

Regional Variation in Successional Trajectories and Rates of Vegetation Change on Glacier Forelands in South-Central Norway

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Abstract

Variability in the vascular plant species composition of four stages of primary succession was investigated on 39 glacier forelands in the Jotunheim and Jostedalbreen regions of south-central Norway. The relative frequencies of species were recorded in the pioneer zone adjacent to the glacier snout, in vegetation on terrain ages of c. 70 years and c. 250 years, and in mature vegetation outside the foreland (approximately 10,000 years since deglaciation). Sørensen dissimilarity, non-metric multidimensional scaling, and cluster analysis were used to compare the relative variability in species composition of these four stages and to identify patterns of succession within four altitudinal belts. Indicator species analysis identified characteristic species within each stage. Variation partitioning was used to quantify the relative influence of altitude and continentality on species composition.

Variability increased between pioneer and later successional stages at all but the highest altitudes, which showed no significant difference in variability between stages. The results suggest that up to an altitude of around 1600 m succession on glacier forelands follows a divergent trajectory: above this altitude little successional change occurs. Rate of successional change also varies with altitude: below about 1000 m, in the sub-alpine belt, the transition from pioneer vegetation to birch woodland occurs within 70 years; above about 1600 m in the high-alpine belt, herbaceous pioneer vegetation can persist indefinitely; at intermediate altitudes, the dwarf-shrub and snowbed vegetation types of the low- and mid-alpine belts develop within c. 250 years. The explanatory power of altitude and continentality on compositional variation and the relative importance of altitude increased with successional stage.

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Introduction

The most important characteristic of primary succession in defining the trajectory and rate of change between pioneer and mature stages is variability in species composition (Glenn-Lewin et al., 1992; Matthews, 1992; Walker and del Moral, 2003). This paper measures for the first time, within and between a large sample of glacier forelands, the relative variability of four successional stages. The main aim is to investigate whether successional trajectories and rates on these glacier forelands exhibit an interpretable pattern. A broad-scale, regional approach is used to address this aim. The main factors investigated are the altitudinal and continentality (oceanic-continentality) gradients in relation to relative within-stage dissimilarity.

The approach taken in this paper is consistent with a geoeological model of succession, which assumes that the establishment of vegetation on recently deglaciated terrain is a component of the developing landscape (Troll, 1971, 1972; Matthews, 1992; Löffler, 2003). In other words, biotic and abiotic factors are both expected to change along a successional trajectory. It was not possible, within the constraints of the project, to collect local-scale environmental data. However, an attempt was made to minimize local environmental variation as far as possible.

SUCCESSIONAL TRAJECTORIES

Successional trajectories are commonly defined in terms of changes in the relative variability of vegetation over time (Glenn-

Lewin et al., 1992; Matthews, 1992; Walker and del Moral, 2003). Relative variability may be defined as a measure of the extent to which similarities in vegetation composition between sites within the same successional stage increase or decrease as succession proceeds. Convergence of the vegetation to a common structure would therefore entail a decrease in relative variability over time. Whether vegetation converges towards a common structure determined by environmental factors remains an important question in community ecology (Fukami et al., 2005). Successional convergence, in which vegetation becomes more homogeneous with time, has been attributed to factors which limit the pool of initial colonizers (e.g. Rydin and Borgegard, 1988), decreasing microsite heterogeneity (e.g. Mori et al., 2008), abiotic stress (e.g. Hatton and West, 1987), or competitive dominance of later colonizers (e.g. Suter et al., 2007; Dolezal et al., 2008). Divergent trajectories, in which vegetation becomes increasingly variable as succession proceeds, have been attributed to stochastic processes affecting initial colonizers (e.g. Drake, 1990), priority effects (e.g. Inouye and Tilman, 1995), environmental heterogeneity (e.g. Matthews and Whittaker, 1987; del Moral et al., 2010), and differences in initial conditions (e.g. del Moral, 2007). Lack of species dominance and vegetative proliferation have also been identified as an explanation of the relative variability of mature vegetation in alpine tundra (Burrows, 1990). Evidence from a grassland experiment has found that apparent trajectories may be partly dependent on the scale of observation, with species composition diverging and species traits converging (Fukami et al., 2005).

Studies on glacier forelands have shown that divergent pathways appear to be associated with relatively severe environments and convergence with relatively strong biotic controls (Matthews, 1992). For example, divergent pathways were identified on Storbreen glacier foreland, southern Norway, (Matthews, 1979a, 1992, 1999) with multiple mature communities developing despite similar initial conditions, a pattern attributed to recurrent disturbance and abiotic stress. Jones and del Moral (2005) also found a relatively homogeneous pioneer stage on the foreland of Coleman Glacier, Washington, compared to the mature vegetation, suggesting successional divergence. However, there is evidence of convergent patterns on some glacier forelands (e.g. Fægri, 1933; Archer, 1973; Birks, 1980; Wardle, 1980; Vetaas, 1994).

