Vegetation of eastern Unalaska Island, Aleutian Islands, Alaska[1]

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Abstract: Plant communities of Unalaska Island in the eastern Aleutian Islands of western Alaska, and their relationship to environmental variables, were studied using a combined Braun-Blanquet and multivariate approach. Seventy relevés represented the range of structural and compositional variation in the matrix of vegetation and landform zonation. Eleven major community types were distinguished within six physiognomic–ecological groups: I. Dry coastal meadows: *Honckenya peploides* beach meadow, *Leymus mollis* dune meadow. II. Mesic meadows: *Athyrium filix-femina – Aconitum maximum* meadow, *Athyrium filix-femina – Calamagrostis nutkaensis* meadow, *Erigeron peregrinus – Thelypteris quelpaertensis* meadow. III. Wet snowbed meadow: *Carex nigricans* snowbed meadow. IV. Heath: *Linnaea borealis – Empetrum nigrum* heath, *Phyllodoce aleutica* heath, *Vaccinium uliginosum – Thamnolia vermicularis* fellfield. V. Mire: *Carex pluriflora – Plantago macrocarpa* mire. VI. Deciduous shrub thicket: *Salix barclayi – Athyrium filix-femina* thicket. These were interpreted as a complex gradient primarily influenced by soil moisture, elevation, and pH. Phytogeographical and syntaxonomical analysis of the plant communities indicated that the dry coastal meadows, most of the heaths, and the mire vegetation belonged, respectively, to the widespread classes Honckenyo–Elymetea, Loiseleurio–Vaccinietea, and Scheuchzerio–Caricetea, characterized by their circumpolar and widespread species. Amphi-Beringian species were likely diagnostic of amphi-Beringian syntaxa, many of these yet to be described.

Key words: community classification, heath, meadow, nonmetric multidimensional scaling, northern boreal, phytogeography.

Résumé : Les auteurs ont étudié les communautés végétales de l'île Unalaska dans l'est des îles Aléoutiennes de l'Ouest, ainsi que leurs relations avec les variables environnementales, en utilisant une combinaison des approches de Braun-Blanquet et multivariée. Plusieurs relevés représentent l'amplitude de la variation des structures et de la composition dans le zonage de la matrice de végétation et du paysage. Les auteurs ont identifié 12 types majeurs de communautés dans six groupes écolo-physiognomiques : I. Prairies côtières sèches : prairie côtière à *Honckenya peploides*, prairie dunaire à *Leymus mollis* II. Prairies mésiques : prairie à *Athyrium filix-femina – Aconitum maximum*, prairie à *Athyrium filix-femina – Calamagrostis nutkaensis*, prairie à *Erigeron peregrinus – Thelypteris quelpaertensis*; III. Prairies humides à congère de neige à *Carex nigricans*; IV. Éricacaie : éricacaie à *Linnaea borealis – Empetrum nigrum*, éricacaie à *Phyllodoce aleutica*, champ d'abattis à *Vaccinium uliginosum – Thamnolia vermicularis*; V. Tourbière : tourbière à *Carex pluriflora – Plantago macrocarpa*, et VI. Fourrée arbustive décidue : fourrée à *Salix barclayi – Athyrium filix-femina*. Les auteurs interprètent ces communautés comme un gradient complexe influencé par l'humidité du sol, l'élévation, et le pH. Les analyses phytogéographiques et syntaxonomiques des communautés végétales indiquent que les prairies côtières, la plupart des éricacaies, et la végétation de tourbière appartiennent respectivement aux classes largement répandues des Honckenyo–Elymetea, Loiseleurio–Vaccinietea et Scheuchzerio–Caricetea, caractérisées par leurs espèces circumpolaires largement répandues. Les espèces amphi-Béringiennes constituent probablement un diagnostic des syntaxons amphi-Béringiens, dont plusieurs restent à décrire.

Mots-clés : des communautés, éricacaie, prairie, échelle non-métrique multidimensionnelle, région boréale nordique, phytogéographie.

[Traduit par la Rédaction]

Introduction

The Aleutian Islands extend in an arc from the northwestern portion of the North America landmass 1900 km into the Pacific Ocean toward Asia (Fig. 1). These windswept, often foggy volcanic islands of the Alaska Maritime National Wildlife Refuge are of considerable phytogeographic interest, because they occur along the southern margin of the Be-

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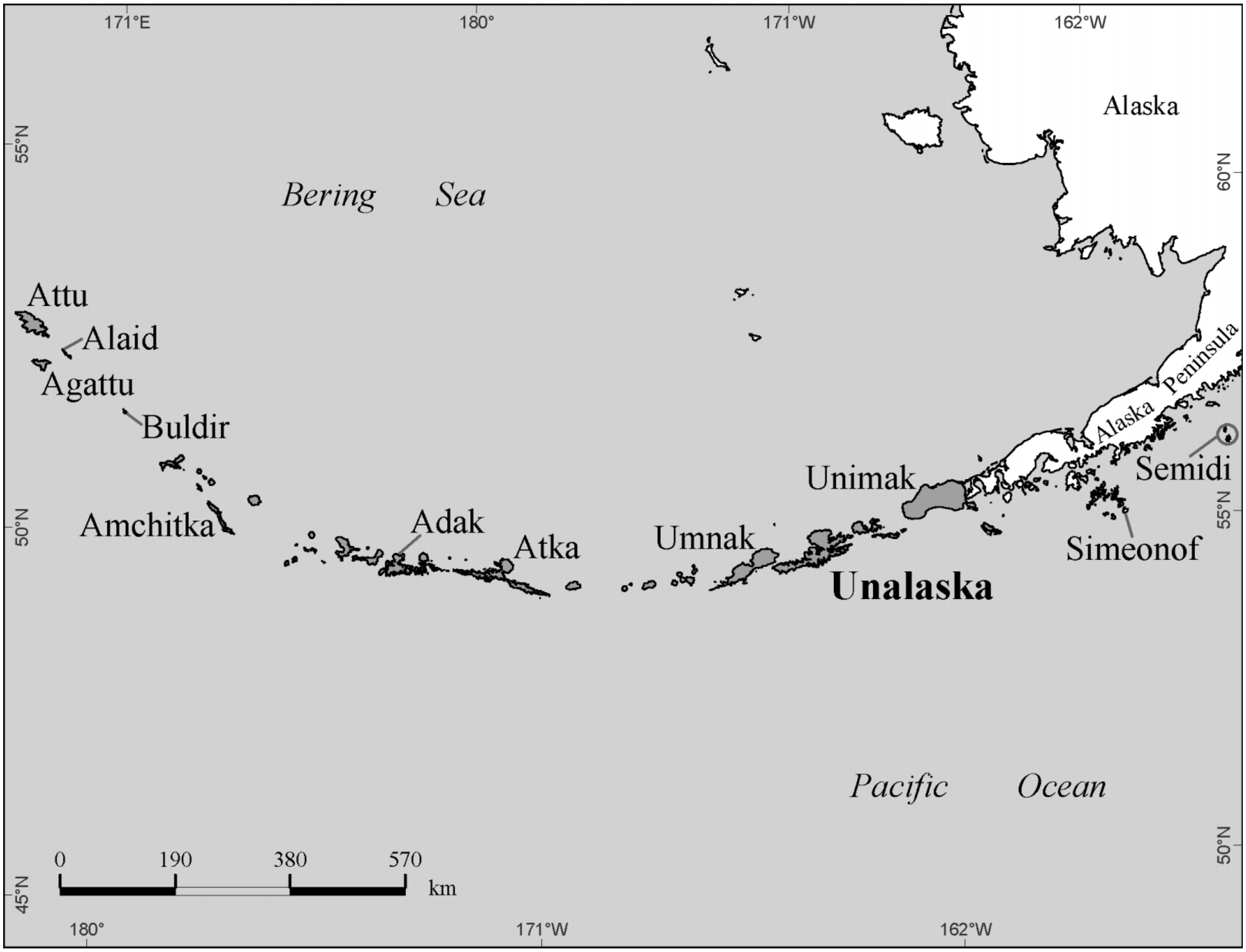
Fig. 1. Location of Unalaska Island and the Aleutian Islands, Alaska along with other islands referenced in the text.



ring Land Bridge and function as an important region for plant dispersal. Species dispersal occurs in at least two directions, westward from North America along the Aleutians and eastward from Asia toward Interior Alaska and the Temperate Pacific Coast; Carlquist (1965) terms this pattern a two-way filter bridge. Hultén (1960) indicates the Aleutian Islands belong to the same floral and vegetational province as the Kamchatka Peninsula of Russia, with the strongest relationships occurring in the westernmost islands of Attu, Agattu, and Alaid. Of the approximately 530 species that make up the Aleutian vascular flora, 70% occur in both Alaska and Kamchatka.

In addition to the important floristic studies of the Swedish botanist E. Hultén (Hultén 1960, 1968), the Japanese botanists M. Tatewaki and Y. Kobayashi (Tatewaki and Kobayashi1934; Tatewaki 1963) provide insights on the vascular flora and give general accounts of the Aleutian vegetation. In general, other descriptions of the Aleutian vegetation are infrequent and usually qualitative and general. Such descriptions include Bank (1951, 1953), Heusser (1990), and Walker (1945), as well as observations of individual islands, such as Adak (Hein 1976; Heusser 1978) and Umnak (Kindschy and O'Connell 1959; Nybakken 1966; Heusser 1973). Quantitative studies are few, except for Amchitka (Amundsen 1977; Shacklette et al. 1969) and Buldir Island (Byrd 1984). Talbot and Talbot (1994) make a quantitative comparison of the coastal vegetation of Attu Island, the westernmost island in the Aleutian Island chain, with others in the chain. The comparison points to a close relationship to the beach and beach-meadow types of the Aleutian Islands and Kamchatka. In a similar manner, Krestov (2004) compares the vegetation of the Commander Islands to Attu Island and other Aleutian Islands and Beringian locations.

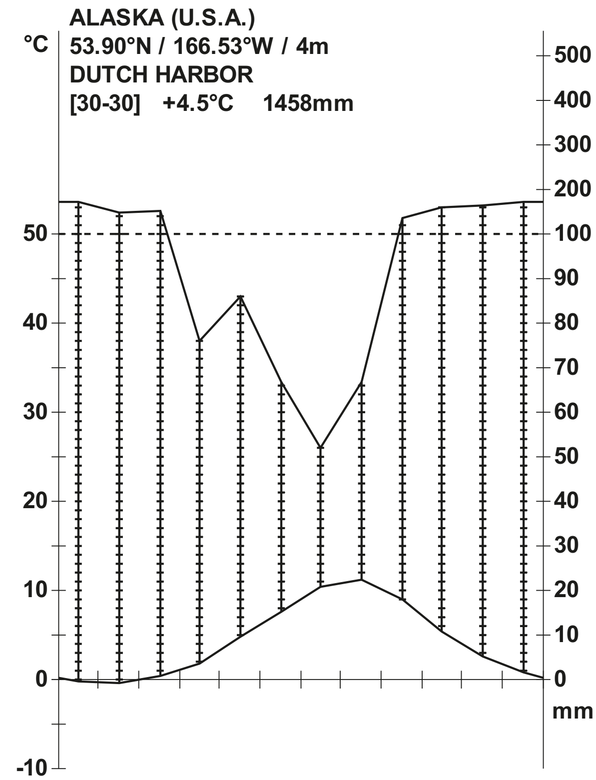
Unalaska Island in the eastern Aleutian Islands is of particular interest because of its relatively close proximity to the Alaska Peninsula, allowing a general comparison between the eastern and western Aleutians, as well as the southern mainland Alaska. Our study presented the first quantitative characterization of the vegetation of Unalaska Island from sea level to alpine. The objectives of our study were (*i*) describe major plant communities of Unalaska Island along environmental gradients; (*ii*) identify the main vegetation types using multivariate methods; (*iii*) interpret the community types in relation to selected site factors; and (*iv*) compare the communities identified for Unalaska Island with those of southern Alaska.

