

Alpine and Subalpine Vegetation Chronosequences following Deglaciation in Coastal Alaska

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Abstract

Glacial recession is a major process in terrestrial ecosystems of the world and an obvious result of global warming. Here we describe the alpine (above tree line) and subalpine forested and wetland/peatland vegetation chronosequences in Glacier Bay National Park and Preserve, Alaska. We derived the results from three products: (1) deglaciation map of 50,000-, 13,000-, and 1- to 246-year-old (Neoglacial) surfaces; (2) a landcover map; and (3) a plant association classification. For the alpine chronosequence, Neoglacial surfaces are dominated by the tall shrub (>1.5 m) (*Alnus* and *Salix*), dwarf shrub (<0.1 m) (*Salix* and *Dryas*), and mesic herbaceous landcover classes. These landcover classes also dominate the 13,000- and 50,000-year-old surfaces but dwarf shrub dominance changes to ericaceous. The subalpine forested chronosequence consists of *Populus balsamifera* ssp. *trichocarpa* and *Picea sitchensis* classes dominating the mid- and late-seral Neoglacial surfaces, then *Tsuga mertensiana* and *Picea sitchensis* classes dominating the 13,000- and 50,000-year-old surfaces. Wetlands/peatlands are rare on the Neoglacial and 13,000-year-old surfaces but common on the 50,000-year-old surface. *Alnus* is rare on the 50,000-year-old surface yet common on the 13,000-year-old surface and, we speculate, is a relict from the end of the Pleistocene.

Introduction

The recession of glaciers and the resulting exposure of new land is a major process in terrestrial ecosystems of the world and one of the most obvious results of global warming. In Glacier Bay National Park and Preserve, Alaska, glacial recession exposes significant areas to species colonization and results in rapid species and structural turnover (Milner et al., 2007). These dramatic ecosystem scale changes provide challenges for the conservation of plant species and ecosystem diversity. Critical empirical information for conservation biology includes species lists, plant association descriptions, and understanding their seral response to disturbance. To this end, numerous government agencies and organizations (U.S. Department of Interior National Park Service, NatureServe, The Nature Conservancy) gather and synthesize this conservation information to identify species and ecosystems of conservation concern and to protect them from extinction.

Studies of the low-elevation vegetation succession in Glacier Bay have a long history and are critical to our understanding of ecology. Cooper (1923, 1939) initially studied recently deglaciated low-elevation surfaces followed by others (Crocker and Major, 1955; Lawrence et al., 1967; Worley, 1975; Chapin et al., 1994; Fastie, 1995). However, they did not describe alpine and subalpine vegetation succession. In nearby areas, however, various studies described alpine and subalpine vegetation but not within a seral context (Martin et al., 1995; DeVelice et al., 1999). The general vegetation zones described include mountain hemlock (*Tsuga mertensiana*) and Sitka spruce (*Picea sitchensis*) dominating the subalpine (defined as the biotic zone immediately below tree line), intermixed with tall shrubs (primarily *Alnus viridis* ssp. *sinuata*),

and peatlands. Moving upslope, the alpine zone (the biotic zone above tree line) starts with tall shrubs, primarily *Alnus viridis* ssp. *sinuata* and *Rubus spectabilis*. These shrubs are commonly mosaicked with mesic herbaceous meadows made up of a diverse array of graminoids or forbs. Common species include *Calamagrostis canadensis*, *Chamerion angustifolium*, and *Nephrophyllidium crista-galli*. Further upslope, dwarf shrubs dominate followed by rock, bare ground, or glaciers. Typical dwarf shrubs include *Cassiope mertensiana*, *Luetkea pectinata*, and *Vaccinium uliginosum*.

Here we describe the alpine and subalpine vegetation chronosequences following deglaciation in Glacier Bay National Park and Preserve, Alaska (Fig. 1). We take a phytosociological approach to describe the chronosequence, emphasizing the classification and mapping of landcover classes and plant associations as a basis for understanding environmental relationships. The deglaciated surface ages range from 1 to 50,000 years ago including a glacial refugia free from ice for approximately 50,000 years, surfaces deglaciated at the end of the Pleistocene approximately 13,000 years ago, and Neoglacial surfaces deglaciated from 1 to 246 years ago. In the discussion section we also evaluate conservation biology concerns.

Methods

STUDY AREA

The alpine and subalpine study area includes all land above 500 m elevation in Glacier Bay National Park and Preserve and encompasses 456,830 ha of which 8% is vegetated, 56% is glacier,