THE EFFECTS OF ALTITUDE ON SUCCESSION

Documented effects of altitudinal factors on vegetation succession include a decrease in species diversity with elevation (Austrheim, 2002; Bruun et al., 2006) and decreasing variability of vegetation with elevation (Dlugosch and del Moral, 1999; del Moral and Ellis, 2004). These patterns are attributed to severe abiotic stress leading to less successful colonizations at higher elevations. The interrelationship between the influences of regional, altitudinal and local topographic gradients on alpine vegetation in Norway have been extensively analyzed by Löffler (2003) and Löffler and Finch (2005). Matthews (1992) summarized the results of individual studies on glacier forelands as follows: in the sub-alpine zone strong biotic controls lead to convergence; in the low- to mid-alpine zone succession is slower and strongly divergent; in the high-alpine zone concepts of convergence and divergence may have little meaning due to high levels of abiotic control. Altitude also appears to influence the rate of succession on glacier forelands, which may proceed more rapidly in the sub-alpine zone than at higher altitudes. Successional trajectories have also been reported as becoming shorter with elevation on volcanic deposits (del Moral, 2007).

Materials and Methods

LOCATION AND REGIONAL ENVIRONMENTAL CONDITIONS

The study area (Fig. 1) includes the Jotunheim and Jostedalsbreen regions of south-central Norway, which lie between latitudes of 61° and 62°N and longitudes of 6° and 9°E. In the Jotunheim region the mean annual air temperature is -3.1 °C, with a July mean of +5.7 °C and a January mean of -10.7 °C, and the mean annual precipitation is 860 mm at an altitude of 1413 m (Sognefjell meteorological station) (Aune, 1993; Forland, 1993). The Jostedalsbreen region, to the west of Jotunheimen, includes the largest ice-cap on mainland Europe. Data from the Bjørkhaug-i-Jostedalen meteorological station (324 m) indicates a mean annual air temperature of +3.7 °C, a July mean of +13.4 °C, a January mean of -4.9 °C, and a mean annual precipitation of 1380 mm (Aune, 1993; Forland, 1993). There is therefore a gradient of oceanic to continental climatic conditions as well as the rise in altitude between the most westerly and most easterly sites sampled.

The glacier forelands studied have an altitudinal range of 80 to 1860 m a.s.l. Sites sampled within the Jotunheim region lie mainly above the tree-line, which occurs at 1100–1200 m, whereas the majority of glacier forelands around Jostedalsbreen occur below the tree-line, which lies at about 850 m. The altitudinal range of typical vegetation within the study area can also be described in terms of alpine belts (e.g. Dahl, 1986, 1987; Moen,

TABLE 1

Altitude (m a.s.l.) and distance east (km) of the glacier foreland study sites. Note that forelands 4, 35, 39, and 42 were omitted from the analyses as data were not available for all four successional stages.

Code	Name	Altitude (m a.s.l.)	Distance east (km)
1	Suphellabreen	80	10
2	Bøyabreen	100	5.7
3	Nigardsbreen	400	29.6
4	Austerdalsbreen	420	19
5	Bergsetbreen	580	24.5
6	Bødalsbreen	700	24.9
7	Fåbergstølsbreen	780	35.2
8	Tuftebreen	880	27.3
9	Haugabreen	900	4.7
10	Ringsbreen	1100	60.5
11	Styggedalsbreen	1280	65.3
12	Vivakulen	1280	39.9
13	Austdalsnutin	1300	40.1
14	Storbreen	1380	80.7
15	Hurrbreen	1380	80.2
16	Storgjuvbreen	1380	88
17	Sandelvibreen	1400	80.6
18	Bøverbreen	1420	74.4
19	Veslbreen	1420	80.4
20	Tverråbreen	1440	90.1
21	Slettmarksbreen	1460	95.7
22	Hellstugubreen	1480	95.3
23	Visbreen	1500	89.6
24	S Illåbreen	1520	84.7
25	Veobreen	1530	100.9
26	Leirbreen	1540	76.3
27	N Illåbreen	1580	85.1
28	Memurbreen	1580	98.7
29	Bukkeholtsbreen	1600	90.1
30	Svartdalsbreen	1600	100
31	Styggebreen	1600	92.2
32	Tjukningsbreen	1600	104.2
33	Austabotbreen	1620	59.8
34	Høgvalgbreen	1620	86.9
35	W Nautgardsbr.	1660	110.6
36	Skautflyibreen	1700	98.2
37	N Veobreen	1700	98.7
38	E Nautgardsbr.	1730	111.7
39	W Grotbreen	1770	99.1
40	E Grotbreen	1780	103.3
41	Besshöbreen	1780	109.9
42	Gråsubreen	1800	104.2
43	Gjuvbreen	1860	90.5

1987). The glacier forelands around Jostedalsbreen are therefore mainly within the boreal and sub-alpine birch belts, while those in Jotunheimen are predominantly within the low-alpine (1100–1450 m) and mid-alpine (1450–1800 m) belts.

