, Poaceae
6	49°22.339'N 154°44.510'E	599	shrub thicket	*Duschekia fruticosa*, *Duschekia maximowiczii* (Call.) Pouzar, Poaceae, *Dryopteris expansa*
7	49°26.686'N 154°44.291'E	233	shrub thicket + dwarf shrub–tundra-like	*Empetrum sibiricum* V. Vassil., *Vaccinium uliginosum* L., *Duschekia fruticosa*, *Salix kurilensis* Koidz., Lichens, Cyperaceae
8	49°23.970'N 154°42.275'E	437	dwarf shrub–tundra-like	*Phyllodoce aleutica* (Spreng.) A. Heller, *Empetrum sibiricum*, *Geranium erianthum* DC., *Salix arctica* Pall. subsp. *crassijulis* (Trautv.) A. Skvorts., *Saussurea riederi* Herd., Poaceae
9	49°23.464'N 154°42.222'E	442	dwarf shrub–tundra-like	*Empetrum sibiricum, Salix arctica* subsp. *crassijulis,* Poaceae
10	49°24.098'N 154°40.653'E	180	dwarf shrub–tundra-like	*Rhododendron camtschaticum* Pall., *Aruncus dioicus* (Walt.) Fern., *Geranium erianthum, Geum calthifolium* Smith., Poaceae
11	49°25.009'N 154°39.909'E	79	meadow	*Senecio cannabifolius* Less., *Geranium erianthum*, *Angelica gmelinii* (DC.) M. Pimen., Cyperaceae, Poaceae, *Empetrum sibiricum*
12	49°24.733'N 154°39.811'E	96	meadow	Cyperaceae, *Angelica gmelinii*, *Thalictrum minus* L., *Heracleum lanatum* Michx.
13	49°22.988'N 154°42.456'E	497	meadow	*Geum calthifolium, Geranium erianthum*, Cyperaceae, *Rhododendron camtschaticum*
14	49°22.744'N 154°43.257'E	534	meadow	Poaceae
15	49°35.551'N 154°48.818'E	78	meadow	Cyperaceae, *Cirsium kamtschaticum* Ledeb., *Geranium erianthum*, *Artemisia* L., *Heracleum lanatum*
16	49°35.608'N 154°48.896'E	91	meadow	Poaceae, Cyperaceae, *Geranium erianthum*, *Angelica gmelinii*, *Cirsium kamtschaticum*, *Pinus pumila*
17	49°35.668'N 154°48.889'E	87	meadow	Cyperaceae, Poaceae, *Geranium erianthum*, *Angelica gmelinii*
18	49°36.150'N 154°48.840'E	39	meadow	Poaceae, *Geranium erianthum*, *Angelica gmelinii*, *Cirsium kamtschaticum*

Pollen analysis

In the 18 surface samples collected from different vegetation community types on Onekotan Island, arboreal pollen dominated the palynological assemblages. Its proportion ranged from 30.3 % (sample 12) to 93.5 % (sample 1), averaging 64.5 % (Fig. 3). Herb pollen varied from 6.0 % (sample 1) to 65.2 % (sample 12), averaging 24.6 %. Spores ranged from 5.2 % (sample 9) to 48.5 % (sample 2), averaging 17.6 %.

Duschekia pollen dominated absolutely, ranging from 14.5 % (sample 16) to 82.99 % (sample 6). The highest values occurred mainly in samples from shrub thicket communities (samples 2, 5, 6), but a high value was also recorded in sample 17. The minimum proportion of *Duschekia* pollen occurred in samples from meadow communities (samples 11, 12, 16, 18).

Pinus subg. *Haploxylon* pollen was present in significant amounts in several samples, ranging from 4.15 % (sample 6) to 56.07 % (sample 1). High percentages were observed in spectra from shrub thickets (samples 1, 4, 5), some dwarf shrub–tundra-like communities (sample 10), and meadow communities in close proximity to dwarf pine (sample 16).

Ericaceae pollen was an important component in samples from dwarf shrub–tundra-like and meadow communities, ranging from 0 % to 52.36 %. The highest values occurred in samples 7 and 18. *Lonicera* pollen occurred as single grains (up to 1.03 % and 0.83 %, respectively).

Among herbaceous taxa, the most significant were: Poaceae, from 1.69 % (sample 5) to 24.12 % (sample 9); Asteraceae, from 0.5 % to 24.5 % (sample 11); Cyperaceae, from 0 % to 5.42 % (sample 7); Apiaceae, from 0 % to 9.07 % (sample 15); and *Thalictrum*, which reached high values in individual samples (up to 37.45 % in sample 12).

Among spores, ferns dominated, ranging from 4.57 % (sample 9) to 48.54 % (sample 2). In individual samples, high percentages were recorded for *Lycopodium clavatum* (up to 6.54 %), *Diphasiastrum complanatum* (up to 14.38 %), *Huperzia* (up to 3.83 %), and *Botrychium* (up to 5.57 %).