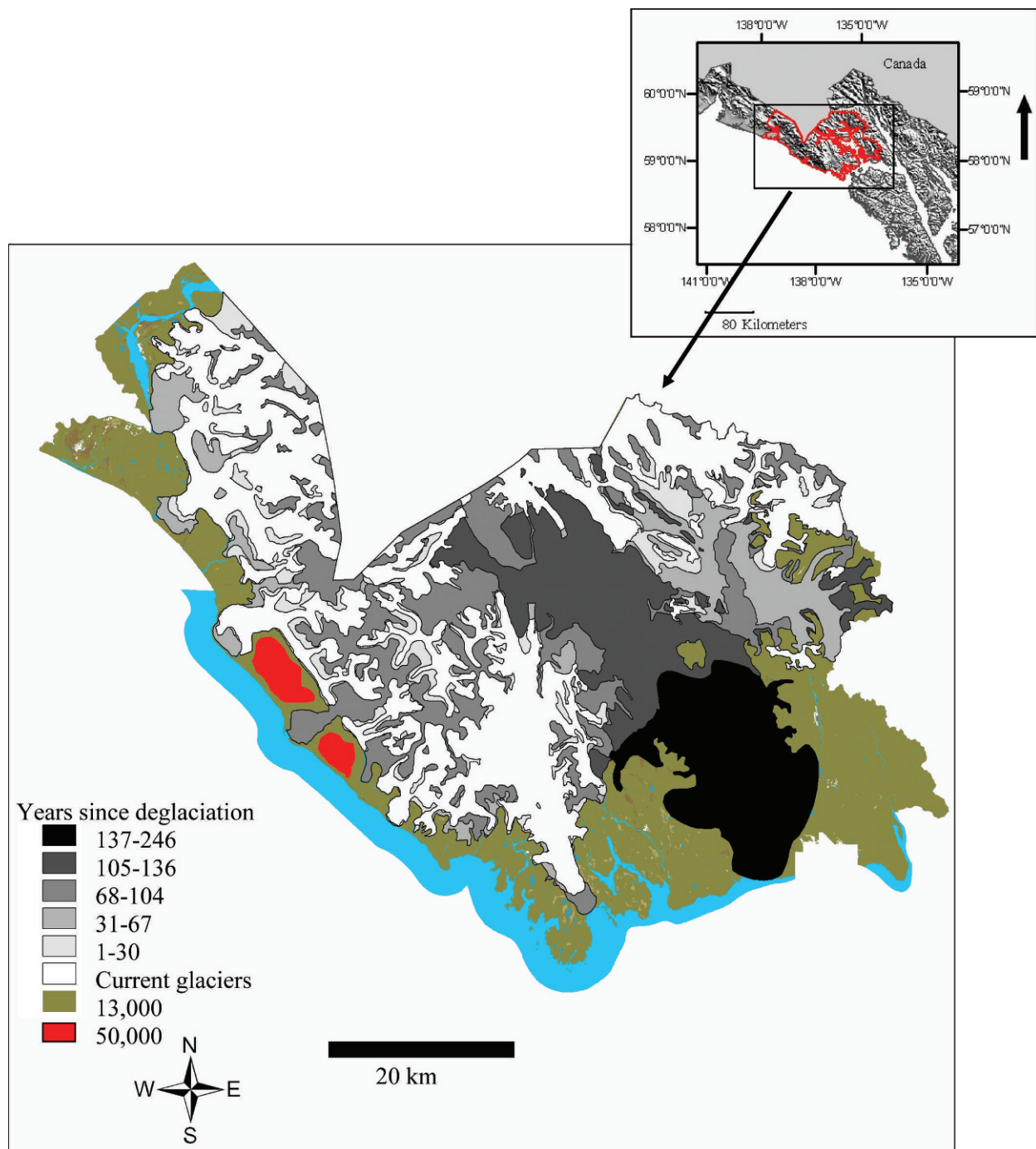


FIGURE 1. Map of the age since deglaciation (Mann, 1983; Manley and Kaufman, 2002). For display purposes, we included all lands within the Glacier Bay National Park and Preserve.

and 36% is rock-bare ground (Fig. 2). The Park is a complex of mountain ranges, coastal fjords, and glaciers. On the outer coast, a low-angle piedmont rises from the Pacific Ocean, culminating in low-elevation peaks (1200 m). Behind the low-elevation peaks is a long straight valley beyond which rise tall mountains up to 4663 m. Throughout the mountain complex are glacially carved valleys and fjords, ice fields, and their exit glaciers commonly extending to sea level. The largest of the valley/fjord systems is Glacier Bay extending 100 km and the second largest is a valley largely filled by the Brady Glacier.

The study area's geology is complex and includes marine mudstones, metasediments, carbonates, metamorphosed volca-

nic, and extensive granitic bodies (Brew, 2008). In general, the prevalence of igneous rocks and degree of metamorphism all increase from southeast to northwest in the study area. The geomorphology is predominantly glacial till, moraines, alluvial fans, and colluviums (Mann, 1983; Manley and Kaufman, 2002).

This area has experienced three major glacial advances in the past 80,000 years (Fig. 1). The earliest ended approximately 50,000 years ago and covered all currently exposed lands in the study area (Manley and Kaufman, 2002). The next advance ended approximately 13,000 years ago and covered nearly all currently exposed land except for two refugia between 25 km² and 60 km² in

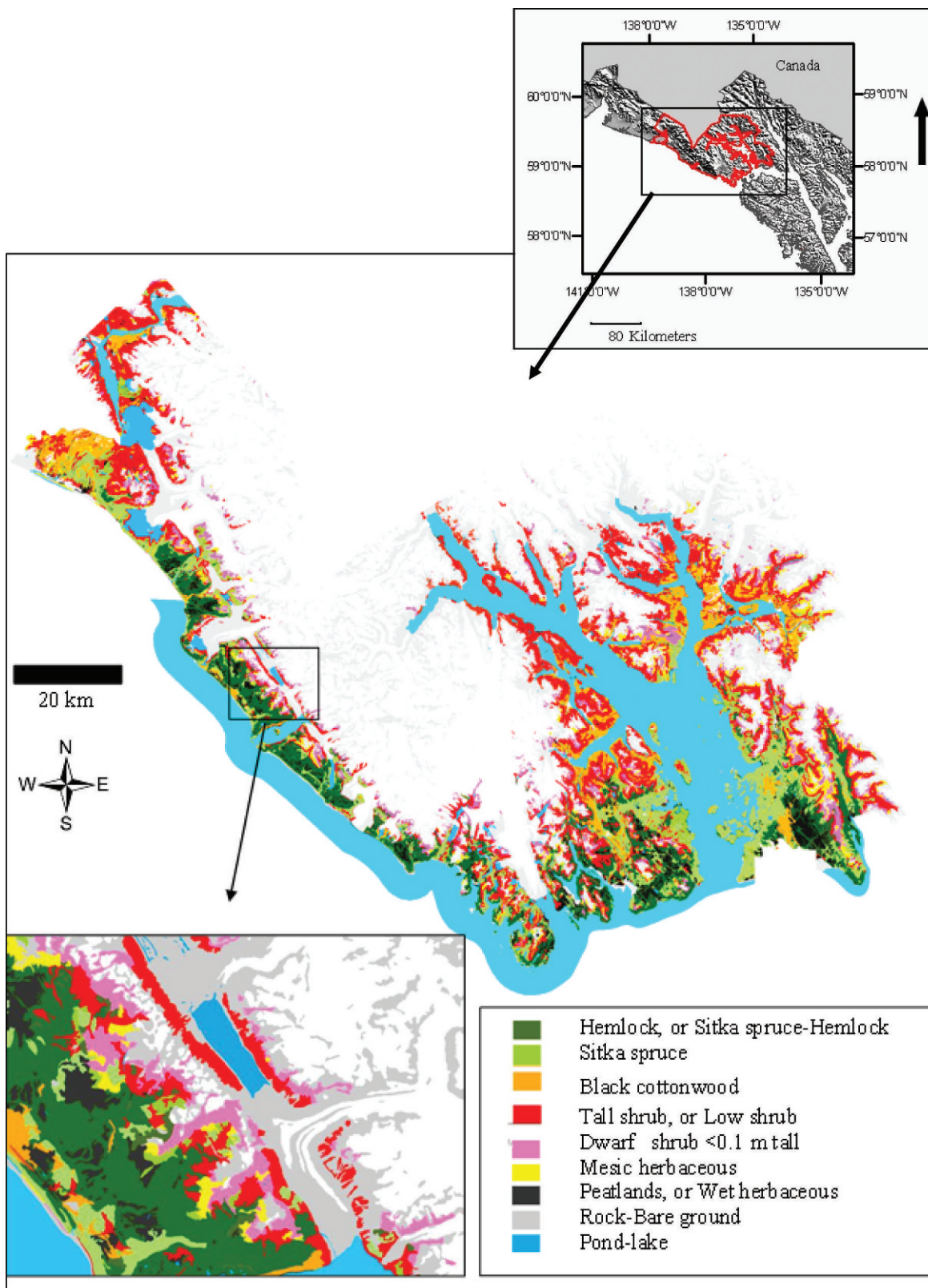


FIGURE 2. Landcover map for Glacier Bay National Park and Preserve. For display purposes, we included all lands within the Park, and reduced the 19 landcover classes for the entire park to 9 general classes.

size on either side of Lituya Bay (Heusser, 1960, Mann, 1983). The last advance ended 246 years ago that filled many of the fjords throughout the study area, including that of Glacier Bay. By 1750 the Glacier Bay glacial terminus began to retreat and by 1879 the retreat had exceeded 60 km (Molnia, 1986). The recession

continued for a total of 100 km up to the present day except for minor advances by some glaciers, and glacier termini also receded on the outer coast although to a far lesser extent.