DATA COLLECTION

A chronosequence approach was used to identify sites at four stages of succession on 39 glacier forelands (Table 1), the relative simplicity of ecosystems found on recently deglaciated terrain and the sampling methods used rendering site-specific conditions less of a confounding factor. The four successional stages (Fig. 2) consisted of: (1) pioneer vegetation on the most recently deglaciated ground (up to about 20 years since deglaciation); (2) early-successional vegetation associated with the 1930 moraine (approximately 70 years since deglaciation); (3) late-successional vegetation associated with the A.D. 1750 moraine (approximately

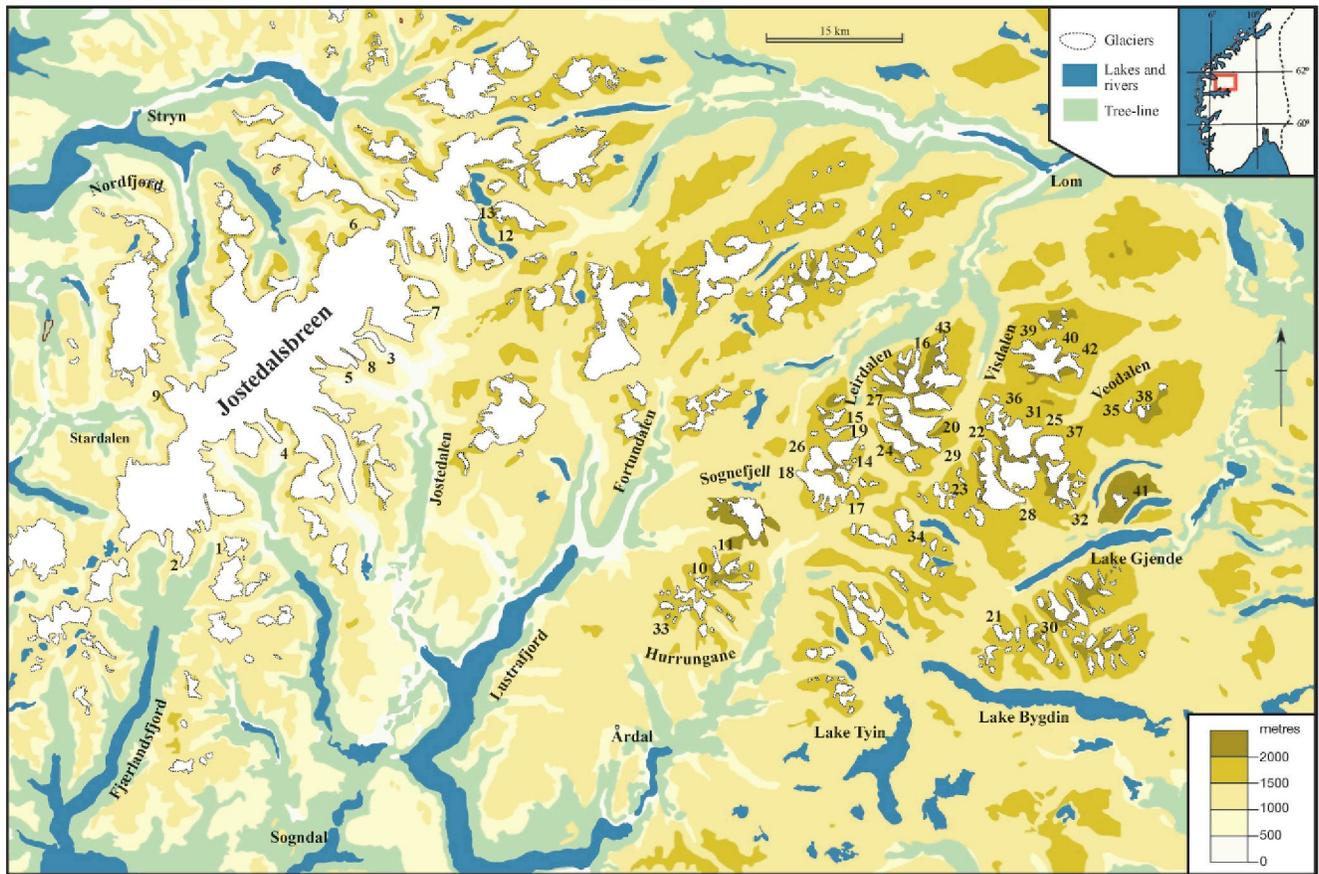


FIGURE 1. Location of the glacier forelands sampled: inset shows southern Norway. See Table 1 for key to numbered sites.