The proportion of allochthonous (long-distance transported) pollen (Figs 3, 4) was generally low, averaging 2.5 % (ranging from 0.4 % in sample 1 to 7.7 % in sample 18). The highest values occurred in samples from meadow communities (sample 18, 7.7 %; sample 11, 5.8 %). Among allochthonous taxa, *Betula* pollen dominated (up to 6.2 % in

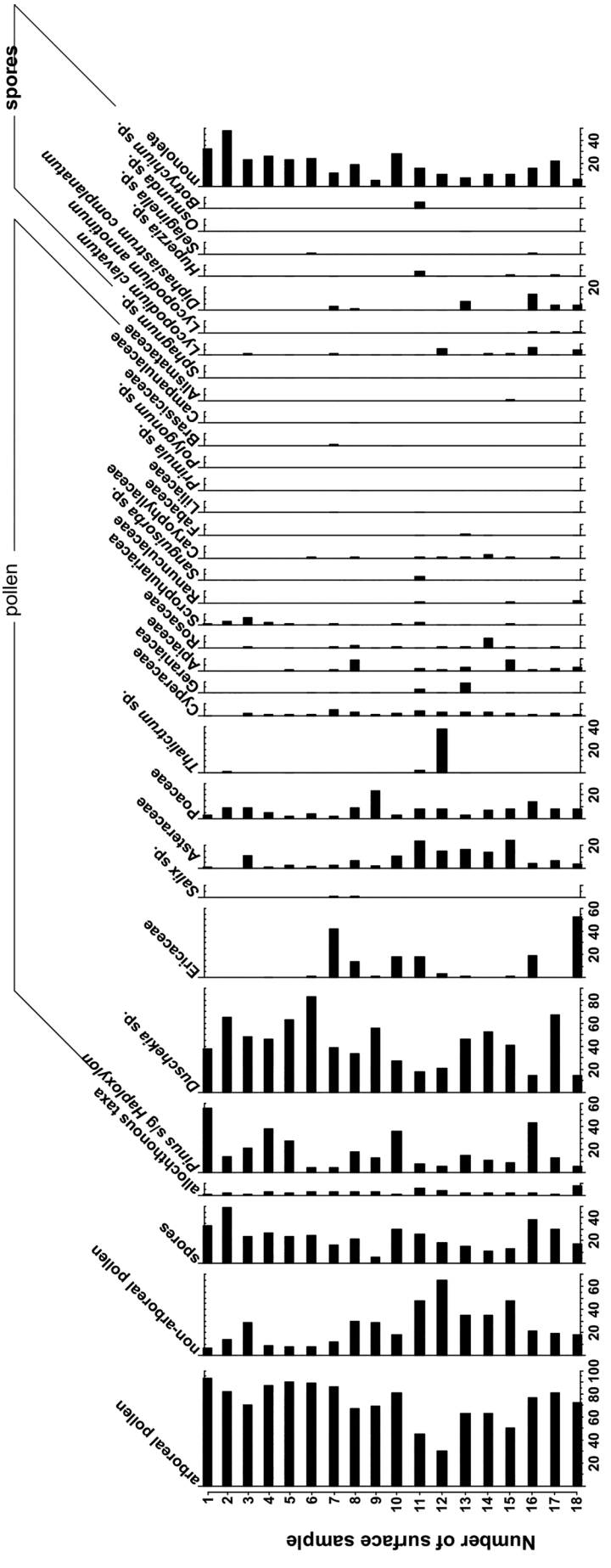


Figure 3 Percentage pollen and spore diagram of subfossil deposits on Onekotan Island. The diagram is based on 18 samples and was constructed using Tilia software (version 2.0.41; Grimm 1991). The diagram shows the main taxa of arboreal, shrub, herbaceous plants, and spores, reflecting changes in landscape conditions in the study area

sample 18), followed by *Pinus* subg. *Diploxylon* (up to 2.3 % in sample 4), *Picea* (up to 0.6 % in sample 11), *Corylus* (up to 0.8 % in sample 11), and *Quercus* (up to 0.4 % in sample 3).

We characterized palynological assemblages from shrub thicket communities (samples 1–6) by the maximum proportion of shrub pollen, averaging 83.8 %. Herb pollen was low, averaging 11.0 %, and spores averaged 30 %. *Duschekia* pollen dominated absolutely, averaging 60 % (ranging from 37.4 % in sample 1 to 83.0 % in sample 6). *Pinus* subg. *Haploxylon* pollen was present in significant amounts, averaging 25.4 %, with maximum values in samples from pine thickets (sample 1, 56.1 %; sample 4, 37.9 %). Ericaceae pollen occurred sporadically, averaging only 0.3 %. Among herbs, Poaceae (averaging 5.2 %) and Asteraceae (averaging 3 %) were most significant. Ferns dominated the spores, averaging 28.9 % and reaching a maximum in sample 2 (48.5 %).

Palynological assemblages from dwarf shrub–tundra-like communities (samples 7–10) showed high proportions of Ericaceae and a decrease in *Duschekia* pollen. Arboreal pollen averaged 70.0 %, herbs 22.1 %, and spores 18 %. Ericaceae was the leading taxon, averaging 23.9 %, with maximum values in sample 7 (41.7 %) and sample 10 (18.1 %). *Duschekia* remained high, averaging 38.4 %, especially in sample 9 (55.3 %). *Pinus* subg. *Haploxylon* occurred in moderate amounts, averaging 18.3 %. Among herbs, the proportions of Poaceae (averaging 9.8 %) and Cyperaceae (averaging 2.9 %) increased. Asteraceae averaged 5.74 %. Ferns dominated the spores (averaging 15.9 %), accompanied by clubmosses: *Diphasiastrum complanatum* (averaging 1.8 %) and *Lycopodium clavatum* (averaging 0.8 %).