The Neoglacial, 13,000-year-old and 50,000-year-old surfaces are all dominated by typical glaciated mountain terrain consisting

of valleys, colluvial slopes, moraines, cirques, and rounded hills. The Neoglacial surface elevation ranges from 500 m to 4663 m, the upper slopes being well above elevations that support vegetation. In contrast, the 13,000-year-old surface elevation ranges from 500 m to approximately 1300 m, and the 50,000-year-old surface extends only up to 1,000 m and nearly the entire surface is vegetated.

In general, the region has a maritime climate with cool summers and mild wet winters at the lower elevations. Annual precipitation at the closest weather station (Gustavus) is 184 cm and monthly precipitation varies between 8 and 30 cm with the wettest months between September and January (National Oceanic and Atmospheric Administration, 1990). Orographic effects create rain shadows and areas of increased precipitation throughout the study area. In addition, snow depth and persistence varies significantly across the study area. Maximum and minimum temperatures at sea level rarely exceed 24 °C and -23 °C, and the mean annual temperature is near 5 °C (Loewe, 1966).

SURFACE AGE MAP

In order to describe the alpine and subalpine chronosequences, we took the approach of producing: (1) a map of the age since deglaciation (referred to as surface age map), (2) a landcover map, and (3) a plant association classification.

We developed a digitized map of the surface age map of the entire Park (Fig. 1) from Manley and Kaufman's (2002) digitized map of the 1- to 246-year-old surface, which divided the surface into 1- to 30-, 31- to 67-, 68- to 104-, 105- to 136-, and 137- to 246-year-old segments. We also digitized a 50,000-year-old glacial refugia mapped by Mann (1983). We delineated lands falling outside of the 0- to 246-year-old and 50,000-year-old glaciated surfaces as deglaciated 13,000 years ago, although minor inclusions of other aged surfaces occur on the outer coast (Engstrom et al., 2000).

Based on field observations, we defined alpine and subalpine as occurring above 500 m elevation. We digitally delineated the alpine and subalpine zone by heads-up digitizing a 500-m-elevation line using ArcView and 1:63,360 digital raster graphics.

LANDCOVER MAP

We also developed a landcover map for the entire Park, from sea level to the highest elevation. The general steps taken were to (1) develop a field sampling design, (2) field sample landcover classes, and (3) photo interpret the landcover classes. Boggs et al. (2008) provided more detailed methods than are given below.

Our sampling goal was to sample a minimum of three transects for each surface age. We systematically selected transect locations by using a grid size that ensured placement of 33 transects across the vegetated portion of the study area on 1:63,360-scale topographic maps, and placed a transect at each grid intersection. This method did not completely capture the needed three transects per surface age. Consequently, we systematically added eight additional transects to fill these gaps for a total of 41 for the study area.

In the mountains, a transect stretched from ridge top to valley bottom up to 3 km long. We delineated transects on 1996 1:65,000 color infrared aerial photos. Along each transect we delineated a subsample of polygons with distinct landcover signatures. We collected aerial and ground-plot data along each transect during the summer of 2001. We used a total of 56 preliminary landcover

classes in the field that, in general, followed *The Alaska Vegetation Classification* system (Viereck et al., 1992). We also revisited the study area for ten days in 2003 and 2005 to evaluate the accuracy of the landcover classes and plant association classification.

Transportation was by helicopter or boat. At each pre-delineated polygon along the transect we recorded percent canopy cover of the dominant species (Brown, 1954; Daubenmire, 1959), dominant species' height, and total percent cover of the following categories: needleleaf trees, deciduous trees, shrubs >1.5 m tall, shrubs 1.5–0.1 m, shrubs <0.1 m, graminoids, forbs, bryophytes, water, bare soil, and bedrock. The total percent for all the categories summed to 100%. Other information included landscape type (e.g. floodplain, cirque), GPS coordinates, photographs, and hydrologic regime (dry, mesic, wet, and aquatic).

After collection of the field data, we reduced the 56 preliminary landcover classes to 19 (for all elevations) based on reviews of the data, air photo interpretation resolution issues, and ecological considerations. We interpreted landcover classes on the 1996 1:65,000 color infrared aerial photos with a stereoscope, and used our field information and LandSat imagery to assist in the air photo interpretation. The minimum mapping unit for wetland and non-wetland landcover classes was 2 and 8 ha. Photo-interpretation procedures conformed to standard conventions and protocols developed by the National Wetlands Inventory for cartography and digitizing (U.S. Fish and Wildlife Service, National Wetlands Inventory, 1995).

The next step was to determine the area of each landcover class within the alpine and subalpine and the seven surface ages (i.e. 1–30, 31–67, 68–104, 105–136, 137–246, 13,000, and 50,000 years old). For this determination, we used the three ARCGIS shape files; alpine and subalpine shape file (determined using the 500 m elevation line), landcover map of the entire Park, and surface age map. Using ARCGIS, we deleted all land below 500 m by clipping the landcover map shape file to the alpine and subalpine shape file. Then, using only the alpine and subalpine portion of the landcover map, we intersected it with our surface age shape file. We then calculated the area of each landcover class within each of the seven surface ages.

PLANT ASSOCIATIONS

The purpose of collecting ground plot data was to provide information to define and describe plant associations and, also, to help develop the landcover map. In 2001 we sampled plots at all elevations along the same transects used for development of the landcover map. Selection of associations to sample was similar to the approach termed "subjective sampling without preconceived bias" as described by Mueller-Dombois and Ellenberg (1974). We based site selection on homogeneous vegetation, and we did not choose the sites with regard to their position in any classification, extant or envisioned. For most plots we also described in what map class it occurred and its general elevation range (low, subalpine, or alpine).

We used a single 10 × 10 m plot to sample each association, and only sampled sites with >10% total cover of vegetation. Taxonomy follows the Integrated Taxonomic Information System (retrieved 2008 from the Integrated Taxonomic Information System online database, <<http://www.itis.gov>>). We ocularly estimated the canopy cover for each species, and the canopy height and strata for the dominant species. Plant specimens not identified in the field were collected and identified in the office or at the University of Alaska Museum Herbarium. Site variables included slope, aspect, landform, and hydrologic regime. We used a soil probe to determine depth of soil peat; A, B, and C horizons; depth to water; and we also

determined pH at 10 cm deep. Other variables included GPS coordinates, photos, and disturbance comments.