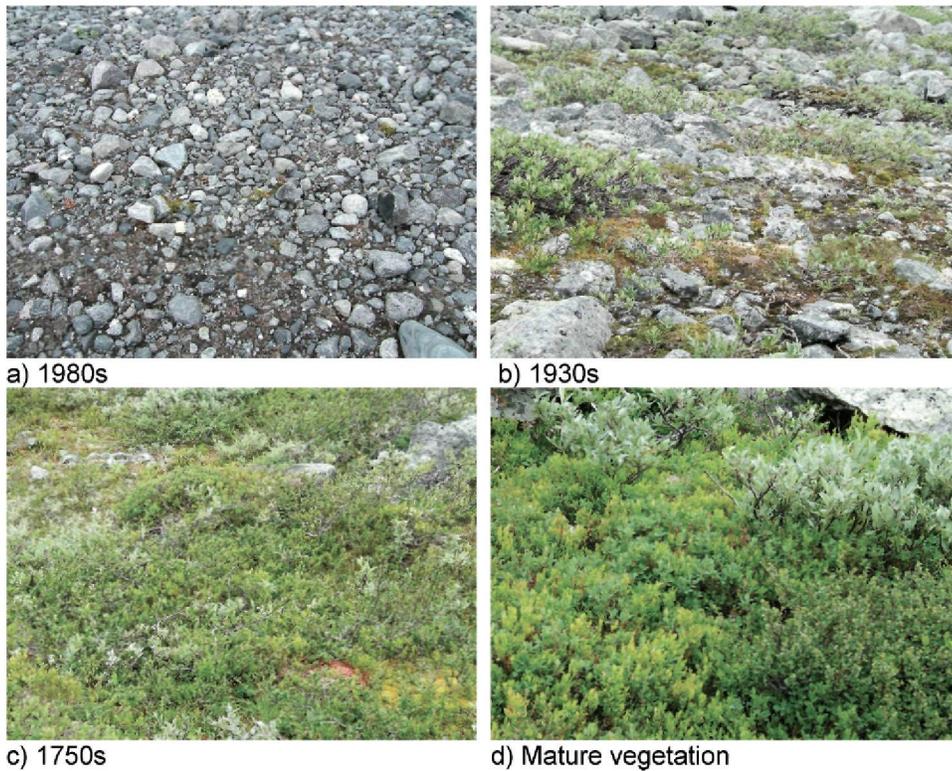


FIGURE 2. (a) to (c) Vegetation associated with dated moraines on Storbreven glacier foreland, and (d) mature vegetation outside the foreland.

250 years since deglaciation); and (4) mature vegetation on ground outside the foreland boundary (deglaciated for approximately 10,000 years). Direct evidence of terrain age was available for about half of the glacier forelands where moraines have been dated using a combination of methods including historical evidence and lichenometry (Bickerton and Matthews, 1992, 1993; Matthews, 2005). At those forelands not dated by these methods, analogue '1930' and '1750' moraines were generally recognizable on geomorphological grounds.

The shoot frequency of vascular plant species was recorded using transects of contiguous $2 \times 0.5 \text{ m}^2$ quadrats aligned at right angles to present and former positions of the glacier snout. The presence of each species in a quadrat was recorded until 100 species occurrences had been recorded within each stage, thus providing a measure of the relative local frequency of each species within each successional stage. This resulted in a larger number of quadrats from the sparsely vegetated pioneer stage than from the more densely vegetated mature vegetation. In other words, sample size was geared to vegetation complexity rather than surface area. Where possible, transects were located to minimize site-specific environmental variation, on ground with an even, stable surface, avoiding stream courses, areas with a high concentration of cobbles and boulders, and major topographic variations. Data collection was confined to vascular plants. Although cryptogams form an important component of the vegetation, detailed research on the Storbreen glacier foreland (Crouch, 1993) has shown that the major vegetation patterns and successional trajectories can be investigated effectively based on the vascular plant species alone.

Nomenclature conforms with Lid and Lid (1994).