Unalaska Island occurs in the "Aleutian Islands Ecoregion," characterized as a naturally treeless region where dwarf shrub communities predominate at higher elevations and on sites exposed to the wind, and where herbaceous communities occur on more protected sites (Gallant et al. 1995). Küchler (1966) classifies the former dwarf shrub communities as "Aleutian heath and barren (*Empetrum–Vaccinium*)", and the latter herbaceous communities as "Aleutian meadows (*Calamagrostis–Anemone*)." The region is composed of a chain of sedimentary islands eroded from older volcanic formations and crowned by steep volcanoes. The topography of Unalaska Island is rugged, with Makushin Volcano, the highest peak on the island, at 2036 m a.s.l.

Unalaska Island occurs within the northern boreal subzone described by Tuhkanen (1984) in the hyperoceanic (O_2) sector and humid (h) province. Mean annual temperature and precipitation recorded for Unalaska are 4.5 °C and 1458 mm, respectively; August is the warmest month, with a mean temperature of 14.8 °C (Arctic Environmental Information and Data Center 1989) (Fig. 2). Multivariate analysis of climate along the southern coast of Alaska indicates that the Aleutian Islands form a distinct climatic group with moderately cool temperatures in the fall, winter, and spring and much colder summers than other coastal stations (Farr and Hard 1987).

The exposed bedrock of andesite, basalt, and granodiorite is primarily of Miocene age (Drewes et al. 1961). The surficial geology of the study area chiefly consists of dominantly coarse rubbly deposits associated with steep-sloped mountains of Quaternary age with high percentage of bedrock exposures (Karlstrom et al. 1964). These deposits include alluvial, beach, and eolian material with terminal and ground moraine till. The dominant soils are Andisols (Rieger et al. 1979); these volcanic soils are mainly Typic Cryandepts.

Fig. 2. Climate diagram for Dutch Harbor, Unalaska Island, Alaska. Abscissa shows the months January to December. Ordinate: the first dash-mark upwards represents 10 °C and 20 mm, respectively. Name of station given in upper left-hand corner with latitude/longitude and elevation given below. Number of years data were collected for temperature and precipitation given in brackets, followed by mean annual temperature and mean annual precipitation. Top curve is mean monthly precipitation and lower curve is mean monthly temperature.



Methods

Study area and study site locations

The location of Unalaska Island (53.90°N, 166.53°W) within the eastern Aleutian Islands is shown in Fig. 1 in relation to other Aleutian Islands referenced in the text. The study area (ca. 35 km^2) is sited within eastern Unalaska Island. Following a reconnaissance of the area, we selected study sites to represent the spectrum of structural and compositional variation in the landscape from sea level to upper elevation. We focused on 13 study site localities (Fig. 3); their location and site characteristics are listed in Table 1.

Vegetational and environmental sampling

This study is based on a set of 70 relevés made according to Braun-Blanquet methods (Westhoff and van der Maarel 1973) from 3–27 August 2007. Plots were laid out in units of homogeneous vegetation so as to represent conspicuous variation in plant communities. Relevé size, 25 m^2, equaled the minimal area for comparable types (Westhoff and van der Maarel 1973). Cover-abundance was estimated for all vascular plants, bryophytes, and macrolichens according to the nine-point ordinal scale of Westhoff and van der Maarel (1973). Plant nomenclature followed USDA-NRCS (2009). Voucher specimens were deposited at several herbaria and determined or confirmed by the following specialists (in parentheses): ALA, miscellaneous vascular plants (Alan R. Batten); BING, *Sphagnum* (Richard E. Andrus); CAN, *Salix* (George W. Argus); ISC, *Botrychium* (Donald R. Farrar); MO, *Epilobium* (Peter C. Hoch); NYS, *Platanthera* (Charles J. Sheviak); RM, *Stellaria* (Ronald L. Hartman); UBC, bryophytes (Wilfred B. Schofield) and lichens (Trevor Goward); and US, Poaceae (Robert J. Soreng).

Environmental factors recorded were aspect (degrees), elevation (m, a.s.l.), litter cover (%), slope inclination (degrees), ecological moisture regime (ordinal values: 1, xeric; 2, subxeric; 3, submesic; 4, mesic; 5, subhygric; 6, hygric; 7, subhydric; and 8, hydric), and mesotopography (Luttmerding et al. 1990). Latitude and longitude were recorded by GPS using WGS84 datum. One soil sample from the rooting zone was collected in the center of each relevé at a depth of 15–20 cm.

Soil analysis

Soils were analyzed by the Kuo Testing Labs, Inc (KTL), Othello, Washington. Methods followed Soil Survey Laboratory Staff (1996). KTL employed an autoanalyzer which simultaneously analyzed the soil pH and soluble salts of the soil sample. Organic matter content was determined by the Walkley–Black method. The orthophosphate analyte was determined after the soil was extracted with 0.5 N sodium bicarbonate solution buffered at pH 8.5 (Olsen's extraction method). The cations, K, Ca, Mg, and Na, were extracted with 1 N ammonium acetate solution buffered at pH 8.5 and assayed with a high precision ICP (inductively coupled plasma) spectrophotometric instrument. These bases were summed to obtain the total bases in $cmol \cdot kg^{-1}$ soil. Both soil nitrate-N and ammonium-N were extracted with 1 N KCl solution; this procedure was followed by flow injection colorimetric analysis using the cadmium reduction method for nitrate-N and phenolic blue method for ammmonium-N determination. The SO_4-S, Boron, Zn, Mn, Cu, and Fe were extracted by DPTA-sorbitol solution with an equilibration time of 2 hours. Absence of effervescence using the method described in Soil Survey Laboratory Staff (1996) suggested a lack of free lime in the soil.

Data analysis

Data from 70 relevés, comprising 332 species, were entered in TURBOVEG (Hennekens and Schaminée 2001) and exported for analysis. First, we used the method OPTIMCLASS in JUICE 6.5 (Tichý 2002) to determine the optimal number of clusters: the partition with maximum number of diagnostic species across all clusters and maximum number of clusters that have a preselected minimum number of diagnostic species. An initial list of diagnostic species was determined based on the *p*-value of 0.001 of the Fisher's exact test (Tichý and Chytrý 2006). Vegetation types were then distinguished with the classification methods of the MULVA-5 program (Wildi 1989; Wildi and Orlóci 1996). Relevé data were transformed based on a square root transformation of the ordinal cover abundance scale and normalized. Resemblance of relevés and species was assessed via the van der Maarel coefficient (similarity ratio) (Wildi and Orlóci 1996). Relevé and species classification were performed using complete linkage (farthest neighbor) clustering. Eleven relevé groups, or vegetation types, and 23 species groups were distinguished. Analysis of concentration (AOC; Feoli and Orlóci 1979) of an 11 × 23 contingency table showed block structure deviated significantly from random expectation; a mean square contingency coefficient of 0.259 indicated that group structure was relatively strong (Wildi and Orlóci 1996).

The 23 species groups were used to discriminate between the vegetation types; these species groups were further refined using diagnostic, constant, and dominant species (cf. Westhoff and van der Maarel 1973) in the final vegetation table into 18 groups. Their determination follows the concepts of Chytrý (2007) based on the following threshold values: diagnostic species were those with Φ coefficient values of 60 or greater; constant species were those with a frequency over 90%; and dominant species were those with a cover value exceeding 20% cover in at least 25% of the relevés. Final table arrangement and syntaxonomical evaluation was according to Braun-Blanquet methodology (Daniëls 1982, 1985; Westhoff and van der Maarel 1973). Vegetation units are termed relevé groups (RG), or vegetation types, because syntaxonomic units within the Braun-Blanquet system should preferably be named based on more data from a variety of localities.

Potential annual direct irradiation (PADI) for relevés based on slope, aspect, and latitude was calculated in JUICE 6.5 (Tichý 2002, Tichý and Holt 2006) as proposed by McCune and Keon (2002) using their equation 3.

An ordination was performed using CANOCO 4.5 (Ter Braak and Šmilauer 2002) with the WinKyst1.0 Add-On (Šmilauer 2003) to provide non-metric multidimensional scaling (NMDS). Prior to analysis, species with fewer than two occurrences were removed; the species data were transformed using a square-root transformation and a distance matrix was calculated using Bray-Curtis distance. The resulting file of 198 species was treated in CANOCO 4.5 and CANODRAW 4.0 as suggested by Šmilauer (2003) with environmental data related to the sample scores in an unconstrained analysis. In addition, discriminant analysis, based on *F* values (Jancey 1979), was used to determine the discrimination power of numeric site factors within the vegetation classification. We used 10 highest *F* values in an ordination biplot.

We listed the geographic distribution type for all species in Tables 2 and 3 (see also supplementary data[4], Table S1, parts *a* and *b*) to illustrate the geographic pattern of species of the Unalaska flora and the phytogeographical position of the plant communities in the Northern hemisphere. The following distribution types were included: A, arctic-alpine; circumpolar occurring in Greenland, Europe, Asia, and North America with some species incompletely circumpolar (absent in one of these categories); B, circumboreal with some species extending into the Temperate and some species incompletely circumboreal (absent in one of these categories); W, widespread; T, Temperate; NA, North America; a-P, amphi-Beringian; a-NA, east Asia and North America; wNA, western North America; E, Europe; and U, unclear.

Results

Geographic pattern of species within the Northern Hemisphere

Forty-three percent of the flora consisted of circumpolar species with most of these boreal in distribution (Table 2). Of the remaining species, ~30% occurred in both Asia and North America, and the major proportion of these were amphi-Beringian (~28%), occurring in eastern Asia and western North America. Fifteen percent of the species were widespread, whereas most of the rest (~11%) were endemic to North America. Thus, species that were also found in Asia comprised a substantial proportion of the Unalaska Island flora.

[4] Supplementary data for this article are available on the journal Web site (http://botany.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5373. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

Fig. 3. Map showing the location of the study area in relation to the rest of Unalaska Island, Alaska. The letters (A–M) show the main study sites described in the study area section and their characteristics are listed in Table 1.