Palynological assemblages from meadow communities (samples 11–18), which occupy coastal lowlands and river valleys, showed maximum herb pollen proportions (averaging 36.7 %) with a corresponding decrease in arboreal pollen (averaging 56.1 %). Spores averaged 21 %. Among shrubs, *Duschekia* pollen dominated (averaging 32.1 %), but its proportion varied considerably, ranging from 14.5 % (sample 16) to 67.2 % (sample 17). *Pinus* subg. *Haploxylon* averaged 15.6 %, and Ericaceae played a notable role (averaging 12.3 %), especially in sample 18 (52.4 %). The herb group was most diverse (Fig. 3). Dominant taxa included: Poaceae (averaging 9.4 %), Asteraceae (averaging 13.21 %), Cyperaceae (averaging 2.3 %), and Apiaceae (averaging 2.4 %). Individual samples showed anomalously high values: *Thalictrum* in sample 12 (37.5 %), Geraniaceae in sample 13 (8.3 %) and *Artemisia* in sample 15 (9.5 %). Fern spores dominated (averaging 12.6 %). Clubmosses reached maximum values: *Lycopodium clavatum* (averaging 2.4 %), *Diphasiastrum complanatum* (averaging 4.0 %), *Huperzia* (averaging 0.9 %), and *Botrychium* (averaging 0.7 %).

The proportion of allochthonous (long-distance transported) pollen was generally low, averaging 2.5 % (ranging from 0.4 % in sample 1 to 7.7 % in sample 18). The highest values occurred in samples from meadow communities (sample 18, 7.7 %; sample 11, 5.8 %). Among allochthonous taxa, *Betula* pollen dominated (up to 6.2 % in sample 18), followed by *Pinus* subg. *Diploxylon* (up to 2.3 % in sample 4), *Picea* (up to 0.6 % in sample 11), *Corylus* (up to 0.8 % in sample 11), and *Quercus* (up to 0.4 % in sample 3).

Cluster analysis

Cluster analysis identified four major compositional patterns among the samples based on the composition of pollen and spore spectra (Fig. 5). The calculated Ward dendrogram showed a cophenetic correlation coefficient of 0.57, indicating a moderate correspondence between the dendrogram structure and the original Euclidean distance matrix. The four groups comprised samples 11 and 12 (Cluster 1), samples 8, 9, 13–15, and 17 (Cluster 2), samples 7, 10, 16, and 18 (Cluster 3), samples 1–6 (Cluster 4).

Cluster 1 included samples 11 and 12, both from meadow communities. These samples were distinguished from the other groups by a stronger contribution of herbaceous pollen, particularly *Thalictrum* and Asteraceae, and by comparatively low proportions of *Pinus* subg. *Haploxylon* and *Duschekia* pollen. Sample 12 was characterized by the

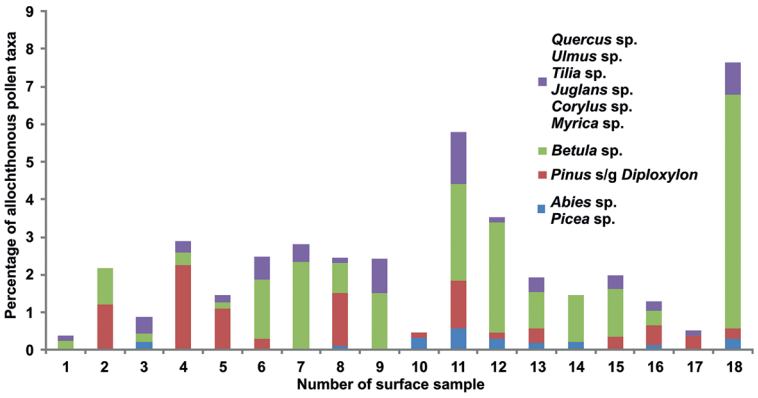


Figure 4 Percentage of allochthonous pollen taxa in subfossil deposits on Onekotan Island

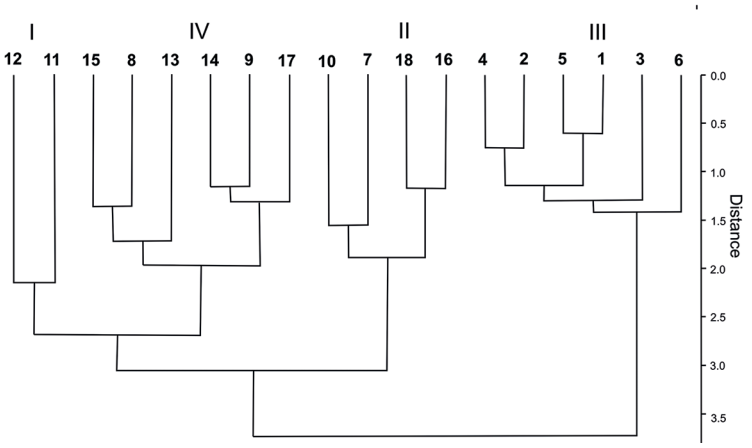


Figure 5 Hierarchical cluster analysis of pollen and spore assemblages from 18 surface samples on Onekotan Island. Bootstrap support values (%) are based on 2 000 replicates. The cophenetic correlation coefficient was 0.57; agreement between Ward clustering and independent k-means classification was moderate (ARI = 0.664)

highest *Thalictrum* contribution in the dataset (37.5 %), whereas sample 11 showed a more balanced representation of Ericaceae, Asteraceae, and fern spores.