DATA ANALYSIS

All data analysis was carried out using PC-ORD Version 4.33 (McCune and Mefford, 1999b). In order to assess the relative variability of vegetation within each successional stage at different altitudes, the glacier forelands were first divided into four altitudinal groups of approximately equal numbers of sites (9–11 forelands). This resulted in the following four altitudinal "belts": <1000 m, 1100–1480 m, 1500–1600 m, and 1620–1860 m. These groups do not correspond exactly with the commonly recognized zonation of alpine vegetation. Therefore, the pioneer and mature stages were also analyzed according to three altitudinal belts: below 1000 m (boreal and sub-alpine), 1100–1480 m (low-alpine), and 1500–1860 m (mid-alpine plus one high-alpine site).

The Sørensen similarity proportion coefficient (also known as the Bray-Curtis or Czekanowski coefficient) converted to percentage dissimilarity was used to characterize changes in the relative variability of vegetation along a chronosequence and according to altitudinal zone. This measure of dissimilarity was chosen because it retains higher sensitivity in heterogeneous data sets and gives lower weight to outliers compared to Euclidean distance (McCune and Grace, 2002). It has also performed well in comparisons with other distance measures (Faith et al., 1987).

A combined ordination of sites from all four stages was carried out to provide a visual representation of the relative variability within each stage and the similarity between stages in terms of species composition. Non-metric multidimensional scaling (NMS) is a method of indirect gradient analysis in which sites are mapped in reduced ordination space according to the rank order of compositional distances between them. NMS therefore has the advantage over other ordination methods of using ranked rather than absolute distances, which improves its ability to extract information from non-linear relationships. This method also overcomes the inherent

limitation of dissimilarity coefficients in expressing large distances when sites with no species in common have a fixed maximum distance. (See Kruskal and Wish [1978] and Mather [1976] for a description of the method and McCune and Grace [2002] for a description of the computational procedure.)

NMS was performed with 40 runs with real data, 50 randomized runs, a maximum of 400 iterations and an instability criterion of 10^{-4} (McCune and Mefford, 1999a). Randomization of the data with a Monte Carlo test allowed assessment of whether the NMS ordination axes have lower stress than expected by chance. Stress levels below approximately 20% were considered to provide a satisfactory quantitative solution (Clarke, 1993), with higher levels within this range providing a qualitative guide to interrelationships between sites.

Detrended correspondence analysis (DCA) (Hill and Gauch, 1980) was also carried out for comparison with NMS. How well the relationships between sites in the solution represent their relationships in the original dissimilarity matrix is assessed by calculating a coefficient of determination (r^2) between distances in ordination space and distances in the original data (McCune and Grace, 2002). This is used to evaluate each ordination, to help assess the optimum number of axes required, and to compare NMS ordinations with those obtained from DCA (although, as some have noted, the meaning of this type of comparison is uncertain).

The most useful NMS ordination diagram was rotated to obtain maximum correlation between axis 1 and successional stage. This enabled the position of sites on axis 1 to be used as a measure of the rate of succession in each altitudinal belt. Centroids were plotted to indicate the mean ordination values for each stage, and confidence ellipses based on two standard deviations (which tend to enclose 95% of the sites in a particular group) were plotted to provide a graphical display of relative variability. Arrows linking the centroids of each stage indicate relative movement along axis one between successional stages.

Cluster analysis (Wishart, 1969; Post and Sheperd, 1974) provided an additional measure of relative variability, the number of vegetation units within each successional stage giving an indication of variability. Hierarchical, polythetic, agglomerative classification (cluster analysis) is a particularly useful complement to NMS ordination because, unlike other methods of classification, it can be based on any distance measure. It can therefore be performed using the same proportion coefficient so that the results are directly comparable with the NMS ordination. Ward's minimum variance method (Ward, 1963) and the unweighted pairs group average technique (UWPGA) (Williams et al., 1966) are the most often used but Kent (2006) criticizes use of the former as it is implicitly based on the squared Euclidean distance coefficient. However, the flexible beta linkage method is considered to produce similar results to Ward's method and is compatible with semi-metric distance coefficients when $\beta = -0.25$ (Lance and Williams, 1967; McCune and Grace, 2002).

Sites were clustered into four vegetation units, and indicator species analysis (Dufrène and Legendre, 1997) was used to identify the most frequent and constant species within each unit. This was primarily for descriptive purposes rather than for identification of vegetation communities in a phytosociological sense. In addition, indicator species analysis was used to detect how far succession has proceeded towards the species composition of the mature vegetation beyond the A.D. 1750 terminal moraine, thus providing an additional measure of the rate of succession.