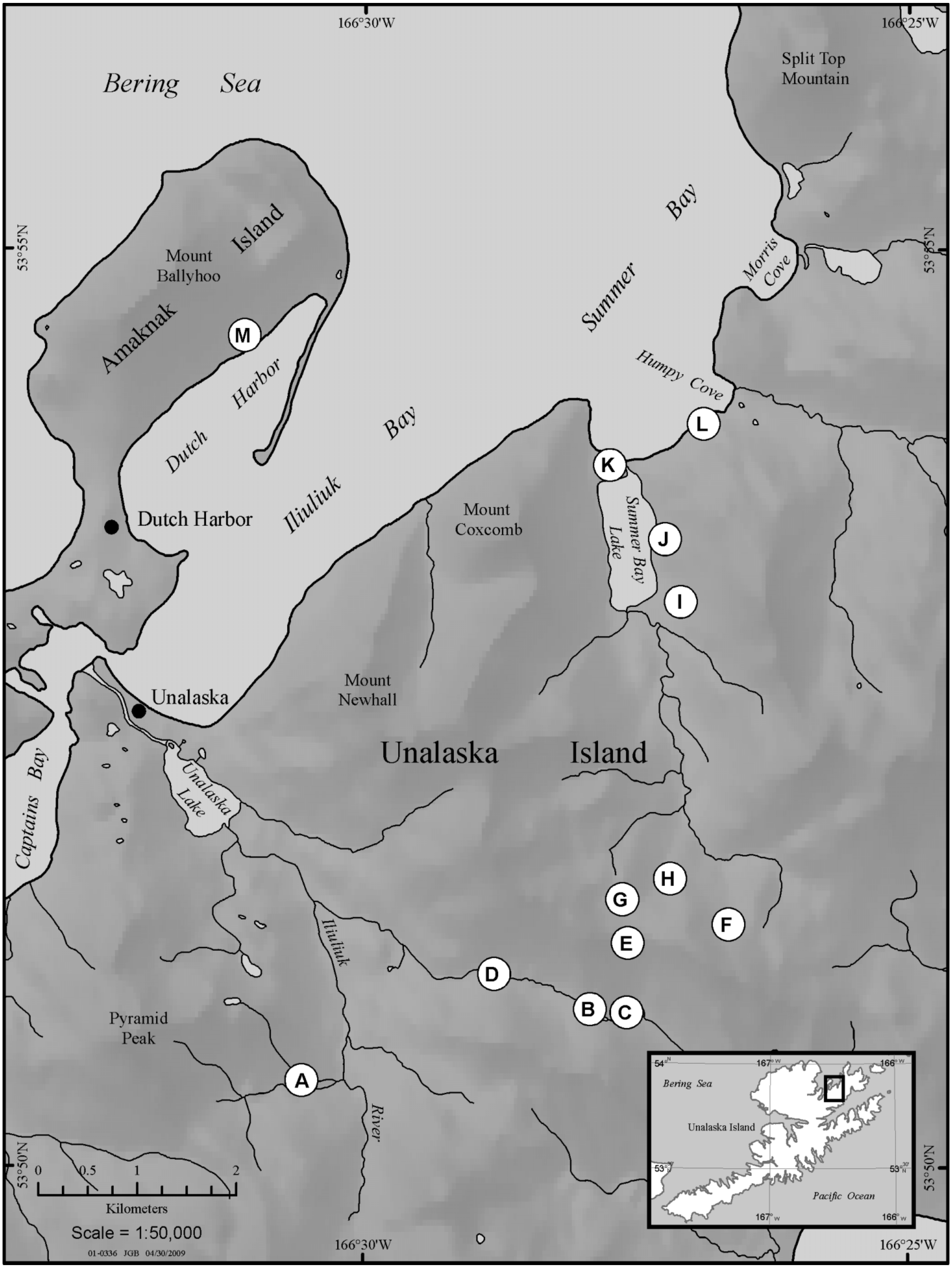


Table 1. Location and site characteristics of the sample sites (see Fig. 2) with geographical coordinates, elevation, landform, and relevé number.

Site	Location	North latitude	West longitude	Elevation (m, a.s.l.)	Landform	Relevé No.
A	Pyramid Peak, Iliuliuk River area	53°50′29″	166°30′34″	122–168	Lower to middle mountain slopes	47–50
B	Head of Ugadaga Bay Trail, Overland Drive mile 1.6	53°50′53″	166°27′56″	234–240	Closed depression by pond	1, 2
C	Valley below Ugadaga Bay Trail, Overland Drive	53°50′54″	166°27′32″	151–214	Alpine valley floor and lower mountain slopes	41–46
D	Lear Road Trail, Overland Drive mile 1.3	53°51′03″	166°28′56″	176–181	Open depression	26–29
E	Below mountain pass, Overland Drive	53°51′10″	166°27′58″	353–402	Upper mountain slope	8, 9, 30–32, 62, 63
F	Mountain pass, Overland Drive	53°51′17″	166°26′29″	267–343	Upper mountain slope	51, 54–56, 59–61, 64–68
G	Alpine valley depression below mountain pass, Overland Drive	53°51′24″	166°27′40″	288–329	Middle and upper mountain slope	34–40, 69
H	Mountain pass, Overland Drive	53°51′34″	166°27′10″	187–213	Middle and upper mountain slope	52, 53, 57–58
I	Summer Bay Lake, Overland Drive	53°53′06″	166°27′09″	39–61	Lower mountain slope	22–25
J	Summer Bay Lake, Overland Drive	53°53′23″	166°27′14″	12–63	Lower mountain slope	3–6
K	Summer Bay Road, Summer Bay	53°53′51″	166°27′46″	2–14	Beach and dunes	10–15, 70
L	Morris Cove Road, Summer Bay	53°53′51″	166°27′46″	1–4	Beach and coastal bluff	16–21
M	Amaknak Island	53°54′32″	166°31′07″	53	Lower mountain slope	7

Classification of vegetation types

Numerical–phytosociological analysis identified 11 vegetation types, or relevé groups (RGs). A quantitative display of relationships among the 11 types is presented in Fig. 4. As indicated in the dendrogram, four major groups were first separated at a high level of dissimilarity. On the top of the dendrogram, the only mire type, RG 1, was clearly distinguished from all other groups. The next major group in the dendrogram was formed of two tall meadow types (RG 2 and 4) and a thicket type with a tall meadow understory, RG 3. These RGs were closely related to each other by the high cover of herb species. The third major group is made up of five RGs; the first division of this group distinguished fellfields with low total vegetation cover, RG 7, from more heavily vegetated types, RGs 8, 9, 10, and 11. The latter were further subdivided into low elevation heaths, RG8, and middle to upper elevation meadows, RGs 10 and 11, and heaths, RG 9. The fourth major type was composed of coastal types; these included beaches, RG 5, and dunes, RG 6. In Table 3 the relevé groups were arranged along a main floristic gradient; in the upper portion of Table 3, diagnostic and dominant (do) species of the plant community types were depicted in light grey pattern; these were followed by dominant species in dark grey pattern. These community types showed differences in composition in diagnostic, constant, and dominant species, community structure (Table 4), and site and soil characteristics (Table 5). A summary of each type follows:

Characterization of vegetation types

Dry coastal meadows (I)

Honckenya peploides beach meadow (RG 5, number of relevés 4) — Diagnostic species, *Honckenya peploides*; dominant species, *H. peploides* and *Senecio pseudoarnica*; constant species, *H. peploides* and *Leymus mollis*.

This beach meadow type occurred at the leading edge of the vegetation along sandy shorelines. It was dominated by fleshy forbs, primarily *H. peploides*, with a minor graminoid component, *L. mollis*; woody shrubs and bryophytes were absent. The mean number of species per relevé (3) was the lowest of all types. The moisture regime was xeric. Soil electrical conductivity (0.8 dS·m^{-1}), strongly alkaline pH (8.90), and Na (1.92 cmol·kg^{-1}) were the highest values of all types. Soil organic matter content was very low, 00.2%.

Leymus mollis dune meadow (RG 6, number of relevés 5) — Diagnostic species, *Lathyrus japonicus* var. *maritimus* and *Senecio pseudoarnica*; dominant species, *L. japonicus* var. *maritimus* and *Leymus mollis*; constant species, *L. mollis* and *S. pseudoarnica*.

This type occurred on sandy dunes along the coast; it formed the second zone inland of *Honckenya peploides* beach meadows. It was dominated by graminoids, 65%, primarily *L. mollis*, and forbs, 49%, such as *L. japonicus* var. *maritimus*; woody plants and bryophytes were absent. The moisture regime was xeric. Moderately alkaline soil pH (8.04) and Na (0.69 cmol·kg^{-1}) content were second highest of all types. Mean number of species per relevé was 6, the second lowest of all types. Soil organic matter content was the second lowest of all types, 0.24%.

Table 2. Geographical distribution of Unalaska Island species (listed in Table 3) in circumpolar regions.

Location	Percentage (*n*)
Circumpolar arctic-alpine and boreal	**43.2 (89)**
Boreal	24.8 (51)
Arctic-alpine	11.6 (24)
Arctic and Boreal	6.8 (14)
Asia and North America	**30.1 (62)**
East Asia and western North America (amphi-Beringian)	27.7 (57)
Asia and North America	2.4 (5)
Widespread	**15.0 (31)**
North America	**11.2 (23)**
East and west coasts of North America	6.8 (14)
Western North America	4.4 (9)
Unclear	**0.5 (1)**
Total	**100 (206)**

Note: Numbers of species are shown in parentheses.

Mesic meadows (II)

Athyrium filix-femina – Aconitum maximum meadow (RG 2, number of relevés 5) — Diagnostic species, *Aconitum maximum*, *Bryhnia hultenii*, *Cirriphyllum piliferum*, *Claytonia sibirica*, and *Galium kamtschaticum*; dominant species, *Athyrium filix-femina*; constant species, *Aconitum maximum*, *Athyrium filix-femina*, *Chamerion angustifolium*, *Claytonia sibirica*, *Heracleum maximum*, and *Rhytidiadelphus squarrosus*.

This lush, tall (0.5–1.0 m) fern meadow occurred on moderately steep ($\bar{x}$ = 24°) lower mountain slopes at a mean elevation of 75 m a.s.l. It was dominated by forbs, primarily *A. filix-femina* and *C. angustifolium*, 92%, with low cover of graminoids such as *Leymus mollis*, 9%, and bryophytes such as *R. squarrosus* and *R. triquetrus*, 5%. The moisture regime was mesic. The soils were strongly acid (pH 5.34); total bases of soils and Ca were the highest of all types, 7.9 and 5.1 cmol·kg^{-1}, respectively. The mean number of species per relevé was 30.

Athyrium filix-femina – Calamagrostis nutkaensis meadow (RG 4, number of relevés 6) — Diagnostic species, *Festuca rubra* and *Polypodium glycyrrhiza*; dominant species, *Athyrium filix-femina* and *Calamagrostis nutkaensis*; constant species, *A. filix-femina*, *C. nutkaensis*, *Carex macrochaeta*, *Chamerion angustifolium*, *Festuca rubra*, *Geranium erianthum*, *Heracleum maximum*, and *Polypodium glycyrrhiza*.

This lush, tall (0.5–1.0 m) fern meadow occurred on moderately steep (19°) lower mountain slopes at a mean elevation of 47 m a.s.l. It was dominated by forbs, primarily *A. filix-femina* and *C. angustifolium*, 70%, with a distinctly higher cover of graminoids, mainly *C. nutkaensis*, 32%, and of bryophytes mainly *Hylocomium splendens*, 16%, than the previous fern meadow. The moisture regime was mesic, and the soils were moderately acid (pH 6.07); total bases of soils and Ca were the second highest of all types, 6.6 and 4.1 cmol·kg^{-1}, respectively. The mean number of species per relevé was 32.

Erigeron peregrinus – Thelypteris quelpaertensis meadow (RG 11, number of relevés 13) — Diagnostic species, *Pedicularis chamissonis*, *Thelypteris quelpaertensis*, and *Vaccinium ovalifolium*; dominant species, *Calamagrostis nutkaensis* and *Erigeron peregrinus*; constant species, *Achillea millefolium* var. *borealis*, *Anemone narcissiflora* var. *villosissima*, *Artemisia arctica*, *Calamagrostis nutkaensis*, *Coptis trifolia*, *Dicranum scoparium*, *Erigeron peregrinus*, *Geranium erianthum*, *Hylocomium splendens*, *Pleurozium schreberi*, *Polygonum viviparum*, *Rhytidiadelphus squarrosus*, and *Trientalis europaea*.

This moderately tall (<0.5 m) meadow was lower in stature than the tall fern types described above, and occurred at higher mean elevations, 273 m a.s.l.; it occurred on moderately steep (27°) middle to middle-upper mountain slopes (Fig. 5). They were dominated by forbs, primarily *E. peregrinus* and *G. erianthum,* 60%, and graminoids, mostly *C. nutkaensis* and *Carex macrochaeta*, 32%, with lower cover of dwarf shrubs such as *Vaccinium ovalifolium*, 8%, and bryophytes such as *H. splendens* and *P. schreberi*, 7%. The moisture regime varied from mesic to sub-hygric. The soils were very strongly acid (pH 5.05) and total bases (1.3 cmol·kg^{-1}) are the lowest of all types. The mean number of species per relevé was relatively high at 48.

Wet snowbed meadow (III)

Carex nigricans snowbed meadow (RG 10, number of relevés 3) — Diagnostic species, *Calliergon stramineum*, *Carex nigricans*, *Epilobium palustre*, *Hippuris montana*, *Juncus drummondii*, *Pseudobryum cinclidioides*, *Rhizomnium nudum*, and *Tritomaria quinquedentata*; dominant species, *Carex nigricans*, *Coptis trifolia*, *Erigeron peregrinus*, *Hippuris montana*, *Salix arctica*; constant species, *Carex anthoxanthea*, *Carex macrochaeta*, *C. nigricans*, *Coptis trifolia*, *Erigeron peregrinus*, *Geum calthifolium*, *Hippuris montana*, *Platanthera convallariaefolia*, *Pleurozium schreberi*, *Rhizomnium nudum*, *Rhytidiadelphus loreus*, *Salix arctica*, *Sanguisorba canadensis*, and *Trientalis europaea*.