Cluster 2 included samples 8, 9, 13, 14, 15, and 17. These samples generally showed a greater contribution of herbaceous pollen, particularly Poaceae and Asteraceae, although *Duschekia* remained an important component. The group was therefore compositionally heterogeneous and included both dwarf shrub–tundra-like samples (8 and 9) and meadow samples (13–15 and 17). The similarity of these samples appears to reflect the combined contribution of regional *Duschekia* pollen and a diverse herbaceous component rather than a single vegetation type.

Cluster 3 comprised samples 7, 10, 16, and 18 and was characterized by a combination of Ericaceae, *Pinus* subg. *Haploxylon*, and *Duschekia* pollen. Ericaceae was particularly abundant in samples 7 and 18, reaching 41.7 % and 52.4 %, respectively, while samples 10 and 16 contained high proportions of *Pinus* subg. *Haploxylon*. Thus, this group combines spectra from dwarf shrub–tundra-like and meadow communities that share a strong ericaceous and/or dwarf-pine signal.

Cluster 4 consisted exclusively of samples 1–6 from shrub thicket communities. Among the four groups, this group showed the most distinctive compositional pattern, with high proportions of *Duschekia* and fern spores and a substantial contribution of *Pinus* subg. *Haploxylon*. The mean proportion of *Duschekia* pollen in this group was 57.1 %, while Polypodiales and *Pinus* subg. *Haploxylon* averaged 29.6 % and 26.9 %, respectively. The group therefore reflects shrub thicket communities associated with alder shrub and dwarf pine, together with the local abundance of ferns.

Bootstrap analysis demonstrated limited stability of the individual clusters. Exact-clade bootstrap support was 16.4 % for Cluster 1, 0.8 % for Cluster 2, 6.5 % for Cluster 3 and 10.1 % for Cluster 4. Thus, none of the four groups reached high bootstrap support when the stability of the complete sample group was tested. Nevertheless, the overall grouping pattern was partly reproduced by an independent k-means analysis. The agreement between the Ward and k-means classifications was moderate, with an adjusted Rand index of 0.664.

Principal component analysis

We performed principal component analysis (PCA) to identify the main gradients in the palynological data. The first two principal components explained the largest proportion of the total variance (Fig. 6). Their cumulative contribution was 63 % of the total variance for the correlation matrix.

PC1 explained the maximum proportion of the variance in the original data (38.3 %). Positive values on PC1 correlated with Ericaceae pollen abundance (loading 0.7). Negative values corresponded to samples with high fern spore abundance (loading -0.7). We interpreted PC1 as a gradient from fern-dominated assemblages (negative scores) to Ericaceae-dominated assemblages (positive scores).

PC2 explained the second largest proportion of the variance (24.6 %). Positive values correlated with abundances of Asteraceae pollen (loading 0.6), Poaceae (0.3), and *Thalictrum* (0.2), as well as other herbs. Negative values corresponded to samples with high abundances of Ericaceae pollen (loading -0.5) and fern spores (loading -0.4). We interpreted PC2 as a gradient separating herb-rich assemblages (positive scores) from assemblages dominated by Ericaceae and ferns (negative scores).

Detrended correspondence analysis

We performed detrended correspondence analysis (DCA) to model the gradual replacement of taxa along environmental gradients, which more accurately reflects successional processes than PCA. The eigenvalues of the first two axes were 0.4005 for Axis 1 and 0.1921 for Axis 2. Together, they explained 100 % of the variance (67.6 % and

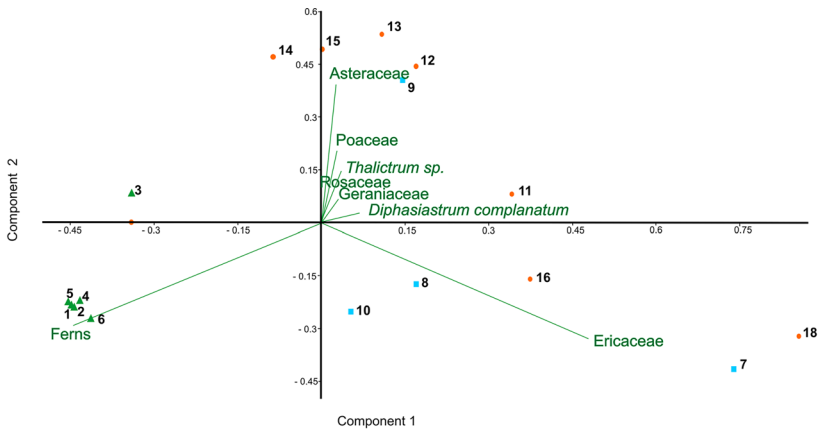


Figure 6 PCA biplot for main pollen taxa, Onekotan Island. Symbols indicate vegetation types: triangle – shrub thicket; square – dwarf shrub–tundra-like; circle – meadow

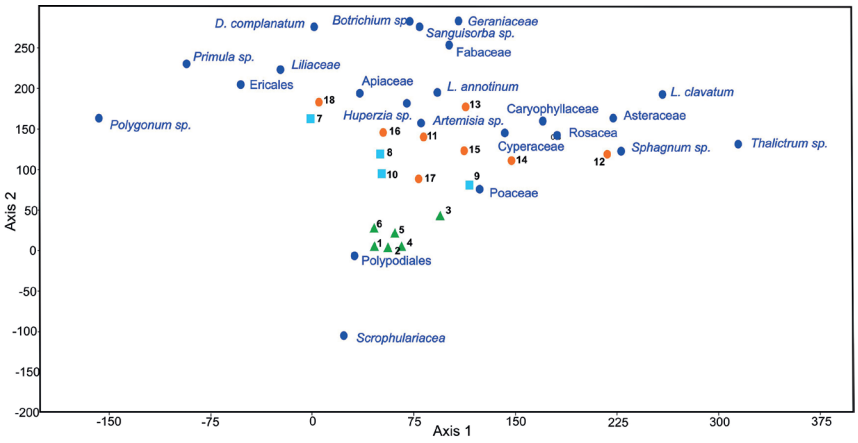


Figure 7 DCA biplot for main pollen taxa (blue circle), Onekotan Island. Symbols indicate vegetation types: triangle – shrub thicket; square – dwarf shrub-tundra-like; red circle – meadow

32.4 %, respectively, when recalculated as a proportion of the sum of both axes) (Fig. 7).