The relative influence of altitude and continentality on species composition were analyzed using variation partitioning. This technique clarifies the extent to which these two variables (otherwise confounded by the regional topography) covary. Variation partition-

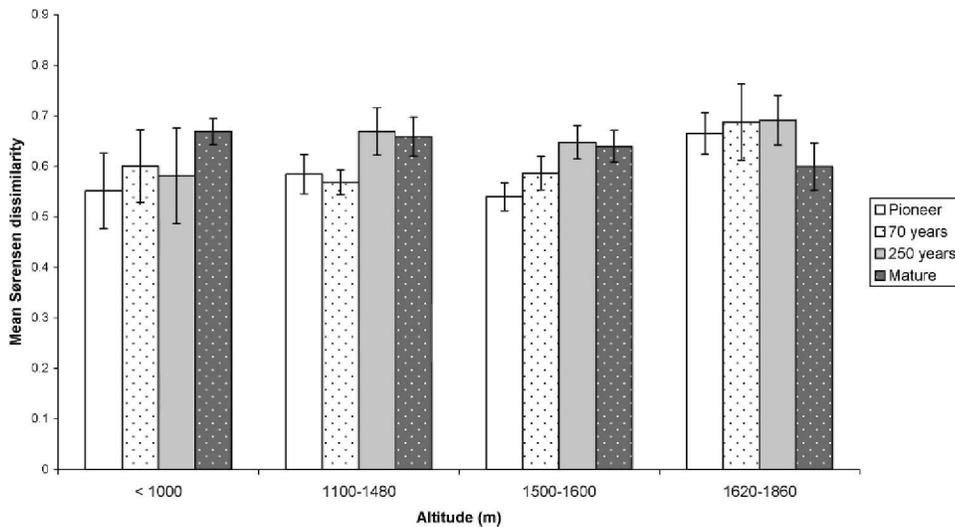


FIGURE 3. Mean Sørensen dissimilarity (between-site variability) and 95% confidence intervals for four successional stages on glacier forelands in four altitudinal zones.

ing was carried out using CCA within Canoco 4.54 software (ter Braak and Šmilauer, 2006). The technique is described in Økland and Eilertsen (1994) and Lepš and Šmilauer (2003). It should be emphasized that this method is used to partition explanatory variables rather than to provide a measure of the amount of total inertia explained by these variables, as recommended by Økland (1999).

Results

SØRENSEN DISSIMILARITY

Figure 3 shows the mean Sørensen dissimilarity for the four successional stages within each altitudinal belt. The lowest altitudinal belt (<1000 m) shows no significant change in variability between the first three stages but a significant difference between pioneer and mature stages. This indicates a divergent trajectory, but not until relatively late in the successional process. However, the broad confidence intervals for the first three stages make it difficult to detect differences, and the high within-stage variability suggested by these confidence intervals could be a result of some sites diverging more rapidly than others.

The 1100–1480 m and 1500–1600 m altitudinal zones show no significant difference in mean Sørensen dissimilarity between the pioneer and 70-year stages but a significant increase between the pioneer and the 250-year stages (followed by no further change). Divergence therefore appears to be beginning earlier and possibly ceasing earlier at these altitudes. For the highest altitudinal belt (>1600 m), there is no significant difference in variability between stages, suggesting parallel trajectories or little successional development.

The sites were also analyzed according to a closer approximation to recognized vegetation belts. In order to have a large enough sample, boreal and sub-alpine sites remain grouped together (the <1000 m group), and the one high-alpine site was analyzed with the mid-alpine forelands (forming a 1500–1860 m group). The remaining sites are situated within the low-alpine belt (1100–1480 m). Thus, the main difference in this analysis was the amalgamation of the two higher altitudinal groups. No significant difference in variability was found between any of the successional stages in the mid- to high-alpine belt: i.e. analysis according to established vegetation belts did not alter the findings.

ORDINATION

Coefficients of determination were calculated for both NMS and DCA ordinations, and the NMS ordination was considered

more useful due to its higher r^2 value (NMS cumulative $r^2 = 0.63$ for 2 axes, 0.82 for 3 axes; DCA cumulative $r^2 = 0.26$ for 2 axes, 0.31 for 3 axes). A single NMS ordination of all four stages of succession on glacier forelands was used to show the relationships between stages in terms of their species composition. This ordination is plotted as four separate diagrams, each representing an altitudinal belt, in Figures 4a–4d. Stress for the two-dimensional NMS ordination is 20% ($p = 0.03$) with an instability of 10^{-4} after 75 iterations. After rotation to obtain maximum correlation between axis 1 and successional stage, $r = 0.79$ ($p < 0.01$). The confidence ellipses, enclosing sites within each successional stage, clarify the degree of clustering at each stage, while the arrows represent the movement of the centroid for each stage along axis 1.

Figure 4a is particularly important in substantiating that, below 1000 m, the greatest successional change (movement along axis 1) occurs early in succession (between the pioneer and 70-year stages) with very little subsequent movement along this axis. The figure also appears to show evidence of early divergence followed by late convergence. This was not detectable from mean within-stage dissimilarities, perhaps due to the broad confidence intervals (Fig. 3).