This snowbed meadow occurred at the base of steep, upper-elevation slopes (32°). This type was dominated by forbs, primarily *C. trifolia* and *H. montana*, 62%, with moderate cover of graminoids, mainly *C. nigricans*, 20%, bryophytes such as *C. stramineum* and *Racomitrium muticum*, 17%, and dwarf shrubs, primarily *Salix arctica*, 16%. The moisture regime was hygric and the soils were very strongly acid (pH 4.93); total bases were low (2.1 cmol·kg^{-1}). The mean number of species per relevé was 36.

Heath (IV)

Linnaea borealis – Empetrum nigrum heath (RG 8, number of relevés 7) — Diagnostic species, *Antitrichia curtipendula* and *Linnaea borealis*; dominant species, *Calamagrostis nutkaensis*, *Empetrum nigrum*, *Linnaea borealis*, and *Vaccinium uliginosum*; constant species, *Achillea borealis*, *Calamagrostis nutkaensis*, *Empetrum nigrum*, *Hylocomium splendens*, *Ptilidium ciliare*, and *Rhytidiadelphus loreus*.

This heath type occurred on lower slopes at mean elevations of 94 m a.s.l; the meso-topography was usually convex, resulting in higher wind exposure than meadow types. Dwarf shrubs dominate, 86%, primarily *E. nigrum* and *L. borealis*, with moderate cover of bryophytes, 18%, such as *H. splendens,* and graminoids, 14%, mainly *C. nutkaensis*. The moisture regime varied from sub-xeric to sub-mesic and the soils were strongly acid (pH 5.34). The mean number of species per relevé was 37.

Phyllodoce aleutica heath (RG 9, number of relevés 10) — Diagnostic species, *Cladina rangiferina*, *Cladonia gracilis* subsp. *vulnerata*, *Lobaria linita*, *Pseudoleskea baileyi*, *Pyrola minor*, *Racomitrium ericoides*, *Sibbaldia procumbens*; dominant species, *Empetrum nigrum*, *Phyllodoce aleutica*, and *Salix arctica*; constant species, *Calamagrostis nutkaensis*, *E. nigrum*, *Erigeron peregrinus*, *Pleurozium schreberi*, *P. baileyi*, *Salix arctica*, and *Sanionia uncinata*.

The heath type occurred on steep (32°) upper mountain slopes at mean elevations of 329 m a.s.l. It was dominated by dwarf shrubs, 74%, primarily *P. aleutica* and *S. arctica,* with moderate cover of forbs, 20%, such as *Arnica unalaschcensis* and *Erigeron peregrinus*, bryophytes, 13%, such as *Barbilophozia floerkii* and *P. baileyi*, and graminoids such as *C. nutkaensis*, 12%; lichen cover was low but accounted for 2%. The moisture regime was sub-mesic to mesic and the soils were strongly acid (pH 5.13). The mean number of species per relevé was 56, the highest of all types.

Vaccinium uliginosum – Thamnolia vermicularis fellfield (RG 7, number of relevés 5) — Diagnostic species, *Alectoria nigricans*, *Andreaea alpestris*, *Antennaria monocephala*, *Anthelia juratzkana*, *Arnica unalaschcensis*, *Calamagrostis sesquiflora*, *Campanula chamissonis*, *Campanula lasiocarpa*, *Carex circinata*, *Cassiope lycopodioides*, *Cetrariella delisei*, *Gymnomitrion pacificum*, *Lagotis glauca*, *Loiseleuria procumbens*, *Lupinus nootkatensis*, *Luzula arcuata* subsp. *unalaschcensis*, *Melanelia agnata*, *Oligotrichum hercynicum*, *Pedicularis capitata*, *Pedicularis langsdorfii*, *Racomitrium lanuginosum*, *Racomitrium macounii*, *Salix ovalifolia* var. *cyclophylla*, *Salix reticulata*, *Salix rotundifolia*, *Sphaerophorus globosus*, *Stereocaulon spathuliferum*, *Thamnolia vermicularis*, *Tofieldia coccinea*, and *Vaccinium uliginosum*; dominant species, *Empetrum nigrum*, *Gymnomitrion pacificum*, *V. uliginosum*; constant species, *A. alpestris*, *A. monocephala*, *A. unalaschcensis*, *C. lasiocarpa*, *C. circinata*, *Carex macrochaeta*, *C. lycopodioides*, *Cladina arbuscula*, *E. nigrum*, *L. procumbens*, *Polygonum viviparum*, *R. lanuginosum*, *R. macounii*, *Rhododendron camtschaticum*, *Salix arctica*, *S. reticulata*, *T. vermicularis*, and *V. uliginosum*.

This type occurred on wind-exposed summit ridges at mean elevations of 356 m a.s.l (Fig. 6). Slopes were moderate, 23°. Total vegetation cover was the lowest of all types, 72%, with approximately 30% composed of rocky debris. Dwarf shrubs were dominant, 53%, primarily *Empetrum nigrum* and *Vaccinium uliginosum*, with moderate cover of bryophytes, 18%, particularly *Anthelia juratzkana* and *Gymnomitrion pacificum*; lichen cover though low achieved their highest values, 3%, primarily *Sphaerophorus globosus* and *Thamnolia vermicularis*. The mean number of species per relevé was 50, the second highest of all types.

Mire (V)

Carex pluriflora – Plantago macrocarpa mire (RG 1, number of relevés 8) — Diagnostic species, *Aulacomnium palustre*, *Carex lyngbyei*, *Carex pluriflora*, *Eriophorum angustifolium*, *Pinguicula vulgaris*, *Plantago macrocarpa*, *Scapania uliginosa*, and *Selaginella selaginoides*; dominant species, *Carex anthoxanthea*, *Eriophorum angustifolium*, *Geum calthifolium*, *Plantago macrocarpa*, and *Vaccinium uliginosum*; constant species, *C. anthoxanthea*, *Equisetum arvense*, *E. angustifolium*, *Geum calthifolium*, *S. selaginoides*, and *Trientalis europaea*.

This mire type was found in middle mountain valleys and upper-middle mountain depressions associated with ponds and streamlets at a mean elevation of 227 m a.s.l. Slopes were mild, 4°. The moisture regime was the wettest of all types, hygric to sub-hydric, and soils were strongly acid (pH 5.15). Graminoids, 66%, primarily *C. pluriflora* and *E. angustifolium,* and forbs, 32%, particularly *G. calthifolium*, were dominant with moderate cover of bryophytes, 15%, such as *Hypnum dieckii*, and dwarf shrubs, 10%. Peat mosses did not dominate but did add to diversity with seven species occurring within the type *Sphagnum alaskense*, *Sphagnum compactum*, *Sphagnum girgensohnii*, *Sphagnum quinquefarium*, *Sphagnum russowii*, *Sphagnum squarrosum*, and *Sphagnum subnitens*. The mean number of species per relevé was 37.

Deciduous shrub thicket (VI)

Salix barclayi – Athyrium filix-femina thicket (RG 3, number of relevés 4) — Diagnostic species, *Anaphalis margaritacea*, *Epilobium hornemannii* subsp. *behringianum*, *Pseudoleskea stenophylla*, *Rhizomnium glabrescens*, *Salix barclayi*, *Thalictrum hultenii*, and *Veronica serpyllifolia*; dominant species, *Calamagrostis canadensis*, *Salix barclayi*, and *Sanguisorba canadensis*; constant species, *Achillea millefolium* var. *borealis*, *A. margaritacea*, *Athyrium filix-femina*, *Carex macrochaeta*, *Chamerion angustifolium*, *E. hornemannii* subsp. *behringianum*, *Geranium erianthum*, *Hylocomium splendens*, *Platanthera convallariaefolia*,

Table 3. Synoptic presence table of vegetation of eastern Unalaska Island, Alaska. Light shading indicates diagnostic species; dark shading indicates dominant species.

		Groups										
Relevé group (RG) number	Distribution type	5	6	7	8	9	11	4	2	3	10	1
Diagnostic and dominant species of RG 5												
Honckenya peploides	A, B	4	III	—	—	—	—	—	—	—	—	—
Diagnostic/dominant species of RG 6												
Senecio pseudoarnica	a-NA	2	V	—	—	—	—	—	—	—	—	—
Lathyrus japonicus var. *maritimus* (do)	A, B	1	III	—	—	—	—	—	—	—	—	—
Diagnostic/dominant species of RG 7												
Cladina arbuscula	W	—	—	V	III	IV	I	—	—	—	1	II
Racomitrium lanuginosum	W	—	—	V	II	III	—	—	—	—	—	II
Cassiope lycopodioides	a-P	—	—	V	—	III	—	—	—	—	—	—
Loiseleuria procumbens	A	—	—	V	—	II	—	—	—	—	—	—
Antennaria monocephala	a-P	—	—	V	—	II	—	—	—	—	—	—
Carex circinata	NA	—	—	V	—	—	—	—	—	—	—	—
Andreaea alpestris	A	—	—	V	—	I	—	—	—	—	1	—
Racomitrium macounii	B	—	—	V	—	II	—	—	—	—	—	—
Campanula lasiocarpa	a-P	—	—	V	I	I	I	—	—	—	—	—
Thamnolia vermicularis	A	—	—	V	II	I	—	—	—	—	—	—
Campanula chamissonis	a-P	—	—	IV	—	I	I	—	—	—	—	—
Pedicularis capitata	a-P	—	—	IV	—	I	—	—	—	—	—	I
Luzula arcuata subsp. *unalaschcensis*	a-P	—	—	IV	I	—	—	—	—	—	—	—
Lagotis glauca	a-P	—	—	IV	—	I	—	—	—	—	—	—
Lupinus nootkatensis	NA	—	—	IV	—	—	—	—	—	—	—	—
Gymnomitrion pacificum (do)	a-P	—	—	IV	—	I	—	—	—	—	—	—
Anthelia juratzkana	A	—	—	IV	—	—	—	—	—	—	—	—
Tofieldia coccinea	A, B	—	—	III	—	—	—	—	—	—	—	—
Sphaerophorus globosus	A	—	—	III	II	—	—	—	—	—	—	—
Calamagrostis sesquiflora	a-P	—	—	III	—	—	—	—	—	—	—	—
Salix ovalifolia var. *cyclophylla*	a-P	—	—	III	—	—	—	—	—	—	—	—
Alectoria nigricans	A	—	—	II	—	—	—	—	—	—	—	—
Oligotrichum hercynicum	A	—	—	II	—	—	—	—	—	—	—	—
Cetrariella delisei	A	—	—	II	—	—	—	—	—	—	—	—
Melanelia agnata	A	—	—	II	—	—	—	—	—	—	—	—
Pedicularis langsdorffii	a-P	—	—	II	—	—	—	—	—	—	—	—
Salix rotundifolia	a-P	—	—	II	—	—	—	—	—	—	—	—
Stereocaulon spathuliferum	A	—	—	II	—	—	—	—	—	—	—	—
Diagnostic/dominant species of RG 8												
Linnaea borealis (do)	B	—	—	—	V	I	I	I	—	1	—	—
Antitrichia curtipendula	B, T	—	—	—	III	—	—	—	—	—	—	—
Diagnostic species of RG 9												
Pseudoleskea baileyi	NA	—	—	I	—	V	III	—	—	—	—	—
Sibbaldia procumbens	A	—	—	III	—	V	II	—	—	—	—	—

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Table 3 (*continued*).