Axis 1 showed positive loadings for *Thalictrum* pollen (318), Asteraceae (222), Rosaceae (180), and spores of *Lycopodium clavatum* (260) and *Sphagnum* (227). Negative loadings occurred for Ericaceae (-53), *Polygonum* (-155), *Primula* sp. (-92), and Liliaceae (-22).

Axis 2 showed positive loadings for Ericaceae (208), *Sanguisorba* (280), Geraniaceae (289), *Diphasiastrum* (279), *Botrychium* (283), Fabaceae (257), Liliaceae (223), *Primula* sp. (231), and Apiaceae (195). Negative loadings occurred for Scrophulariaceae (-108).

Palynological richness

We recorded the minimum palynological richness in assemblages from shrub thicket communities (averaging 11 taxa), which we attribute to the dominance of *Duschekia* and *Pinus* subg. *Haploxylon* combined with minimal herb pollen. The lowest value of palynological richness (8 taxa) occurred in samples 1 and 2.

In assemblages from dwarf shrub–tundra-like communities, richness increased to an average of 16.5 taxa, due to the presence of Ericaceae pollen, grasses, and forbs.

We observed the maximum palynological richness in assemblages from meadow communities, averaging 19.3 taxa, with a maximum of 26 taxa in sample 11. This high richness reflects the high floristic diversity of coastal and valley meadow assemblages (Table 2).

DISCUSSION

Dominance of the regional background over the local signal

Pollen of highly productive pollen taxa, alder shrub (*Duschekia fruticosa*) and Siberian dwarf pine (*Pinus pumila*), creates a strong regional background that masks the local vegetation signal at some sampling sites, which influenced our cluster analysis results. Even in meadow communities (samples 11–18), where the average proportion of *Duschekia* pollen is 32.1 %, its contribution remains significant, making it difficult to identify pure herbaceous associations from pollen data alone. Similar patterns have been reported for the Northern Kuril Islands, where *Pinus pumila* and *Duschekia kamtschatica* pollen dominate the spectra, creating a regional background capable of masking local vegetation (Anderson & Lozhkin 2017). On Ketoy Island (Central Kurils), dominance of dwarf pine pollen (up to 70 %) and alder pollen (up to 81 %) has also been recorded in spectra from different sediment types, reflecting the widespread distribution of shrub thickets (Mokhova 2024). Our data from Onekotan Island show the same pattern: the average proportion of *Duschekia* in shrub thicket communities reaches 60 %, and *Pinus* subg. *Haploxylon* reaches 25 %, confirming that such proportions are typical for the Northern and Central Kuril Islands.

Reflection of local vegetation in the assemblages

Cluster analysis indicates that pollen assemblages reflect both local vegetation and the regional pollen background. The shrub-thicket samples formed the most coherent group, characterized by abundant *Duschekia*, *Pinus* subg. *Haploxylon*, and fern spores. In contrast, meadow and dwarf shrub–tundra-like samples showed greater overlap, largely because they shared herbaceous and ericaceous components.

The clustering therefore does not support a one-to-one correspondence between pollen assemblages and vegetation types. Samples from different communities may converge in multivariate space when they are influenced by the same highly productive regional taxa, particularly *Duschekia fruticosa* and *Pinus pumila*. Local dominants are nevertheless reflected where pollen productivity is high or local deposition is favoured, as indicated by the strong herbaceous signal in several meadow samples.

The low bootstrap support of the individual clusters indicates that their exact composition is not highly stable, although the moderate agreement between Ward clustering and k-means (ARI = 0.664) supports the presence of broad compositional structure. Accordingly, the four groups are best interpreted as major pollen-compositional patterns rather than discrete vegetation types. These results confirm the value of multivariate pollen analysis for distinguishing broad environmental settings, while emphasizing that vegetation reconstruction must account for regional pollen transport, taxon-specific productivity, and local habitat conditions.

According to our PCA results, the palynological assemblages were distributed along the first two axes in accordance with vegetation community types (Fig. 6). We interpret PC1 as a gradient from closed shrub thicket communities (negative values for fern spores) to open dwarf shrub–tundra-like and meadow communities (positive values for Ericaceae and herbs). PC2 reflects a gradient from dwarf shrub–tundra-like communities to herbaceous meadows, with positive loadings also recorded for the herb group. Some samples did not fully conform to this pattern. Sample 9, classified as dwarf shrub–tundra-like, shifted into the positive region of both PC1 and PC2. We attribute this to high Poaceae pollen content (24.12 %) combined with extremely low Ericaceae pollen (0.64 %). In contrast, samples 16 and 18 (meadow communities) lie in the positive region of PC1 and the negative region of PC2 due to elevated Ericaceae pollen (18.76 % and 52.36 %, respectively). We suggest that such deviations are related to vegetation mosaic, microecological

Table 2. Surface pollen assemblages: richness and taxa by vegetation type, Onekotan Island.