Figure 4b shows that, for the 1100 to 1480 m belt, the greatest movement along axis 1 occurs between the 70- and 250-year stages. It also shows greatest divergence between these two stages. In contrast, there is little movement along axis one between the 250-year and mature stage centroids.

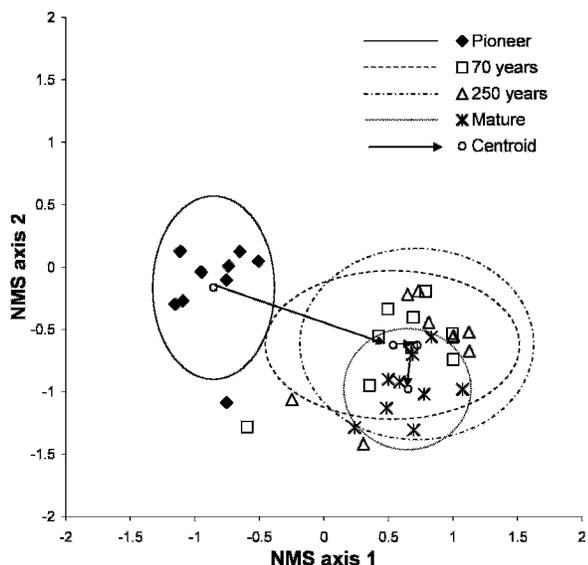
In the 1500 to 1600 m belt (Fig. 4c), mean movement along axis 1 is large between the pioneer and 70-year stages and also between the 70- and 250-year stages, with the greatest variability in the 70-year stage occurring along axis 1. This suggests relatively high variability in the degree of successional development during the 70-year stage. Distance along axis 1 between the 250-year and mature stage centroids is greater than in the two lower zones, suggesting later successional development. However, in both these intermediate altitudinal belts divergence appears to occur in mid-succession.

Figure 4d shows a less clear pattern at the highest altitudes (1620–1860 m) with less overall movement along axis 1 between pioneer and mature stages compared with lower altitudinal zones. This indicates less successional development.

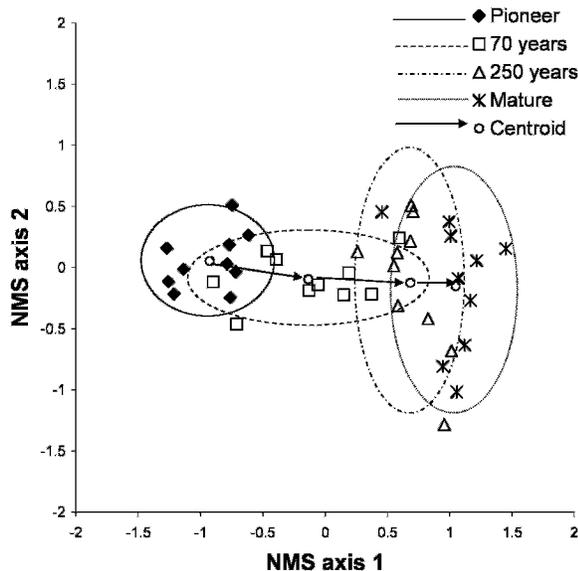
CLUSTER ANALYSIS AND INDICATOR SPECIES ANALYSIS

Cluster analysis combined with indicator species analysis allows further assessment of the species composition of sites,