We defined associations using the ground plots collected in 2001 and plots collected by the National Park Service in 1985. Two plant association classifications describing mature forest (Martin et al., 1995) and low-elevation wetland/peatland (Shepherd, 1995) associations existed for adjacent regions. We consequently used these classifications to key those plots that fit the previously defined associations. These classifications did not, however, define alpine associations or early- and mid-seral subalpine forest associations.

We classified the remaining plots into associations using a stepwise procedure of successive approximations (Pfister and Arno, 1980). We created association tables of the preliminary dominance-type groupings by using the species and cover data. We used detrended correspondence analysis (Hill and Gauch, 1980) and hierarchical clustering (average linkage, percentage difference, and dissimilarity) for further approximations of plot groupings. Naming of the association followed the frequently used system of a binomial with the dominant over-story species separated from the dominant or diagnostic indicator of the undergrowth by a slash (Mueller-Dombois and Ellenberg, 1974).

We also assigned a surface age to each ground plot using the surface age map. We used this information to summarize the ground plot information—including soils and species—in a chronosequence from young to old. Late-seral communities were determined using various criteria. The plots occurred on the 13,000- or 50,000-year-old surfaces, the sites were stable exhibiting no signs of mass wasting or blow-down, forested plots were old growth, and wetland plots had significant peat development.

ORDINATION AND GROUP TESTS

Using ground plot data from all elevations, we used nonmetric multidimensional scaling (NMS) with Sørensen distance to express the relationship of the ground plots (species list and cover) to surface age, and to evaluate the relationship of landcover classes to surface age (McCune and Mefford, 2006). We assessed the relationship of environmental variables to the ordination axes by using overlays (for categorical variables) and Pearson correlations (for quantitative variables). Environmental variables included in the analysis were elevation, surface age (natural log-transformed midpoints of the 7 age classes), surface age category (Neoglacial, 13,000-year-old, and 50,000-year-old surfaces), moisture category (mesic or wet), and slope. To reduce the heterogeneity within the data set, we removed aquatic and wet herbaceous plots and deleted rare species that occurred three or fewer times in the data set. To equalize the importance of common and uncommon species, we relativized species cover by the maximum value for each species.

We also used multiresponse permutation procedures (MRPP) with Sørensen distance to test the hypothesis that there was no difference between plots grouped by surface age (McCune and Mefford, 2006). The effect size (A) describes the chance-corrected within-group agreement. When all items are identical within groups, $A = 1$; when with-group heterogeneity exceeds that expected by chance, $A = 0$.

Results

For clarity within the text, we used plant common names when referring to landcover classes and scientific names when referring to plant associations.

LANDCOVER MAP

We based the final landcover classes (from sea level to the highest elevation) on reviews of the aerial polygons ($n = 197$) and the ground plot data ($n = 211$) (Fig. 2 and Table 1). Of the 211 ground plots, 73 occurred in the alpine and subalpine and 138 plots below 500 m elevation. Boggs et al. (2008) provide full landcover class descriptions, aerial and ground plot locations, digital landcover map, and a qualitative review of landcover class accuracy. Landcover classes that had accuracy problems included the two peatland classes (peatland, dwarf tree; and peatland, shrubs) that were often confused with each other during air photo interpretation. In addition, the wet herbaceous class was typically a peatland and often occurred as a mosaic within the other peatland types. To reduce this confusion we generally treat these three classes as a group (referred to as “wetland/peatland”) within the text. There was also confusion of young stands of black cottonwood (*Populus balsamifera* ssp. *trichocarpa*) with the tall shrub (>1.5 m) class, and the Sitka spruce class being confused with the Sitka spruce–black cottonwood ($>25\%$ cover) class.

ORDINATION AND GROUP TESTS

To reduce the heterogeneity within the data set, we removed aquatic and wet herbaceous plots from the analysis. For the three-dimensional ordination, model stress was 19.4 and instability was <0.0001 . The axes extracted were stronger than those expected by chance ($P = 0.004$) based on a Monte Carlo test. The first three axes accounted for 37% of the variance in the data set, with Axis 2 and Axis 3 contributing the majority (15% and 16%). Surface age was positively correlated with Axis 2 ($r = 0.76$), and elevation was negatively correlated with Axis 3 ($r = -0.61$). An overlay of landcover classes on the ordination showed that the landcover classes were grouped according to the environmental gradients displayed by the ordination axes (Fig. 3). At this coarse scale, the ordination generally expressed and supported the plot groupings used to define the landcover classes and plant associations.

ALPINE AND SUBALPINE DELINEATION

The alpine and subalpine zone, of course, did not precisely correspond to the 500 m elevation line. Alpine begins at various elevations due to different environmental conditions. To evaluate the level of overlap of alpine landcover classes into the lower elevations we selected two landcover classes [dwarf shrub (<0.1 m) and mesic herbaceous] that should have a high fidelity for the alpine on the 13,000- and 50,000-year-old surface ages. We did not use the Neoglacial surfaces in the error evaluation because it was not clear as to whether forests on the Neoglacial surfaces were seral to forest or alpine vegetation. The *a priori* 500 m elevation lines were adequate for separating the alpine vegetation from the lower elevations. The combined dwarf shrub and mesic herbaceous class cover at lower elevations was 5% on the 13,000-year-old surface and 2% on the 50,000-year-old surface, showing little overlap of alpine classes into the low elevations.

For the subalpine, *Tsuga mertensiana* associations are generally considered subalpine in Alaska with *Tsuga herterophylla* dominating lower elevations (Viereck and Little, 1972). Eleven of our 12 total *Tsuga mertensiana* plots for the Park occurred above 500 m elevation. In addition, seven of the *Tsuga mertensiana* plots were either treed krummholz vegetation or subalpine species (*Cassiope* spp., *Nephrophyllidium crista-galli*) dominated by the understory (Table 3).

TABLE 1

Percent cover of landcover class on the subalpine-alpine (above 500 m elevation) landscape per surface age. The vegetated classes are given as a percentage of the total vegetated surface, whereas the pond-lake class and rock-bare ground class are the percent of the study area not including the glacier class. We arranged the vegetated classes in a chronosequence from young to old.

Dominant species–lifeform	% cover species–lifeform	Surface age—Years before present					
		1–30	31–67	68–104	105–246*	13,000	50,000
Alpine classes							
Mesic herbaceous		5	8	10	21	21	21
Dwarf shrub (<0.1 m)	>25	43	34	37	28	32	16
Low shrub (0.1–1.5 m)	>25	<1	1	5	7	1	—
Tall shrub (>1.5 m)	>25	38	38	36	37	33	17
Subalpine forest classes							
Black cottonwood	>10	<1	2	3	1	<1	—
Sitka spruce-black cottonwood	10–25	—	<1	3	<1	<1	—
Sitka spruce-black cottonwood	>25	<1	—	—	<1	<1	—
Sitka spruce	10–25	3	6	2	2	2	4
Sitka spruce	>25	7	12	5	4	5	6
Hemlock or Sitka spruce-hemlock	>25	1	—	—	—	5	19
Wetland/peatland classes							
Aquatic herbaceous	>10	—	—	<1	—	<1	—
Wet herbaceous	>25	<1	<1	1	<1	<1	4
Peatland, shrub	>25	—	—	—	—	<1	2
Peatland, dwarf tree	>10	—	—	—	—	<1	11
Total % vegetated surface		8	47	12	32	56	91
Rock-Bare Ground		92	53	88	68	44	9
Pond-lake		<1	<1	<1	<1	<1	<1
Total vegetated surface (ha)		3769	3122	2158	5013	19,340	1536

* The 137–246 surface had little area (176 ha) and, consequently, we collapsed it with the 105–136 surface.