Vegetation type	Pollen richness	Representation by taxa and plant groups, %				
		Duschekia	*Pinus* subg. *Haploxylon*	Ericaceae	Herbs	Long-distance transported
Shrub thicket	11.0	60.0	25.4	0.28	11.0	1.75
Dwarf shrub–tundra-like	16.5	38.4	18.3	18.68	22.1	2.15
Meadow	19.3	32.1	15.6	11.64	36.7	2.85

conditions (slope aspect, drainage patterns, proximity to local pollen sources), as well as landscape openness and the strong wind regime characteristic of the island.

The distribution of samples on the DCA diagram agrees with our cluster and PCA results and allowed us to identify the main ecological gradients, most likely moisture and openness. Samples from dwarf shrub thicket group 1–6 formed a cluster near zero values on both Axes 1 and 2. Samples 7 and 18 occupied the region of high positive values on Axis 2 and near-zero values on Axis 1, corresponding to Ericaceae dominance. Sample 12 (meadow with maximum *Thalictrum* abundance) lay in the far positive region of Axis 1, reflecting the high score of this taxon. Samples 13, 14, 15, and 17 clustered in the region of moderate positive values on Axis 1, indicating similarity in their dominant taxa (fern spores, Asteraceae).

We interpret Axis 1 as a gradient from dwarf shrub–herb communities with ericaceous plants, primrose, and knotweeds (negative values) to dwarf shrub–meadow associations with meadow-rue, Asteraceae, Rosaceae, clubmoss, and sphagnum mosses (positive values). The positive pole of Axis 1 probably corresponds to more moist habitats (wetland valleys, stream banks). Consequently, Axis 2 separates communities dominated by ericaceous plants, burnet, Geraniaceae, clubmosses, and Fabaceae (positive values) from habitats where alder and Scrophulariaceae dominate (negative values). We interpret this axis as reflecting an openness and moisture gradient: the positive pole corresponds to open dwarf shrub and meadow communities with diverse forbs, the negative pole to more closed alder thickets with ferns.

As our multivariate analysis showed, Ericaceae effectively reflect crowberry heath and rhododendron tundra communities. For the Northern Kurils, it was shown that Ericaceae reaches maximum values (5–8 %) precisely on the northern islands, reflecting the importance of ericaceous communities (Anderson & Lozhkin 2017). Fern spores predictably dominate in spectra from sites with developed of *Dryopteris expansa* (samples 1–6). Polypodiaceae is the dominant spore type and reflects the frequent occurrence of ferns in communities with *Duschekia* and *Pinus pumila* (Anderson & Lozhkin 2017). The local abundance of *Thalictrum* in sample 12 (37.5 %) and Geraniaceae in sample 13 (8.3 %) exemplifies the successful detection of local flowering peaks. Apiaceae pollen was recorded in spectra from meadow sites (sample 15, 9.1 %), consistent with its presence in vegetation descriptions. In our data, the proportion of Poaceae in meadow communities averaged 9.4 %, which is substantially lower than their actual abundance in the herb layer, confirming a pattern observed in modern spectra from the Kuril Islands (Anderson & Lozhkin 2017). For example, the proportion of Poaceae in palynological assemblages does not correspond to their actual participation in coastal meadows and *Sasa kurilensis* thickets.

Evidence of long-distance pollen transport

An important aspect of analyzing surface palynological assemblages from Onekotan Island is the presence of long-distance transported pollen, confirmed by comparison with the island's floristic lists. This has implications for interpreting modern vegetation and transport processes in the region.

In the studied assemblages, allochthonous pollen includes both deciduous (*Betula*, *Quercus*, *Ulmus*, *Juglans*, *Tilia*, *Corylus*) and coniferous (*Picea*, *Abies*, *Pinus* subg. *Diploxylon*) taxa. *Betula* pollen dominates this group, which we attribute to atmospheric transport from neighboring territories. Possible sources include the northern Kuril Islands and the Kamchatka Peninsula, where birch is widely represented in both tree and shrub forms (Krestov 2003). For example, on Paramushir Island, the shrub birch *Betula paramushirensis* Barkalov, a hybrid of *B. exilis* Sukacz. and *B. ermanii*, occurs (Grishin & Barkalov 2009). Pollen of *Corylus*, *Quercus*, *Juglans*, *Tilia*, and *Ulmus* arrives from more southern regions, including the southern Kuril Islands, Sakhalin Island, and Hokkaido (Box & Fujiwara 2012, Krestov 2003). Coniferous pollen is also allochthonous. We suggest that its presence is related to long-distance atmospheric transport from various regions of the Northwestern Pacific. *Pinus* subg. *Diploxylon* pollen, apparently represented by *Pinus sylvestris*, arrives from continental areas, whereas *Picea* and *Abies* originate from Kamchatka, the southern Kuril Islands, Sakhalin, and Hokkaido (Box & Fujiwara 2012, Krestov 2003). The influx of allochthonous pollen is related to the predominance of westerly air mass transport as well as the displacement of atmospheric fronts from southern regions (Fig. 1).