Relevé group (RG) number	Distribution type	Groups 5	6	7	8	9	11	4	2	3	10	1
Racomitrium ericoides	B	—	—	—	I	V	II	—	—	—	—	—
Cladina rangiferina	W	—	—	II	II	V	—	—	—	—	—	—
Cladonia gracilis subsp. *vulnerata*	a-P	—	—	—	I	III	—	—	—	—	—	—
Lobaria linita	A	—	—	—	—	III	—	—	—	—	—	—
Pyrola minor	B	—	—	—	—	III	I	—	—	—	—	—
Diagnostic species of RG 11												
Vaccinium ovalifolium	a-NA	—	—	—	—	III	IV	—	—	—	—	—
Thelypteris quelpaertensis	B	—	—	—	—	II	IV	—	—	1	—	—
Pedicularis chamissonis	a-P	—	—	—	—	—	II	—	—	—	—	—
Diagnostic species of RG 4												
Festuca rubra	W	—	1	IV	III	—	—	V	I	—	—	—
Polypodium glycyrrhiza	a-P	—	—	—	—	—	—	V	I	—	—	—
Diagnostic species of RG 2												
Aconitum maximum	a-P	—	—	—	—	—	I	III	V	2	—	—
Claytonia sibirica	wNA	—	—	—	—	—	—	I	V	—	—	—
Bryhnia hultenii	a-P	—	—	—	—	—	—	—	III	—	—	—
Cirriphyllum piliferum	B	—	—	—	—	—	—	—	II	—	—	—
Galium kamtschaticum	a-NA	—	—	—	—	—	—	—	II	—	—	—
Diagnostic/dominant species of RG 3												
Epilobium hornemannii subsp. *behringianum*	a-P	—	—	—	—	I	I	II	IV	4	—	—
Salix barclayi (do)	NA	—	—	—	—	—	—	—	—	4	—	—
Anaphalis margaritacea	W	—	—	—	III	—	—	II	—	4	—	—
Thalictrum hultenii	a-P	—	—	—	—	—	—	II	—	3	—	—
Calamagrostis canadensis (do)	NA	—	—	1	—	—	I	I	IV	3	—	—
Pseudoleskea stenophylla	NA	—	—	—	—	—	—	—	—	3	—	—
Veronica serpyllifolia	W	—	—	—	—	—	—	—	—	2	—	—
Rhizomnium glabrescens	NA	—	—	—	—	—	—	—	—	2	—	I
Diagnostic/dominant species of RG 10												
Hippuris montana (do)	a-P	—	—	—	—	II	II	—	—	—	3	II
Tritomaria quinquedentata	B	—	—	—	—	III	II	—	—	—	3	I
Rhizomnium nudum	a-P	—	—	—	—	III	V	—	—	—	3	—
Carex nigricans (do)	a-P	—	—	—	—	—	I	—	—	—	3	—
Calliergon stramineum	B	—	—	—	—	—	—	—	—	—	2	II
Juncus drummondii	wNA	—	—	—	—	—	—	—	—	—	2	—
Pseudobryum cinclidioides	B	—	—	—	—	—	—	—	—	1	2	—
Epilobium palustre	A, B	—	—	—	—	—	—	—	—	—	2	—
Diagnostic/dominant species of RG 1												
Selaginella selaginoides	B	—	—	—	—	I	IV	—	—	—	1	V
Eriophorum angustifolium (do)	W	—	—	—	—	—	—	—	—	—	1	V

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Table 3 (*continued*).

Relevé group (RG) number	Distribution type	Groups 5	6	7	8	9	11	4	2	3	10	1
Scapania uliginosa	B	—	—	—	—	—	—	—	—	—	—	V
Carex pluriflora	a-P	—	—	—	—	—	—	—	—	—	—	V
Plantago macrocarpa (do)	a-P	—	—	—	—	—	—	—	—	—	—	V
Carex lyngbyei	Bd	—	—	—	—	—	—	—	—	—	—	IV
Aulacomnium palustre	W	—	—	—	I	—	—	—	—	—	—	IV
Pinguicula vulgaris	A, B	—	—	—	—	—	—	—	—	—	—	III
Dominant species of vegetation types												
Leymus mollis	A, B	4	V	—	II	—	—	—	III	—	—	—
Vaccinium uliginosum	A,B	—	—	V	III	II	—	—	—	—	—	III
Empetrum nigrum	B	—	—	V	V	V	II	—	—	—	—	IV
Calamagrostis nutkaensis	wNA	—	—	I	V	V	V	V	II	3	1	II
Phyllodoce aleutica	a-P	—	—	IV	—	V	II	—	—	—	1	I
Salix arctica	A	—	—	V	I	V	IV	—	—	—	3	I
Erigeron peregrinus	a-P	—	—	—	II	V	V	II	—	2	3	V
Athyrium filix-femina	W	—	—	—	I	—	II	V	V	—	—	—
Sanguisorba canadensis	a-P	—	—	—	II	II	IV	IV	III	4	3	V
Coptis trifolia	A, B	—	—	—	II	V	V	—	—	—	3	IV
Geum calthifolium	a-P	—	—	I	I	IV	IV	—	—	—	3	V
Carex anthoxanthea	a-P	—	—	—	—	IV	V	—	—	—	—	V
Other differential species groups												
Arctostaphylos alpina	A	—	—	II	III	I	—	—	—	—	—	—
Vaccinium vitis-idaea	B	—	—	II	II	—	—	—	—	—	—	—
Dicranum spadiceum	A	—	—	II	II	—	—	—	—	—	1	—
Salix reticulata	A, B	—	—	V	I	III	I	—	—	—	—	I
Cetraria islandica subsp. crispiformis	B	—	—	III	II	IV	I	—	—	—	1	II
Artemisia arctica	a-P	—	—	IV	I	V	V	—	—	—	1	—
Rhododendron camtschaticum	a-P	—	—	V	—	V	IV	—	—	—	1	II
Arnica unalaschcensis	a-P	—	—	V	—	III	IV	—	—	—	—	—
Veronica wormskjoldii	NA	—	—	IV	—	V	V	—	—	—	—	—
Anemone narcissiflora var. *villosissima*	a-P	—	—	III	IV	IV	V	—	—	—	—	—
Polygonum viviparum	A, B	—	—	V	III	IV	V	—	—	—	2	III
Vahlodea atropurpurea	W	—	—	I	I	IV	V	—	—	—	1	II
Ptilium crista-castrensis	B	—	—	—	IV	—	—	III	—	—	1	—
Arctostaphylos uva-ursi	B	—	—	—	III	—	—	I	—	—	—	—
Frullania nisquallensis	a-P	—	—	—	II	—	—	—	—	—	—	—
Lycopodium alpinum	B	—	—	—	IV	III	IV	—	—	—	1	—
Lycopodium clavatum	W	—	—	—	III	III	IV	II	—	—	1	—
Luzula multiflora subsp. *frigida*	A, B	—	—	—	IV	II	III	—	—	—	—	I
Barbilophozia lycopodioides	B	—	—	—	I	III	III	—	—	—	—	—
Lycopodium sitchense	a-NA	—	—	—		III	III	—	—	—	1	—
Ptilidium ciliare	W	—	—	I	V	III	I	II	—	—	—	—

Table 3 (*continued*).

		Groups										
Relevé group (RG) number	Distribution type	5	6	7	8	9	11	4	2	3	10	1
Rhytidiadelphus triquetrus	B	—	—		V	IV	I	II	IV	1	1	I
Dactylorhiza aristata	a-P	—	—	—	I	I	IV	—	—	—	—	II
Rhinanthus minor	a-P	—	—	—	—	I	III	—	—	—	—	—
Platanthera chorisiana	a-P	—	—	I	I	—	V	—	—	—	—	III
Chamerion angustifolium	W	—	II	—	V	I	III	V	V	4	—	—
Heracleum maximum	a-P	—	—	—	I	—	—	V	V	3	—	—
Ranunculus occidentalis var. *brevistylis*	wNA	—	—	—	I	—	I	IV	III	3	—	—
Bromus aleutensis	wNA	—	—	—		—	—	IV	III	2	—	—
Rubus spectabilis	a-P	—	—	—	III	—	I	IV	III	2	—	—
Cardamine oligosperma var. *kamtschatica*	a-P	—	—	—	—	—	I	II	IV	2	—	—
Galium triflorum	W	—	—	—	—	—	—	III	IV	3	—	—
Brachythecium frigidum	NA	—	—	—	—	I	I	II	IV	3	—	I
Phegopteris connectilis	B	—	—	—	—	I	I	IV	I	—	—	—
Gymnocarpium dryopteris	B	—	—	—	I	—	—	III	I	—	—	—
Luzula parviflora	W	—	—	—	I	—	I	I	IV	3	—	—
Anemone richardsonii	B	—	—	—	—	I	I	—	II	3	—	I
Equisetum arvense	W	—	III	—	I	I	II	—	I	2	1	V
Leptarrhena pyrolifolia	wNA	—	—	—	—	III	III	—	—	—	—	V
Juncus mertensianus	a-P	—	—	—	—	—	I	—	—	—	1	III
Trichophorum cespitosum	W	—	—	—	—	—	—	—	—	—	—	II
Campylium stellatum	B	—	—	—	—	—	—	—	—	—	—	II
Juncus falcatus	a-P	—	—	—	—	—	—	—	—	—	—	II
Sphagnum alaskense	NA	—	—	—	—	—	—	—	—	—	—	II
Sphagnum russowii	B	—	—	—	—	—	—	—	—	—	—	II
Sphagnum warnstorfii	B	—	—	—	—	—	—	—	—	—	—	II
Sarmenthypnum sarmentosum	A	—	—	—	—	—	—	—	—	—	—	II
Aneura pinguis	W	—	—	—	—	—	—	—	—	—	—	II
Philonotis fontana	B	—	—	—	—	—	—	—	—	—	—	II
Limprichtia revolvens	B	—	—	—	—	—	—	—	—	—	—	II
Equisetum palustre	A, B	—	—	—	—	—	—	—	—	—	—	II
Sphagnum subnitens	B	—	—	—	—	—	—	—	—	—	—	II
Warnstorfia exannulata	B	—	—	—	—	—	—	—	—	—	—	II
Achillea millefolium var. *borealis*	NA	—	II	II	V	V	V	IV	II	4	—	I
Carex macrochaeta	a-P	—	—	V	V	V	V	V	III	4	3	—
Platanthera convallariaefolia	a-P	—	—	—	III	IV	V	II	III	4	3	—
Geranium erianthum	a-P	—	—	—	—	III	V	V	IV	4	—	—
Deschampsia beringensis	a-P	—	—	—	III	IV	III	IV	II	3	1	II
Trientalis europaea	a-P	—	—	I	III	IV	V	V	II	2	3	V
Hylocomium splendens	W	—	—	I	V	V	V	IV	II	4	2	IV
Rhytidiadelphus squarrosus	W	—	—	—	—	IV	V	IV	V	4	2	II
Dicranum scoparium	W	—	—	II	IV	V	V	IV	I	3	2	II

Table 3 (*continued*).