PLANT ASSOCIATIONS

For all elevations within the Park, we defined 70 plant associations using the 211 ground plots. Martin et al. (1995) and Shephard (1995) had previously described 45 of these associations from adjacent areas, but had not described the remaining 25 associations. These 25 newly described associations were primarily alpine types and early- and mid-seral subalpine forests. Boggs et al. (2008) provided full descriptions of each association. Tables 2 and 3 include all plant associations sampled above 500 m elevation, plus plant associations we observed above 500 m elevation but sampled the actual plot below 500 m (the plots are represented by * in the table).

The rarity of plots on the young Neoglacial surfaces (Tables 2 and 3) was because we placed transects systematically. Consequently, on the sparsely vegetated early-seral deglaciated surfaces (8% vegetated on the 1- to 30-year-old surface) transects often did not intersect vegetation above 500 m elevation (Table 1). This was not true at elevations below 500 m where vegetation quickly invaded the sites (56% on the 1- to 30-year-old surface).

ALPINE CHRONOSEQUENCES

In the following sections we describe the alpine (above tree line) and subalpine vegetation (forest and wetland/peatlands) chronosequences using the surface age map, landcover map, and plant association classification. In Table 1, we give the vegetated classes as a percentage of the total vegetated surface, whereas the pond-lake and rock-bare ground classes are the percent of the study area not including the glacier class. On the early-seral Neoglacial surfaces, it was not possible to determine what vegetation was seral to any specific late-seral vegetation on the 13,000- or 50,000-year-old surfaces. Once trees established or

wetlands developed we placed them in their respective forest and wetland/peatland chronosequence descriptions. Otherwise, we speculate that most of the early-seral classes and associations could be seral to alpine, forest, or wetland/peatland classes and associations.

The alpine chronosequence is as follows. The immediate post-melt substrate was generally bedrock or unstable morainal and glacial till deposits. The first associations to colonize the sites were *Dryas drummondii* and *Salix* spp./early seral that supports depauperate *Salix alaxensis*, *S. commutata*, *S. barclayi*, *S. sitchensis*, *S. arctica*, and *Shepherdia canadensis* (Table 2). This was followed by tall shrub associations dominated by *Alnus viridis* ssp. *sinuata* and *Salix sitchensis*. Additional associations occurred on the older Neoglacial surfaces (105- to 136- and 137- to 246-year-old surfaces) including the mesic herbaceous association *Geranium erianthum*–*Lupinus nootkatensis*–*Sanguisorba canadensis*, the dwarf shrub associations *Salix arctica*, *S. reticulata* ssp. *reticulata*, and *Vaccinium uliginosum*, and the low-shrub (0.1–1.5 m) association *Shepherdia canadensis* (Table 2).

The dwarf shrub and tall shrub landcover classes dominated the vegetated surface of all the Neoglacial surface ages (Table 1). The dwarf shrub class ranged from 28% to 43% and the tall shrub class remained relatively constant (36% to 38%). The low-shrub class increased from <1% to 7% and the mesic herbaceous class increased from 5% to 21%. We collapsed the 137- to 246-year-old surface landcover data with the 105- to 136-year-old landcover data because the 137- to 246-year-old surface had only 176 ha while all the other surface ages had greater than 1536 ha.

The dwarf shrub and tall shrub classes also dominated the 13,000-year-old surface. However, a dramatic shift in plant association species dominance occurred. Various *Salix* species and *Dryas drummondii* dominated the Neoglacial dwarf shrub

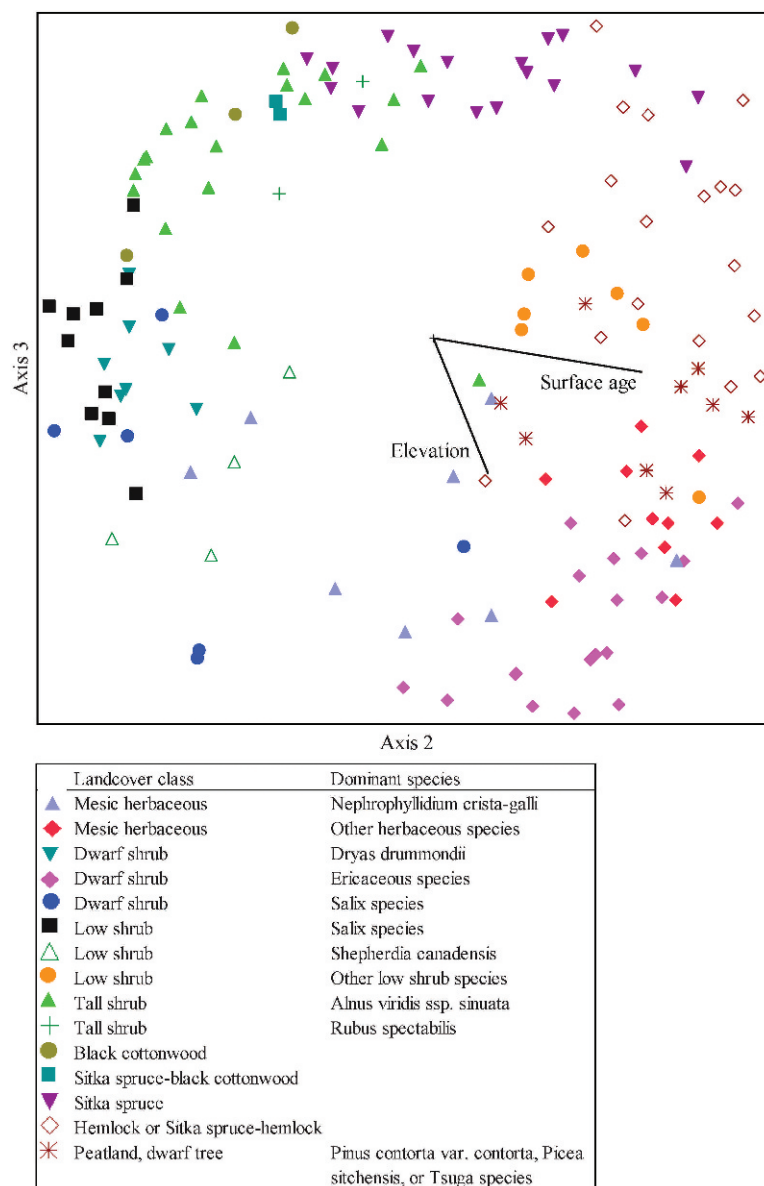


FIGURE 3. Nonmetric multidimensional scaling ordination of 145 plots across the study area with landcover class displayed as the grouping variable. Vectors show the direction and strength of correlation of environmental variables. Surface age is positively correlated with Axis 2 ($r = 0.76$), and elevation is negatively correlated with Axis 3 ($r = -0.61$). To reduce the heterogeneity within the data set, we removed aquatic and wet herbaceous plots and deleted rare species that occurred three or fewer times in the data set.

associations whereas ericaceous species (*Cassiope mertensiana*, *Phyllodoce aleutica*, *Empetrum nigrum*, *Harrimanella stelleriana*, and *Vaccinium uliginosum*) and *Luetkea pectinata* dominated the 13,000- and 50,000-year-old surfaces. The *Salix reticulata* ssp. *reticulata* and *Vaccinium uliginosum* associations occurred on both the Neoglacial and 13,000-year-old surfaces.