The presence of allochthonous pollen in modern palynological assemblages is a common phenomenon on island vegetation communities. As Anderson & Lozhkin (2017) noted, the presence of broadleaved pollen (*Quercus*, *Ulmus*, *Juglans*, *Tilia*, *Corylus*) in spectra from the Northern Kuril Islands indicates long-distance wind transport, because these taxa are absent from the local vegetation. According to other studies, the proportion of allochthonous pollen on the Kuril Islands varies widely. On Shikotan Island, the proportion of allochthonous *Pinus pumila* pollen reaches 5 %, oak 3 %, and on small islands 7–45 % (Mokhova 2021). On Ketoy Island, the proportion of allochthonous pollen of broadleaved (*Quercus*, *Carpinus*) and dark coniferous (*Abies*, *Picea*) taxa usually does not exceed 1–2 % (Mokhova 2024). These values are comparable with our data from Onekotan Island, where the average proportion of allochthonous taxa is approximately 2.5 %. This confirms the regional character of long-distance pollen transport processes within the Kuril island system.

Mokhova (2024) noted that palynological assemblages from the upper sediment layer of small lakes on Ketoy Island generally reflect the surrounding vegetation but contain an elevated proportion of allochthonous pollen (up to 10–15 %), related to the accumulation of material from a large catchment area. Unlike lake sediments, soil spectra are less affected by long-distance transport and more fully reflect local vegetation. Nevertheless, even in soil spectra, the influence of allochthonous pollen remains noticeable. The maximum content and diversity of allochthonous taxa occurred in samples from coastal meadow communities (sample 18, 7.7 %; sample 11, 5.8 %), which we attribute to more efficient trapping of long-distance transported pollen

in open sites. In contrast, the high pollen productivity of dwarf shrub thicket communities creates a strong regional background that dilutes the relative proportion of allochthonous pollen. This confirms the significant influence of local vegetation composition on the formation of palynological assemblages.

Thus, allochthonous pollen is a consistent component of palynological assemblages on Onekotan Island, and its formation is determined both by regional atmospheric processes and by habitat type. This must be considered when interpreting modern assemblages and conducting paleoecological reconstructions.

Reflection of vegetation cover in subfossil assemblages: possibilities and limitations

Despite the strong regional background, the application of multivariate statistics allows us to analyze the proportions of pollen from shrubs, herbaceous plants (especially grasses, sedges, Geraniaceae, Apiaceae, *Thalictrum*), and spores. This facilitates the identification of shrub thickets, dwarf shrub–tundra-like, and meadow communities at specific sampling points. Our quantitative diversity indices and the proportions of major taxa adequately reflect ecological differences among the identified vegetation types and can be used for paleoecological reconstructions (Table 3). However, the influence of sediment type and depositional environment should not be completely disregarded, as differences in sediment genesis may affect the representation and preservation of individual pollen taxa. Published data from other islands in the Kuril chain suggest that this effect may be less pronounced on small islands than on continental territories with developed river networks, and palynological assemblages clearly differentiate forested and treeless areas; for instance, on Shikotan Island, arboreal pollen content in soil spectra reaches 98 % under developed forest vegetation, whereas in the southern part of the island occupied by meadow–marsh communities, its proportion falls below 32 % (Mokhova 2021). Similarly, on Ketoy Island, spectra from various substrates (soils, peatlands, lake sediments, alluvial silts) reliably reflect local vegetation and differentiate biotope types, with peat and soil spectra recording local biocenoses more distinctly and lake sediments showing higher allochthonous pollen (up to 10–15 %) due to larger catchments (Mokhova 2024). This indicates that soil spectra, like spectra from other sediment types, can provide useful information on vegetation patterns at the biome level.

The spectra from all sampling sites largely reflect the island's vegetation composition; however, we identified several discrepancies, which we suggest may be related to low pollen productivity, insect pollination, or poor pollen preservation. Mokhova (2021) noted that even in forest communities on Shikotan Island, the pollen productivity of different taxa does not always correspond to their actual participation in the tree stand: for example, the proportion of spruce pollen in spectra is lower than its actual abundance. We observed a similar situation on Onekotan. Despite the abundance of *Geranium erianthum* in vegetation descriptions for samples 9 and 16, it is absent from the pollen assemblage of sample 9 and occurs in very low proportion in sample 16 (0.4 %). Anderson & Lozhkin (2017) explained the incomplete reflection of herbaceous flora in palynological assemblages by limitations in taxonomic identification of pollen, differences in pollination modes and pollen productivity. Entomophilous plants generally produce smaller amounts of pollen than wind-pollinated taxa and therefore make a limited contribution to the regional pollen rain (Faegri & Iversen 1989). In addition, the relatively large and heavy pollen grains of *Geranium* are less effectively transported over long distances, increasing the importance of local depositional processes. Thus, the low proportion of *G. erianthum* pollen in the spectra does not necessarily indicate a low abundance of this species in the surrounding vegetation. Similarly, *Rhododendron camtschaticum*, described at samples 9 and 11, is represented by ericaceous pollen in sample 9 (0.6 %), which is significantly lower than in sample 7 (41.7 %) and sample 18 (52.4 %), suggesting uneven flowering or local distribution patterns. The relatively low representation of Poaceae pollen in the pollen spectra, despite the high abundance of grasses in meadow vegetation, may result from several interacting factors. Although Poaceae are anemophilous plants and can produce large absolute amounts of pollen (Sjögren et al. 2015), their relative pollen productivity is lower than that of several dominant arboreal taxa (Broström et al. 2008). In particular, *Alnus* (including *Duschekia*) and *Pinus* are highly productive pollen sources and may contribute disproportionaly to the regional pollen rain. Consequently, even relatively limited local cover of *Duschekia* and *Pinus pumila* may dilute the contribution of locally produced grass pollen in the pollen spectra.