Relevé group (RG) number	Distribution type	Groups 5	6	7	8	9	11	4	2	3	10	1
Pleurozium schreberi	B	—	—	II	V	V	V	IV	—	2	3	II
Rhytidiadelphus loreus	B	—	—	—	V	V	V	III	I	1	3	III
Polytrichastrum alpinum	B	—	—	II	III	IV	V	I	I	1	1	II
Sanionia uncinata	W	—	—	I	I	V	V	—	—	3	2	II
Listera cordata	B	—	—	—	IV	IV	IV	I	—	1	2	II
Castilleja unalaschcensis	wNA	—	—	—	II	II	IV	—	—	2	—	IV
Viola langsdorfii	a-P	—	—	II	II	III	V	—	—	1	2	V
Phleum alpinum	A	—	—	—	II	I	III	IV	—	1	—	—
Huperzia selago	B	—	—	III	I	I	II	—	—	—	1	III
Lycopodium annotinum	B	—	—	—	IV	I	II	III	—	—	—	—
Pyrola asarifolia	A, B	—	—	—	II	I	II	IV	—	4	—	I
Primula cuneifolia	a-P	—	—	III	—	III	I	—	—	—	1	II
Racomitrium muticum	a-P	—	—	I	—	III	II	—	—	—	1	II
Platanthera stricta	wNA	—	—	—	II	I	III	—	—	—	1	II
Angelica lucida	W	—	I	—	III	—	I	III	II	1	—	—
Cornus suecica	B	—	—	—	III	II	II	—	—	2	—	—
Hieracium triste	a-P	—	—	II	II	II	II	—	—	—	—	—
Peltigera membranacea	W	—	—	—	II	I	—	III	III	—	—	—
Rubus arcticus s. stellatus	a-P	—	—	—	II	I	II	—	—	2	1	II
Conioselinum gmelinii	a-NA	—	—	—	I	I	II	II	III	—	—	—
Anthoxanthum odoratum	W	—	—	—	III	—	—	II	—	3	—	I
Fritillaria camschatcensis	a-P	—	—	—	—	—	III	—	II	1	—	—
Climacium dendroides	B	—	—	—	—	I	—	II	I	2	1	I
Claopodium bolanderi	NA	—	—	—	—	II	II	I	—	1	—	—
Diplophyllum taxifolium	B	—	—	II	—	II	II	—	—	—	—	—
Sanionia orthothecioides	A	—	—	—	II	II	II	—	—	—	—	—
Agrostis exarata	wNA	—	—	III	—	I	—	—	—	—	—	III
Streptopus amplexifolius	B	—	—	—	—	—	I	III	II	—	—	—
Artemisia vulgaris var. *kamtschatica*	a-P	—	I	I	—	—	—	III	I	1	—	—
Trisetum spicatum	A	—	—	II	II	I	I	—	—	—	—	—
Nardia scalaris	B	—	—	III	—	I	—	—	—	—	2	—
Agrostis mertensii	A, B	—	—	II	—	II	I	—	—	—	—	—
Epilobium anagallidifolium	A	—	—	I	—	III	I	—	—	—	—	—
Lophozia bantriensis	B	—	—	I	I	III	I	—	—	—	1	I
Ligusticum scoticum	B	—	—	I	I	I	I	I	I	—	—	—
Luzula multiflora subsp. *multiflora* var. *kobayasii*	a-P	—	II	—	II	—	II	—	—	—	—	—
Sphagnum girgensohnii	B	—	—	—	—	—	I	—	—	—	1	III
Barbilophozia floerkei	W	—	—	—	—	II	I	—	—	—	1	—
Plagiochila porelloides	B	—	—	—	—	I	I	—	I	2	—	—
Cladonia scabriuscula	W	—	—	—	I	—	II	I	—	—	—	—
Stereocaulon alpinum	A	—	—	I	I	II	—	—	—	—	—	—

Table 3 (*concluded*).

Relevé group (RG) number	Distribution type	Groups 5	6	7	8	9	11	4	2	3	10	1
Peltigera aphthosa	W	—	—	—	I	II	—	—	—	—	1	—
Plagiomnium insigne	NA	—	—	—	—	I	I	—	II	—	—	—
Plagiothecium laetum	B	—	—	—	—	—	I	—	—	2	1	—
Hypnum dieckii	a-P	—	—	—	—	—	—	—	—	—	1	II
Diplophyllum imbricatum	U	—	—	II	—	I	—	—	—	—	—	I
Sphagnum squarrosum	W	—	—	—	—	—	—	—	—	—	1	II
Cladina stygia	B	—	—	I	I	I	—	—	—	—	—	—
Poa arctica	A	—	—	—	II	—	I	—	—	—	—	—
Cladonia uncialis	W	—	—	II	I	I	—	—	—	—	—	—
Spiranthes romanzoffiana	NA, E	—	—	—	—	—	I	—	—	—	—	II
Polytrichum commune	W	—	—	—	III	I	—	—	—	—	—	—
Hypnum lindbergii	B	—	—	—	—	—	I	—	—	—	—	II
Cladonia albonigra	a-P	—	—	—	—	I	I	—	—	—	—	—
Hypnum callichroum	B	—	—	—	—	II	—	—	—	—	—	I
Cladonia ecmocyna subsp. *occidentalis*	A	—	—	I	—	II	—	—	—	—	—	—
Moerkia blytii	A	—	—	I	—	I	—	—	—	—	—	II
Stellaria calycantha	B	—	—	—	—	—	I	—	II	—	—	—
Number of relevés		**4**	**5**	**5**	**7**	**10**	**13**	**6**	**5**	**4**	**3**	**8**
Mean number of species		**3**	**6**	**50**	**37**	**56**	**48**	**35**	**30**	**40**	**36**	**37**

Note: —, no data; do, diagnostic and dominant. Key to relevé groups: 1, *Carex pluriflora – Plantago macrocarpa* mire; 2, *Athyrium filix-femina – Aconitum maximum* meadow; 3, *Salix barclayi – Athyrium filix-femina* thicket; 4, *Athyrium filix-femina – Calamagrostis nootkatensis* meadow; 5, *Honckenya peploides* beach meadow; 6, *Leymus mollis* dune meadow; 7, *Vaccinium uliginosum – Thamnolia vermicularis* fellfield; 8, *Linnaea borealis – Empetrum nigrum* heath; 9, *Phyllodoce aleutica* heath; 10, *Carex nigricans* snowbed meadow; 11, *Erigeron peregrinus – Thelypteris quelpaertensis* meadow. Key to distribution types: A, arctic-alpine; B, boreal; a-P, amphi-Beringian; aNA, east and west coasts of North America; wNA, western North America; NA, North America; T, temperate; W, widespread; U, unclear; d, disjunct. Presence values are shown as Roman numerals for relevé groups with five releves or more: I, 0%–20%; II, 21%–40%; III, 41%–60%; IV, 61%–80%; and V, 81%–100%, and as Arabic numbers for groups with fewer than five relevés. The full table of 70 relevés is presented as supplementary data[4].

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Fig. 4. Classification dendrogram of eleven relevé groups (community types) from Unalaska Island, Alaska, obtained using the van der Maarel coefficient and complete linkage (farthest neighbor) clustering (Wildi and Orlóci 1996) of 70 relevés. The dendrogram was prepared using CLUSTANGRAPHICS7 (Wishart 2003).

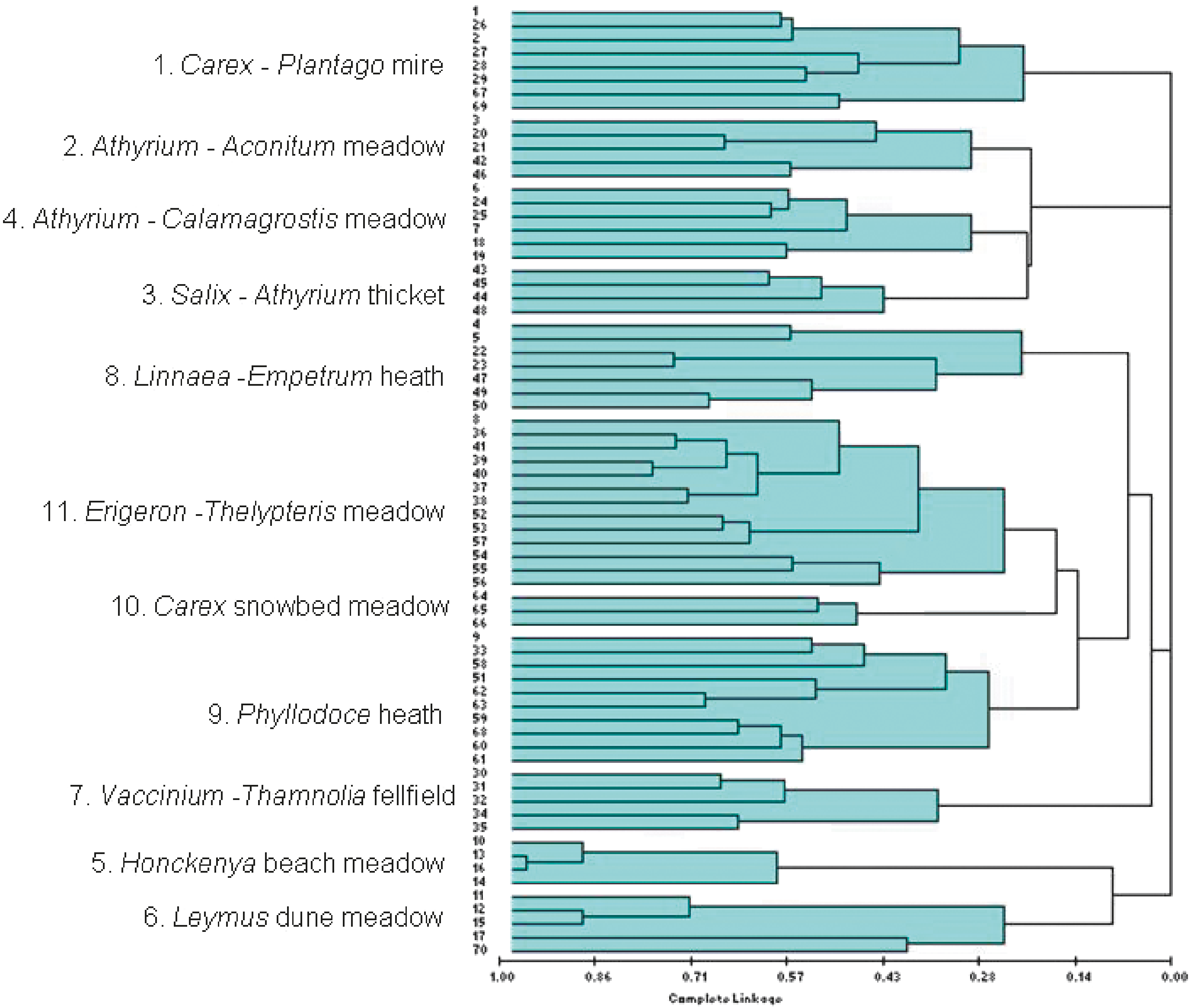


Table 4. Vegetation structure of 11 community types from Unalaska Island, Alaska.

Vegetation type	Total cover	Low shrub (0.5–2.0 m)	Dwarf shrub (<0.5 m)	Forb	Graminoid	Bryophyte	Lichen	Litter
1	99	—	10	32	66	15	—	65
2	100	2	—	92	9	5	1	91
3	100	74	1	39	25	5	1	90
4	100	1	2	70	32	16	—	81
5	91	—	—	85	3	—	—	1
6	99	—	—	65	49	—	—	35
7	72	—	53	2	2	18	3	3
8	100	—	86	9	14	18	1	2
9	100	—	74	20	12	13	2	23
10	90	—	16	62	20	17	—	24
11	98	—	8	60	32	7	—	76

Note: Entries are expressed as mean percent values.

Pyrola asarifolia, *Rhytidiadelphus squarrosus*, *S. barclayi*, and *S. canadensis*.

This deciduous thicket occurred at the base of a wind-protected mountain valley at a mean elevation of 146 m on slopes averaging 13°. Low shrubs (0.5–2.0 m), *S. barclayi*, 74% cover, predominated over a rich hemi-cryptophytic understory of forbs, primarily *C. angustifolium* and *S. canadensis*, 39%, and graminoids, such as *C. canadensis* and *Luzula parviflora*, 25%, and low cover of bryophytes, 5%. The moisture regime was sub-hygric and the soils were moderately acid, pH 5.45. The mean number of species per relevé was 40.

Ordination of relevés

Nonmetric multidimensional scaling ordination (Fig. 7) showed 70 relevés in 11 relevé groups. The primary NMDS solution for two dimensions was found with 45 iterations out of 100, stress = 0.10872 indicating a good fit. The eigenvalues of the first two axes of PCA, applied to NMDS configuration to rotate it so that the spread of relevés was maximized along the two axes, showed that the resulting first axis had pronounced explanatory value, compared with the second one (0.756 vs. 0.244).

The 11 relevé groups were relatively distinct and there was separation between them, which indicated they were well-defined. The ordination biplot (Fig. 7) indicated ecological moisture regime (EMR), elevation, and pH were the three most important factors. Further support for the importance of these factors was based on an alternative approach of discriminant analysis; *F* values (Jancey 1979; Wildi and Orlóci 1996) of the 21 environmental variables indicated that with respect to their specific resolving potential of the 11 Unalaska Island community types, the three most important factors were the same as in the NMDS ordination (Table 6).