For the tall shrub class, various *Alnus viridis* ssp. *sinuata* associations were common on both the Neoglacial and 13,000-year-old surfaces. But, as with the dwarf shrub associations, the *Salix* species component was common on the Neoglacial surface but rare on the 13,000-year-old surface. We also first recorded the tall shrub *Rubus spectabilis* association on the 13,000-year-old surface. The low-shrub class was rare (1%) on the 13,000-year-old surface, and we first recorded the low shrub *Elliotia pyroliflorus* association on the 13,000-year-old surface.

The mesic herbaceous class covered 21% of the vegetated surface on the 13,000-year-old surface (Table 1). For all surface ages we only defined two mesic herbaceous associations. *Nephrophyllidium crista-galli* occurred only on the 13,000- and 50,000-year-old surfaces. However, the *Geranium erianthum*–*Lupinus nootkatensis*–*Sanguisorba canadensis* association occurred on the Neoglacial and 13,000-year-old surfaces. We expected this

because it colonizes early-seral sites—such as alluvial fans—and also occurs on stable alpine sites throughout southern coastal Alaska (DeVelice et al., 1999; Boggs et al., 2008).

The mesic herbaceous, dwarf shrub and tall shrub landcover classes were common on the 50,000-year-old alpine surface (Table 1). The mesic herbaceous class cover remained the same (21%) between the 13,000- and 50,000-year-old surfaces. The dwarf shrub class changed from 32% to 16% and the tall shrub class changed from 33% to 17% cover. *Elliotia pyroliflorus* was the only low-shrub association sampled, and *Rubus spectabilis* was the only tall shrub association sampled. We did not sample or observe *Alnus viridis* ssp. *sinuata* associations on this surface age.

SUBALPINE FOREST AND WETLAND/ PEATLAND CHRONOSEQUENCE

The subalpine forest chronosequence is as follows. In Glacier Bay proper—not including the outer coast—we speculate that newly deglaciated surfaces seral to subalpine forests were colonized by the same plant associations and landcover classes given in the alpine chronosequence (Tables 1 and 2). We occasionally found

TABLE 2

Number or occurrence of plant association plots on the alpine landscape per surface age. We arranged the associations in a chronosequence from young to old.

Landcover class	Plant associations	Surface age—Years before present						
		1–30	31–67	68–104	105–136	137–246	13,000	50,000
Dwarf shrub (<0.1 m)	<i>Dryas drummondii</i>	*	*	*	*	—	—	—
Low shrub (0.1–1.5 m)	<i>Salix</i> spp./Early seral	*	1	—	1	—	—	—
Tall shrub (>1.5 m)	<i>Alnus viridis</i> ssp. <i>sinuata</i>	—	*	*	*	1	—	—
Tall shrub (>1.5 m)	<i>Alnus viridis</i> ssp. <i>sinuata</i> – <i>Salix sitchensis</i>	—	*	1	1	1	1	—
Tall shrub (>1.5 m)	<i>Salix sitchensis</i>	—	*	—	—	—	—	—
Mesic herbaceous	<i>Geranium erianthum</i> – <i>Lupinus nootkatensis</i>	—	—	—	1	—	5	—
Low shrub (0.1–1.5 m)	<i>Shepherdia canadensis</i>	—	—	—	*	*	—	—
Dwarf shrub (<0.1 m)	<i>Salix arctica</i>	—	—	—	1	—	—	—
Dwarf shrub (<0.1 m)	<i>Salix reticulata</i> ssp. <i>reticulata</i>	—	—	—	—	1	1	—
Dwarf shrub (<0.1 m)	<i>Vaccinium uliginosum</i>	—	—	—	—	1	2	1
Mesic herbaceous	<i>Nephrophyllidium crista-galli</i>	—	—	—	—	—	8	2
Dwarf shrub (<0.1 m)	<i>Cassiope mertensiana</i>	—	—	—	—	—	3	—
Dwarf shrub (<0.1 m)	<i>Cassiope mertensiana</i> – <i>Luetkea pectinata</i>	—	—	—	—	—	5	2
Dwarf shrub (<0.1 m)	<i>Cassiope mertensiana</i> – <i>Phyllodoce aleutica</i>	—	—	—	—	—	1	—
Dwarf shrub (<0.1 m)	<i>Empetrum nigrum</i>	—	—	—	—	—	1	1
Dwarf shrub (<0.1 m)	<i>Harrimanella stelleriana</i>	—	—	—	—	—	1	—
Dwarf shrub (<0.1 m)	<i>Phyllodoce aleutica</i> – <i>Luetkea pectinata</i>	—	—	—	—	—	1	1
Low shrub (0.1–1.5 m)	<i>Elliottia pyroliflorus</i>	—	—	—	—	—	5	1
Low shrub (0.1–1.5 m)	<i>Menziesia ferruginea</i>	—	—	—	—	—	1	—
Tall shrub (>1.5 m)	<i>Alnus viridis</i> ssp. <i>sinuata</i> /Athyrium filix-femina	—	—	—	—	—	1	—
Tall shrub (>1.5 m)	<i>Alnus viridis</i> ssp. <i>sinuata</i> /Phyllodoce aleutica	—	—	—	—	—	*	—
Tall shrub (>1.5 m)	<i>Alnus viridis</i> ssp. <i>sinuata</i> /Rubus spectabilis	—	—	—	—	—	1	—
Tall shrub (>1.5 m)	<i>Rubus spectabilis</i>	—	—	—	—	—	1	1

* We observed these associations above 500 m elevation but we sampled the plots below 500 m.