Differences in pollen preservation may further contribute to the underrepresentation of some herbaceous taxa, as pollen preservation in soils varies among taxa and depositional environments (Havinga 1984). In the acidic soils of the Kuril Islands (pH 3.7–5.5), pollen is generally well preserved due to the suppression of bioturbation and microbial activity (Miyake et al. 2000). However, even under such conditions, differential resistance of various taxa to chemical oxidation is observed: pollen of conifers (*Pinus*, *Picea*) with thick, sporopollenin-rich exine is more resistant to hydrolysis, whereas pollen of herbs with thin exine (Poaceae, *Geranium*) is more susceptible to chemical degradation (Havinga 1984, Lebreton et al. 2010). This also may explain the systematic underestimation of herb pollen proportions in the soil spectra of Onekotan Island relative to their actual abundance in plant communities.

Sampling points located above the closed canopy of *Pinus pumila* and *Duschekia fruticosa* would be expected to show a decrease in their pollen proportions. However, on Onekotan Island, all sampling points lie within the dominance belt of these shrubs (from 39 to 599 m a.s.l.); therefore, the altitudinal gradient in the spectra is weakly expressed. The upper boundary of the alder belt reaches 900–1000 m (Grishin & Barkalov 2005), which exceeds the maximum sampling elevation (599 m). Consequently, all studied sites are within the zone of active deposition of alder and dwarf pine pollen, explaining the dominance of these taxa even in spectra from meadow communities.

Modern pollen spectra as analogues for Holocene vegetation reconstruction

Comparison with Holocene palaeovegetation records from Onekotan Island (Razjigaeva et al. 2011, 2013, 2014), together with regional palaeoecological evidence from the Kuril Islands and the southern Russian Far East (Razjigaeva et al. 2019), demonstrates the value of the modern pollen spectra obtained in this study as analogues for palaeogeographic interpretation. Previous reconstructions based on three peat sections identified eight phases of Holocene vegetation development and showed that vegetation changes largely involved shifts in the distribution and relative importance of plant communities that are still present on the island. During the Early Holocene, heath communities with scattered graminoids and shrubs were widespread, whereas during the Middle Holocene herb–forb meadows, wetlands, and *Duschekia* thickets became more prominent, with *Pinus pumila* and *Duschekia* expanding during warmer or more humid phases. Vegetation development was also strongly influenced by volcanic activity, particularly by tephra deposition associated with the Tao-Rusyr eruption at approximately 7.5 ka BP.

The comparison indicates that modern pollen spectra are best used as analogue assemblages rather than as direct quantitative measures of vegetation composition. *Duschekia* and *Pinus* subg. *Haploxylon* form a strong regional pollen background and occur in substantial proportions even in meadow communities, potentially masking the contribution of locally occurring herbaceous taxa. Conversely, Poaceae may be underrepresented in the pollen spectra relative to their abundance in the herb layer. Allochthonous pollen of *Betula*, *Picea*, *Abies*, and broadleaved taxa, which is regularly recorded in fossil assemblages and interpreted as the result of long-distance transport, is also present in the modern spectra.

Several similarities between the modern spectra and the Holocene records further support their use as a reference dataset. For example, the substantial contribution of *Duschekia* in our meadow spectra is comparable to the continued representation of alder-shrub pollen in the upper peat layers of the Chernoye Lake section, whereas the relatively high proportion of Ericaceae in dwarf shrub–tundra communities is consistent with the importance of heath vegetation during intervals interpreted as cooler. Thus, modern surface pollen spectra provide a useful analogue framework for identifying broad vegetation changes in Holocene records from Onekotan. However, their quantitative interpretation should remain cautious because pollen representation is strongly influenced by regional pollen production, dispersal, preservation, and the dilution of local signals.

CONCLUSION

Surface pollen spectra of Onekotan Island represent a typical example of assemblages formed under conditions of dominance of wind-pollinated shrubs. We demonstrate that pollen of shrub thicket vegetation dominates the surface palynological assemblages of Onekotan Island (averaging 64.5 %). *Duschekia* is the absolute dominant, ranging from 14.5 % to 83.0 %. *Pinus* subg. *Haploxylon* pollen occurs in all community types (averaging 15–25 %). Despite the strong regional background created by pollen of highly productive pollen taxa (*Duschekia* and *Pinus* subg. *Haploxylon*), the application of multivariate statistics reveal broad compositional differences among the sampled vegetation communities (shrub thicket, dwarf shrub–tundra-like, meadow) based on their palynological assemblages. Several taxa were particularly characteristic of the pollen spectra associated with different vegetation types: *Duschekia* pollen and fern spores in shrub-thicket communities; Ericaceae in dwarf shrub–tundra-like communities; and herbaceous taxa (Asteraceae, Poaceae, Apiaceae, *Thalictrum*) in meadow communities. Allochthonous pollen is an integral component of palynological assemblages on Onekotan Island and originates from long-distance atmospheric transport from northern, southern, and continental regions. Its contribution depends on habitat conditions and is highest in open coastal communities, whereas it is reduced in shrub communities due to the filtering role of the vegetation cover. The proportion of allochthonous pollen does not exceed 8 %, allowing the use of surface assemblages for characterizing modern vegetation. However, in fossil palynological assemblages, its contribution could lead to erroneous interpretations of past vegetation and climatic conditions. Modern surface pollen spectra provide a reference framework for palaeoecological interpretation of Onekotan records. However, quantitative reconstruction should account for the strong regional pollen background, long-distance transport, and taxon-specific differences in pollen production and preservation.

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