The ordination showed seven relevé groups along axis one, with RGs 5 and 6 on the right end nearest to the sea and characterized by low elevation, low EMR, and high pH. At the other end (left side) were RGs 1, 8, 9, and 10 characterized by higher elevation, higher EMR and organic matter, and low pH). RGs 2, 3 and 4 were clearly separated from the others; these three types had abundant tall meadow components and the highest values for total bases of all types. RG 7 was also clearly separated from the others with low total bases and the highest elevation values.

Discussion

Geographic pattern of the flora and plant communities within the Aleutian region and southern Alaska

This research represented an essential contribution to understanding the plant community composition and structure in a strategic location that bridges the flora of North America and Asia. While Hultén (1960) enumerates the distributional data of species in the Aleutians, Lindroth (1963) and Tatewaki (1963) attempt a phytogeographic synthesis of Aleutian vascular plant patterns. In spite of a strong overlay of holarctic species across the island chain, Lindroth (1963: 122, Fig. 1) illustrates a progressive decrease of Asiatic species eastward and North American species westward. Tatewaki (1963) divides the floristic area he names "Hultenia" (Commander Islands and Aleutian Islands) into four districts and calculates the total number of species for each district. These include: I. The Commander Islands (300 species, represented by Bering Island); II. Near Islands (278 species, represented by Attu Island); III. Rat and Andreanof islands (244 species, represented by Atka Island); and IV. The Fox Islands and the Islands of the Four Mountains (390 species, represented by Unalaska). Tatewaki (1963) detected a distinct decrease in shared species between the Commander Islands (I) and the Aleutian Islands (II, III, IV). Although this decrease is transitional, he considers the flora of the Commander Islands to belong to the eastern Asiatic region and the Aleutian Islands to the North American region.

Our description of the vegetation of Unalaska (Tatewaki's floristic district IV) that included vascular plants, bryophytes, and lichens suggested only 11% of the species were endemic to North America; almost 90% of species were circumpolar, amphi-Beringian, or cosmopolitan. Thus, a substantial portion of the species that comprise the vegetation of Unalaska also occurred in Asia. North American vascular plant species from the Unalaska study area accounted for 17% of the flora, while the flora of this group from coastal Attu Island was only 9% (S. Talbot & S. Talbot, unpublished data). Floristic studies of the vascular flora from Tuxedni Wilderness in south central Alaska (Talbot et al. 1995) indicated 20% were North American, and from Izembek National Wildlife Refuge on the westernmost Alaska Peninsula, 13% (Talbot et al. 2006). Data from other Aleutian Islands are required to fully understand the westward and eastward pattern of community assembly and therefore polarity of species dispersal in this region. Future studies addressing this are currently underway.

Our comparison focuses primarily on the vegetation of southern Alaska within four of the phytogeographical districts of delimited by Hultén (1941–1950: 5): Aleutian Islands, Western Pacific Coast, Central Pacific Coast, and Eastern Pacific Coast. Phytogeographic community comparisons of this region, which follow, suffer from a lack of quantitative data, incomplete species lists, or failure to determine of taxa below the level of genus, absence of information on bryophytes and lichens, and different sampling methodologies. For these reasons the validity of comparison of the communities defined for Unalaska by numerical methods with those from other non-numerical studies with partial species lists should be considered tentative and for heuristic purposes. Thus, we made qualitative comparisons:

Dry coastal meadows

Leymus mollis dune meadow and the *Honckenya peploides* beach meadow are referred to by Hultén (1960) as the "*Elymus* association." Hultén (1960: 39) noted that the association "is about the same as in other places in the North Pacific" and Batten and Murray (1993) provide an overview of the dry coastal ecosystems of Alaska. Using the broad classification concept given above, similar types are reported in southern Alaska as "*Elymus arenarius*" and "*Elymus arenarius* – *Senecio pseudoarnica* – *Lathyrus maritius*" (Bank 1951), "*Honckenya peploides* vegetation" and "*Elymus mollis* dune vegetation" on Simeonof Island (Daniëls et al. 1998), "*Honckenya peploides*, *Leymus mollis*, and *Senecio pseudoarnica*" on Bogoslof Island (Byrd et al.

Table 5. Ecological data for 11 community types of Unalaska Island vegetation.

Vegetation type[a]	Elevation (m, a.s.l.)	Slope (°)	OM (g·kg^{-1})	pH	EC (1:1) (dS·m^{-1})	NO_3 (mg·kg^{-1})	NH_4	P	SO_2
1	227	4	71.1	5.15	0.34	1.3	16.8	10	23
2	75	24	59.6	5.34	0.26	3.3	23.7	10	23
3	146	13	77.1	5.45	0.2	6.4	15.2	6	13
4	47	19	48.6	6.07	0.22	4.7	12.8	5	16
5	2	7	0.2	8.9	0.8	8.3	0.3	6	29
6	5	18	2.4	8.04	0.18	8	1.3	5	9
7	356	11	52.8	5.24	0.12	1.5	8.8	2	28
8	94	12	74.4	5.34	0.23	4.5	13.7	8	16
9	329	23	56.6	5.13	0.15	0.7	17.2	4	18
10	321	32	80.4	4.93	0.35	1.2	26.2	13	49
11	273	27	68.9	5.05	0.18	2	16.8	5	23

Note: Entries are expressed as mean values. OM, organic matter; EMR, ecological moisture regime; PADI, potential annual direct irradiation.
[a]Description of vegetation types in text.

Fig. 5. *Erigeron peregrinus – Thelypteris quelpaertensis* meadow on a steep, south-facing slope of a mountain bowl at an elevation of 288 m a.s.l, Unalaska Island, Alaska (11 August 2007).

1980), "*Elymus* association" on Atka Island (York 1950); "*Elymus arenarius – Honckenya peploides*" in the Barren Islands (Manuwal 1979); "*Arenaria* (*Honckenya*) *peploides*," "*Lathyrus maritimus – Elymus mollis*" and "*Elymus mollis – Senecio pseudoarnica*" on Attu Island (Talbot and Talbot 1994); "*Honckenya peploides – Senecio pseudoarnica* community" on Amchitka Island (Shacklette et al. 1969); "*Honckenya peploides"* at the Port of Valdez (Crow 1977); "*Elymus arenarius* type" (DeVelice et al. 1999).

Mesic meadows

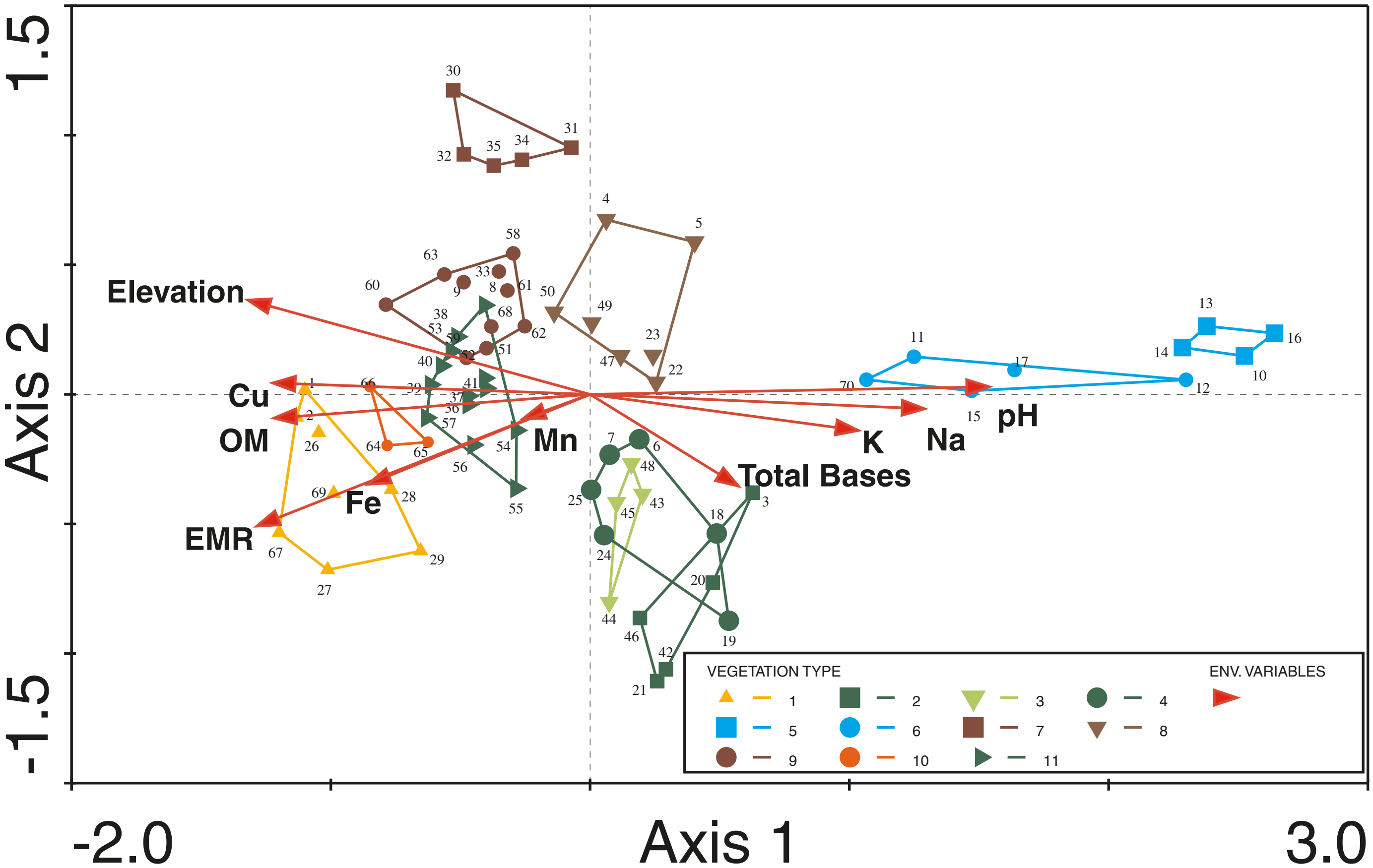
General descriptions of similar types are reported as the "*Calamagrostis* association" on Atka Island (York 1950)

B	Zn	Mn	Cu	Fe	K	Ca	Mg	Na			
					(cmol·kg^{-1})				Total bases	EMR	PADI
0.7	3.5	8	4	315	0.378	2.6	1	0.3	4.3	6.8	0.798
0.92	3	22	3.2	332	0.32	5.1	1.9	0.54	7.9	4	0.635
0.74	3.6	29	5.3	271	0.238	3.9	1.2	0.26	5.5	5	0.842
0.8	5.3	23	3.7	285	0.417	4.1	1.8	0.4	6.6	4	0.743
0.65	0.6	2	0.2	14	0.775	1.7	1.2	1.92	4.4	1	0.75
0.32	0.3	2	0.2	16	0.639	2.8	0.9	0.69	5	1	0.65
0.31	0.5	10	4	127	0.169	0.8	0.3	0.18	1.4	1.4	0.735
0.87	3.2	30	4.2	333	0.309	2.4	1.5	0.36	4.6	2.9	0.766
0.64	1.8	22	5	239	0.233	1.4	0.5	0.2	2.3	3.8	0.722
0.98	4.2	5	5.7	368	0.522	0.8	0.5	0.3	2.1	6	0.734
0.61	1.4	16	5.6	223	0.263	0.6	0.2	0.17	1.3	4.6	0.72

Fig. 6. *Vaccinium uliginosum – Thamnolia vermicularis* fellfield (foreground) on a rounded ridge below the summit at an elevation of 402 m a.s.l, Unalaska Island, Alaska (10 August 2007). In the background is seen the pattern of heath vegetation on wind-exposed ridges and meadows in more wind-protected sites.

and the "*Calamagrostis–Heracleum–Ranunculus*-Association" on Unalaska Island (Tatewaki and Kobayashi 1934). For the Aleutian Islands the "*Coelopleurum–Carex–Artemisia*-Association" (Tatewaki and Kobayashi 1934) represents a broad spectrum of Aleutian meadows and includes species such as *Cacalia kamtschatica* and *Veratrum oxysepalum* that are restricted to the western Aleutians, but other species are typical of Unalaska meadows. Similarly for Attu Island, the mesic meadows "*Athyrium filix-femina – Streptopus amplexifolius*" and "*Artemisia tilesii – Veratrum album*" (Talbot and Talbot 1994) share many species with Unalaska meadows, but differ in that there is a significant component of

Fig. 7. Non-metric multidimensional scaling ordination (Šmilauer 2003, Ter Braak and Šmilauer 2002) of 70 relevés with projected environmental variables from Unalaska Island, Alaska. The scatterplot shows the 11-cluster model of community types identified in classification dendrogram (Fig. 4). Colors distinguish the physiognomic–ecological groups indicated by Roman numerals and colored symbols distinguish relevé groups (RG). Key to types: I. Dry coastal meadows (blue): RG 5. *Honckenya peploides* beach meadow, RG 6. *Leymus mollis* dune meadow; II. Mesic meadows (dark green): RG 2. *Athyrium filix-femina – Aconitum maximum* meadow, RG 4. *Athyrium filix-femina – Calamagrostis nutkaensis* meadow, RG 11. *Erigeron peregrinus – Thelypteris quelpaertensis* meadow; III. Wet snowbed meadow (orange): RG 10. *Carex nigricans* snowbed meadow; IV. Heath (brown): RG 7. *Vaccinium uliginosum – Thamnolia vermicularis* fellfield, RG 8. *Linnaea borealis – Empetrum nigrum* heath, RG 9. *Phyllodoce aleutica* heath; V. Mire (gold): RG 1. *Carex pluriflora – Plantago macrocarpa* mire; and VI. Deciduous shrub thicket (light green): RG 3. *Salix barclayi – Athyrium filix-femina* thicket.