Picea sitchensis, *Populus balsamifera* ssp. *trichocarpa*, and *Tsuga mertensiana* seedlings on the youngest surface ages, but *Populus balsamifera* ssp. *trichocarpa* associations did not develop until the 31- to 67-year-old surface, and *Picea sitchensis* associations until the 68- to 104-year-old surface (Table 3). We did not, however, record *Tsuga mertensiana* associations or upper canopy trees until the 13,000-year-old surface. The slow development of *Populus balsa-*

mifera ssp. *trichocarpa* and *Picea sitchensis* stands in Glacier Bay was primarily due to the newly deglaciated sites being far from established forests and thus a seed source (Fastie, 1995). In contrast, on the outer coast the newly deglaciated sites were near established forests and thus a seed source and—based on the landcover map data—*Populus balsamifera* ssp. *trichocarpa* and *Picea sitchensis* associations colonized some of the newly deglaciated sites (Table 1).

TABLE 3

Number or occurrence of plant association plots on the subalpine (forest and wetland/peatland) landscape per surface age. All of the alpine neoglacial associations given in Table 2 are potentially seral to these subalpine associations. We arranged the associations in a chronosequence from young to old.

Landcover class	Plant associations	Surface age—Years before present						
		1–30	31–67	68–104	105–136	137–246	13,000	50,000
Forest associations								
Black cottonwood	<i>Populus balsamifera</i> ssp. <i>trichocarpa</i>	—	*	—	1	1	—	—
Sitka spruce	<i>Picea sitchensis</i> /Bryophyte	—	—	*	*	*	*	—
Sitka spruce	<i>Picea sitchensis</i> / <i>Alnus viridis</i> ssp. <i>sinuata</i>	—	—	—	*	*	*	—
Hemlock-spruce	<i>Picea sitchensis</i> - <i>Tsuga mertensiana</i> / <i>Vaccinium</i> **	—	—	—	—	—	1	*
Hemlock-spruce	<i>Tsuga mertensiana</i> / <i>Cassiope</i>	—	—	—	—	—	1	—
Hemlock-spruce	<i>Tsuga mertensiana</i> / <i>Elliottia pyroliflorus</i> / <i>Cassiope</i>	—	—	—	—	—	1	1
Hemlock-spruce	<i>Tsuga mertensiana</i> / <i>Krummholz</i>	—	—	—	—	—	3	—
Hemlock-spruce	<i>Tsuga mertensiana</i> / <i>Vaccinium ovalifolium</i>	—	—	—	—	—	1	*
Hemlock-spruce	<i>Tsuga mertensiana</i> / <i>Vaccinium</i> **/ <i>Nephrophyllidium</i> **	—	—	—	—	—	1	—
Wetland/peatland associations								
Wet herbaceous	<i>Carex pyrenaica</i> ssp. <i>micropoda</i>	—	—	—	—	—	1	—
Wet herbaceous	<i>Eriophorum angustifolium</i>	—	—	—	—	—	2	—
Wet herbaceous	<i>Nephrophyllidium crista-galli</i> / <i>Trichophorum cespitosum</i>	—	—	—	—	—	1	*
Wet herbaceous	<i>Trichophorum cespitosum</i>	—	—	—	—	—	1	—
Peatland, dwarf tree	<i>Picea sitchensis</i> / <i>Sphagnum</i>	—	—	—	—	—	*	*

* We observed these associations above 500 m elevation but we sampled the plots below 500 m.

** *Vaccinium* = *Vaccinium ovalifolium*, and *Nephrophyllidium* = *Nephrophyllidium crista-galli*.

TABLE 4

Soil characteristics on the subalpine-alpine (above 500 m elevation) landscape per surface age.

Soil characteristic	Surface age—Years before present		
	0–246	13,000	50,000
% on bedrock-no over burden	0	2	0
% on mineral soil-no organic layer	40	8	20
% with shallow organic layer over mineral soil	40	77	60
% with peat development	20	13	20
Peat depth \pm SD (cm)*	3.2 \pm 2.8	4.9 \pm 19.1	3.8 \pm 8.6
Range in peat depth (cm)	0 to 5	0 to 86	0 to 19
Number of plots	8	40	5

* The maximum depth of the soil cores was 86 cm and some sites had peat depths greater than 86 cm.

However, the high combined Sitka spruce class cover (10%) on the youngest surface was partially due to overlap error between the landcover map and the surface age map on the outer coast. On the Neoglacial surface, the combined Sitka spruce class cover ranged from 18% to 6%, the black cottonwood class was 3% or less, and the combined Sitka spruce-black cottonwood class cover was also 3% or less.

On the 13,000-year-old surface, *Tsuga mertensiana* and *Picea sitchensis* associations dominated, and *Populus balsamifera* ssp. *trichocarpa* associations were rare or absent (Table 3). Four of the six *Tsuga mertensiana* associations were dominated by typical alpine species in the understory such as *Cassiope* spp. and *Nephrophyllidium crista-galli*. The hemlock or Sitka spruce–hemlock class cover increased from 0 to 5% from the Neoglacial to the 13,000-year-old surface, and cover of the other forested landcover classes remained relatively stable (Table 1).

On the 50,000-year-old surface, *Tsuga mertensiana* and *Picea sitchensis*–*Tsuga mertensiana* associations also dominated (Table 3). The hemlock or Sitka spruce–hemlock class cover increased from 5% on the 13,000-year-old surface to 19%, and the combined Sitka spruce cover remained relatively stable from 7% to 10% (Table 1).

The following is the subalpine wetland/peatland chronosequence. On the Neoglacial surface-age, the aquatic herbaceous class and wet herbaceous class percentage of the vegetated surface ranged from 0% to 1% (Table 1). We did not sample any wetland or peatland associations above 500 m elevation on the Neoglacial surface (Table 3). At lower elevations, however, *Equisetum* species dominated the wetlands. On all surface ages, the pond-lake class remained at <1%.

The wetland/peatland landcover classes were also rare on the 13,000-year-old surface (<1%), but supported numerous wetland/peatland associations. They included *Carex pyrenaica* ssp. *micro-poda*, *Eriophorum angustifolium*, *Nephrophyllidium crista-galli*, *Trichophorum cespitosum*, and *Trichophorum cespitosum* (Table 3).

On the 50,000-year-old surface, the combined cover of the wetland/peatland classes increased from <1% to 17% of the vegetated surface (Table 1). Again, this dramatic increase in the wetland/peatland classes was partially due to the 50,000-year-old surface having little high-elevation landscape. We recorded two wetland/peatland plant associations: *Nephrophyllidium crista-galli*, *Trichophorum cespitosum* and *Picea sitchensis*/Sphagnum.

Of the 37 associations described in this study, seven were restricted to the Neoglacial surfaces, 24 to the 13,000 and

50,000 year-old surfaces and six occurred on both the Neoglacial surfaces and the older surfaces.

SOILS

For soils on the Neoglacial surfaces, we recorded shallow peat development (up to 5 cm) in two of our eight plots (Table 4). The remaining soil profiles were either mineral soil (C horizon) with no organic layer or a shallow organic layer (litter) over mineral soil. For the older surfaces, peat development occurred on 13% to 20% of the plots sampled, and peat depth ranged to 86 cm, the maximum depth of our soil cores. Most of the remaining soil profiles had a shallow organic layer over mineral soil (77% to 60% of plots sampled).

Discussion

To our knowledge, this is the first paper to describe the alpine and subalpine chronosequences following deglaciation for coastal Alaska. For the alpine chronosequence (maximum elevation of our plot data is 1006 m), the early-seral stages are similar to that described for low-elevation (<500 m) landscapes of Glacier Bay (Cooper, 1923, 1939; Crocker and Major, 1955; Lawrence et al., 1967; Worley, 1975; Chapin et al., 1994; Fastie, 1995). In general, both start with *Dryas drummondii*, *Alnus viridis* ssp. *sinuata*, various *Salix* species, and *Shepherdia canadensis*. But this similarity ends by the 68- to 104-year surface age with trees (*Populus balsamifera* ssp. *trichocarpa* and *Picea sitchensis*) invading the lower elevations, and, eventually, *Picea sitchensis* dominating the oldest low-elevation Neoglacial surfaces.

In contrast, the subalpine forest chronosequence on the Neoglacial surface is similar to that described for low elevations (<500 m). The subalpine vegetation, however, on the 13,000- and 50,000-year-old surfaces is generally distinct from that found below 500 m elevation, the major difference being the subalpine *Tsuga mertensiana* associations dominate and below 500 m *Tsuga heterophylla* associations dominate. We expected this given that *Tsuga heterophylla* occurs on warmer sites than *Tsuga mertensiana* (Viereck and Little, 1972). For wetland/peatland associations, in general the low-elevation wetlands/peatlands are more diverse (14 associations) than in the subalpine (5 associations) (Boggs et al., 2008).

Primary succession following deglaciation on the 50,000- and 13,000-year-old surfaces likely did not follow the same seral stages as given on the Neoglacial surfaces because the environmental conditions and potential pool of species were initially different. Pollen studies and radiocarbon dates suggest that tundra-like vegetation perhaps similar to that of modern islands in the Bering Sea dominated the study area's 50,000-year-old glacial refugia during the Pleistocene (Mann, 1983). After the glaciers receded 13,000 years ago, tundra and open pine (*Pinus*) forests with alders (*Alnus*) and ferns invaded the deglaciated surfaces (Manley and Kaufman, 2002). Pines spread throughout much of southeastern Alaska by ca. 12,400–12,000 years ago. *Picea sitchensis* largely replaced pines between about 11,000 and 10,000 years ago, and *Tsuga heterophylla* and *Tsuga mertensiana* established throughout much of southeastern Alaska soon after, resulting in a flora that is similar to the modern flora. In our study area, peatlands apparently did not begin developing until 9500 to 10,700 years ago, even on the 50,000-year-old surface (Mann, 1983).

Though each surface age (Neoglacial, 13,000, and 50,000) has evolved from unique primary succession pathways, we contend that the late-seral vegetation on the 13,000 and 50,000 surfaces

represent, in general, the potential vegetation of the Neoglacial surfaces. Certain problems, however, exist concerning this assumption. The chronosequence approach to evaluating succession infers that the abiotic characteristics of the sampled surface ages be similar. The 13,000- and 50,000-year-old surfaces occur on the outer coasts, and climate models indicate that they share similar annual mean temperatures and annual precipitation (Manley and Daly, 2005). However, the climate in Glacier Bay—encompassing most of the Neoglacial surfaces—is generally drier. The local climate of sites formally adjacent to glaciers also changes following glacier retreat and the consequent distancing from the glacier climate. Arguing that the potential vegetation of the outer coast and far inland Neoglacial surfaces are the same, consequently, poses certain challenges and it is likely not possible to accurately predict succession on any specific recently deglaciated site.

Another limitation of our study and others of the study area is the lack of intermediate surface ages from 246 years post-deglaciation to approximately 13,000 years. During this temporal gap, many seral stages occurred leading to the development of *Tsuga mertensiana*-dominated forests, alpine ericaceous dwarf shrub-dominated associations, and peatlands.

An unsolved question for the conservation of peatland plant species for all recently deglaciated regions of the Pacific Northwest is to understand where peatlands will develop over time. Within our study area, isolated wet depressions do occur on the Neoglacial surfaces and, below 500 m elevation *Equisetum* species rapidly colonize the sites (Boggs et al., 2008). Several studies have explored the possible causes of paludification in spruce forests at lower elevations in the study area (Ugolini and Mann, 1979; Bormann and Sidle, 1990; Noble et al., 1984). They speculated that it results from pedogenic processes that are causing the water table to rise, and that colonization by *Sphagnum* begins 175 to 600 or more years following the initiation of primary succession. None of our Neoglacial plots have *Sphagnum* (even at low elevations) indicating that the conversion of sites to peatlands is an uncommon process at this stage. Our results also clearly show that the 50,000-year surface supports more peatlands than the 13,000-year-old surface, suggesting that paludification will continue on the 13,000-year surface.

A unique finding is that *Alnus viridis* ssp. *sinuata*-dominated associations are rare on the 50,000-year-old surface. Yet, they dominate the lower alpine throughout southern Alaska, including this study's Neoglacial and 13,000-year-old surfaces. The occurrence of *Alnus viridis* ssp. *sinuata* associations on the Neoglacial and 13,000-year-old surfaces may be partly due to it invading mass wasting, avalanche paths, wind-throw, and other disturbances. On stable sites, however, alder is a "climax" association (Griggs, 1936; Mitchell, 1968; Talbot et al., 2005; Kojima, 2006). The rarity of alder-dominated associations on the 50,000-year-old surface is not due to lack of seed source because alder occurs adjacent to the 50,000-year-old surface. Mass wasting may decrease on older surfaces, but avalanche paths are still common. Based on this lack of alder we speculate that the "climax" *Alnus viridis* ssp. *sinuata* associations on the 13,000-year-old surface may actually be relicts from the end of the Pleistocene that are seral (over long time spans) to other associations. Pedogenic processes, soil grain-size, and moisture may also play a role as the soils continue to evolve over time.

To conserve all alpine and subalpine species and habitats, conservation biologists and land managers must understand the seral response of species and ecosystems to receding glaciers. We found that most associations have a high fidelity to either the Neoglacial surfaces or the 13,000- and 50,000-year-old surfaces.

Most early- to mid-seral associations on the Neoglacial surfaces have a limited lifespan and their continued existence is dependent primarily on rates of deglaciation. Because deglaciated surfaces are more common since the end of the Little Ice Age (ending in approximately 1850), we speculate that these associations were rare prior to the Neoglacial and their distribution and extent are now expanding. In contrast, we assume that most old-growth forests and wetlands/peatlands on the 13,000- and 50,000-year-old surfaces have a lifespan of hundreds to thousands of years. These old landscapes will also support many of the early-seral associations as a minor part of the landscape because disturbances initiating primary succession do occur such as mass wasting and avalanches (Nowacki and Kramer, 1998; Snyder et al., 2008). These results highlight the importance of not only the older landscapes for conserving ecosystem diversity, but also that of newly deglaciated surfaces.

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