Asian species both in dominance and constancy on Attu Island.

The *Erigeron peregrinus – Thelypteris quelpaertensis* meadow (RG 11) appears to be a unique type; no reference was found to this type in the literature.

Heaths

As used here, "heath" includes species within the Ericaceae, Empetraceae, and Diapensiaceae (sensu Bliss 1979). "*Empetrum*/Lichen community" on Umnak Island (Nybakken 1966); "*Salix–Vaccinium*" and "*Empetrum*-lichen" on Atka Island (York 1950), "*Empetrum–Rhacomitrium–Cladonia* association" on Atka Island (Tatewaki and Kobayashi 1934); "*Arctostaphylos–Salix*-Association" on Amaknak Island adjacent Unalaska Island (Tatewaki and Kobayashi 1934);

The *Vaccinium uliginosum – Thamnolia vermicularis* fellfield (RG 7) corresponds to the "*Vaccinium–Empetrum*–Lichen association" (Hultén 1960) of the upper alpine, where heaths are often patchy alternating with bare earth. For the Aleutians all the species mentioned by Hultén (1960: 42) are contained in our Unalaska fellfield type. The "*Empetrum–Vaccinium–Cladonia*–Moss-Association" (Tatewaki and Kobayashi 1934) of dry, upper mountain sides or hill tops of the Aleutians also seems related.

Important dwarf shrubs such as *Cassiope lycopodioides*, *Empetrum nigrum*, *Linnaea borealis*, *Loiseleuria procumbens*, *Salix reticulata*, *Vaccinium uliginosum*, and *Vaccinium vitis-idaea* in the flora of the Unalaska heaths indicate similarities with those of communities of the Western and Central Pacific Coast districts of Hultén (1941–1950) as seen in the "Dwarf Shrub Landcover Class" of Boggs et al. (2003) for the eastern Alaska Peninsula and the "Dwarf Scrub Type" (DeVelice et al. 1999). However, noteworthy is the absence of a number of dwarf shrubs in heaths of the Aleutian Islands that are present in both Hultén's (Hultén 1941–1950) southern phytogeographical districts of Alaska and Asia: *Arctostaphylos rubra*, *Betula nana*, *Cassiope tetragona*, *Diapensia lapponica*, *Dryas integrifolia*, *Dryas octopetala*, *Ledum palustre* subsp. *decumbens*, and *Luetkea pectinata* (Hultén 1960, 1968). Other dwarf shrub species occur in the types of Boggs et al. (2003) and DeVel-

Table 6. Discriminant analysis based on *F* values (Jancey 1979; Wildi and Orlóci 1996) of 21 environmental variables with respect to their specific resolving potential of the 11 Unalaska Island community types (df1 = 10, df2 = 59).

Rank	Variable	*F* value
1	Ecological moisture regime (EMR)	66.117**
2	Elevation (m, a.s.l.)	41.579**
3	pH	22.463**
4	Na	13.059**
5	Cu	11.080**
6	Organic matter (OM)	9.6345**
7	Fe	6.6542**
8	K	6.6121**
9	Mn	5.2906**
10	Total bases	4.6254**
11	Electrical conductivity (EC)	4.4971**
12	Mg	4.4781**
13	SO_2	4.3647**
14	Ca	4.1615**
15	Zn	3.9722**
16	B	3.2218**
17	Slope (°)	2.6094**
18	P	2.5512
19	NH_4	2.2824
20	NO_3	1.5319
21	Potential annual direct irradiation (PADI)	0.98439

Note: **, significant at $p < 0.01$.

ice et al. (1999) but are only present in the eastern Aleutians and Asia: *Arctostaphylos alpina*, *Arctostaphylos uva-ursi*, and *Cassiope stelleriana*.

Mires

For the Aleutian Islands, Tatewaki and Kobayashi (Tatewaki and Kobayashi 1934) refer to a "*Plantago–Primula*-Association" and a "*Lycopodium–Carex–Cladonia*–Moss-Association" that may represent a broader pattern. Floristic similarities are seen in the "*Vaccinium uliginosum – Empetrum nigrum*" (Talbot and Talbot 1994) on wet organic soils of Attu Island and the "*Carex–Sphagnum* association" on Atka Island (York 1950). No other references to this type have been published.

Several woody shrubs that are important in the mires of Hultén's (Hultén 1941–1950) southern phytogeographical districts are notably absent in the Aleutians: *Andromeda polifolia*, *Chamaedaphne calyculata*, and *Myrica gale* (Hultén 1968).

Salix thicket

Salix barclayi thickets may be classed in an international context as "Subalpine or subpolar deciduous thicket *with primarily hemicryptophytic undergrowth*, mainly forbs" (Ellenberg and Mueller-Dombois 1966). Hultén (1960) reported the type on Unalaska and eastwards; he noted that with the exception of these thickets, American species not found in Asia have not been able to establish a single association of their own in the Aleutians. Golodoff (2001) states that *S. barclayi* grows together with *S. commutata* and *S. pulchra* in sheltered Unalaska lowlands and valleys and Tatewaki and Kobayashi (1934) noted the presence of *S. barclayi* thickets over an area greater than 4 km in circumference near Unalaska Lake, Unalaska Island. For south-central Alaska, DeVelice et al. (1999) describe a "*Salix baclayi*/*Calamagrostis canadensis*" tall scrub type of flood plains, valley floors, non-disturbed foot slopes, and rounded mountains that shares a number of species related to Unalaska. In Katmai National Park and Preserve of the upper Alaska Peninsula, Boggs et al. (2003) described two willow types of dry to mesic sites that are related to Unalaska, the "*Salix barclayi*/*Calamagrostis canadensis* Plant Association" and the "*Salix barclayi*/Mixed Herbceous Plant Association." For southeast Alaska, Shephard (1995) described several *Salix barclayi* thickets for the Yakutat Foreland. Of these, the type most similar to Unalaska willow thicket is the "*Salix barclayi*/mixed herb Community Type," but the southeast Alaska type occurs in different habitats, namely flood plains, distal outwash, and uplifted tidal flats. In the Copper River Delta and also in southeast Alaska, Boggs (2000) described a similar type, the "*Salix barclayi*/mixed herb Community Type" associated with dunes and levees of outwash plains. Del Moral and Watson (1978) report *S. barclayi* thickets in the Stikine Flats of southeast Alaska. Despite the common occurrence of *S. barclayi* thickets in Alaska, Hultén (1960) states there is no corresponding occurrence in eastern Asia.

Alnus viridis thickets occur throughout the Alaska Peninsula (Talbot et al. 2005) but, for the most part, are absent in the Aleutian Islands until they appear on Kamchatka (Hultén 1960).

Syntaxonomical position of the plant communities

The *Honckenya* beach meadow (RG 5) and *Elymus* dune meadow (RG 6) are assigned to the well established circumboreal alliance Honckenyo–Elymion Tx 1966 (Elymetalia arenarii Br.-Bl. et Tx 1943, Honckenyo – Elymetea arenariae Tx 1966). The North American and amphi-Beringian distribution of the Unalaska relevé groups might be expressed at the association level by *Senecio pseudoarnica* as a geographical differential species (cf. Daniëls 1985; Lepping and Daniëls 2007; Talbot et al. 2005).

The wind-exposed *Vaccinium uliginosum – Thamnolia vermicularis* fellfield (RG 7) is assigned to the Carici-Empetretum, a dwarf shrub heath described from higher elevations of Simeonof Island, Shumagin Islands (Daniëls et al. 2004). The association is assigned to the circumpolar arctic – northern alpine alliance Loiseleurio–Diapension (Br.-Bl. et al. 1939) Daniëls 1982 belonging to the arctic-alpine circumpolar Rhododendro-Vaccinietalia Br.-Bl. in Br.-Bl. et Jenny 1926, Loiseleurio-Vaccinietea Eggler ex Schubert 1960. This likely amphi-Beringian association is characterized by both amphi-Beringian and widespread circumpolar arctic-alpine species of wind exposed habitats.

The *Linnaea borealis – Empetrum nigrum* heath (RG 8) is floristically and ecologically similar to the Rubo-Empetretum (Rhododendro–Vaccinietalia Br.-Bl. in Br.-Bl. et Jenny 1926, Loiseleurio–Vaccinietea Eggler ex Schubert 1960) from the mesic lowlands of Simeonof Island, Shumagin Islands (Daniëls et al. 2004). This probable amphi-Beringian association is considered the zonal vegetation of Simeonof Island and the Shumagin Islands.

The *Phyllodoce aleutica* snowbed heath (RG 9) is diagnostically very distinct. However, the syntaxonomical position of this pronounced amphi-Beringian vegetation type within a broader context is still difficult to assess, owing to the lack of sufficient phytosociological knowledge.

The *Athyrium filix-femina – Calamagrostis nutkaensis* meadow (RG 4) and *A. filix-femina – Aconitum maximum* meadow (RG 2), as well as the *Salix barclayi* thickets (RG 3) are floristically strongly related; these probably belong to a same association (group) that is yet to be described. Preliminarily, they are classified within the circumboreal-montane tall forb and related shrub vegetation of the class Mulgedio–Aconitetea Hadac et Klika in Klika et Hadac 1944 (syn. Betulo–Adenostyletea Br.-Bl. et Tx 1943) (cf. Talbot et al. 2005).

Erigeron peregrinus – Thelypteris quelpaertensis meadow (RG 11) is floristically strongly related to the *Phyllodoce aleutica* snowbed heath (RG 9) and might belong to a same higher syntaxon. The syntaxonomy of the snowbed meadow (RG 10) needs further field study.

The Unalaska mire vegetation types could be certainly assigned to the azonal, mainly northern, widespread mire class Scheuchzerio–Caricetea fuscae Tx 1937. However, the present mire type and others from the Aleutian Islands and Eastern Asia, will most likely be grouped into their own syntaxa, differentiated by amphi-Beringian species.

Analysis of geographic distribution patterns of the species showed that 43% of the flora consists of circumpolar species with most of these boreal in distribution, while another 15% is widespread. Most of these species are diagnostic species for widespread higher syntaxa such as the well-known classes Honckenyo–Elymetea, Loiseleurio–Vaccinietea, and Scheuchzerio–Caricetea. The other species likely have potential diagnostic value for mainly lower syntaxonomical units (orders, alliances, associations) that are still to be described from amphi-Beringia or parts of it. More phytosociological research is needed in these areas to verify this hypothesis.

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