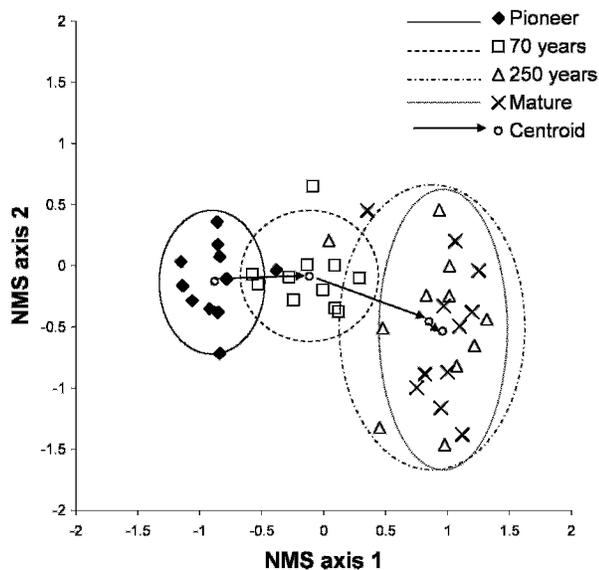
a. < 1000 m



c. 1500 – 1600 m



b. 1100 - 1480 m



d. 1620 – 1860 m

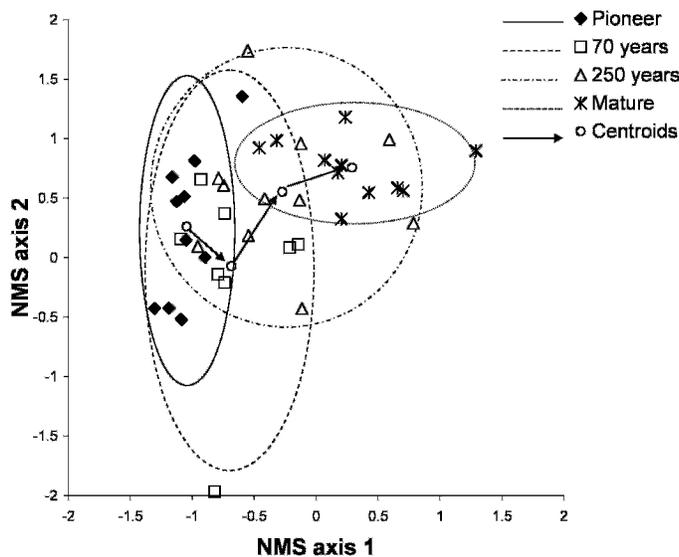


FIGURE 4. Non-metric multidimensional scaling of glacier foreland sites from four successional stages within each altitudinal belt: ellipses indicate ± 2 standard deviations from each stage centroids; arrows connect the centroids of the four stages; stress = 20% ($p = 0.03$); and instability = 10^{-4} after 75 iterations. The ordination has been rotated to obtain maximum correlation between axis 1 and successional stage, $r = 0.792$ ($p < 0.01$).

relative variability within each stage, and the rate of succession. The four-group level of clustering was chosen to define broad vegetation units and allow an assessment of the relationship between stages in terms of their characteristic species (Tables 2 and 3). All but one of the pioneer sites belong to a single vegetation unit, with *Poa alpina* and *Oxyria digyna* as the key species (hereafter referred to as the Poa-Oxyria unit) (Fig. 2a). Other significant indicator species for this group are *Deschampsia alpina*, *Cerastium alpinum*, *Trisetum spicatum*, and *Ranunculus glacialis*. Sites in the three later stages are distributed between at least three vegetation units; the Poa-Oxyria unit; the Betula-

TABLE 2

The distribution of the four vegetation units (cluster analysis groups) in relation to successional stage.

Group	Stage			
	Pioneer	70 years	250 years	Mature
1	38	17	3	0
2	1	10	10	10
3	0	12	18	14
4	0	0	8	15

TABLE 3

Significant indicator species and their indicator values for the four vegetation units (cluster analysis groups).

Species	Indicator Value	p-value
GROUP 1		
<i>Poa alpina</i>	77	0.00
<i>Oxyria digyna</i>	72	0.00
<i>Deschampsia alpina</i>	69	0.00
<i>Cerastium alpinum</i>	67	0.00
<i>Trisetum spicatum</i>	46	0.00
<i>Ranunculus glacialis</i>	42	0.00
<i>Saxifraga stellaris</i>	34	0.00
<i>Saxifraga cespitosa</i>	33	0.00
<i>Arabis alpina</i>	31	0.00
<i>Epilobium anagallidifolium</i>	25	0.00
<i>Saxifraga oppositifolia</i>	21	0.01
<i>Phleum alpinum</i>	16	0.00
<i>Saxifraga rivularis</i>	14	0.01
<i>Mimuartia biflora</i>	12	0.01
GROUP 2		
<i>Vaccinium myrtillus</i>	72	0.00
<i>Betula pubescens</i>	71	0.00
<i>Calluna vulgaris</i>	55	0.00
<i>Melampyrum sylvaticum</i>	48	0.00
<i>Sorbus aucuparia</i>	48	0.00
<i>Alchemilla alpina</i>	34	0.00
<i>Trientalis europea</i>	34	0.00
<i>Athyrium distentifolium</i>	30	0.00
<i>Cryptogramma crista</i>	25	0.00
<i>Potentilla crantzii</i>	25	0.00
<i>Nardus stricta</i>	22	0.00
<i>Solidago virgaurea</i>	21	0.00
<i>Ahnus glutinosus</i>	19	0.00
<i>Lotus corniculatus</i>	19	0.00
<i>Chamerion angustifolium</i>	18	0.00
<i>Cornus suecica</i>	16	0.00
<i>Pinguicula vulgaris</i>	16	0.00
<i>Juncus sp</i>	13	0.00
<i>Maianthemum bifolia</i>	13	0.00
<i>Viola riviniana</i>	13	0.01
<i>Orthilia secunda</i>	12	0.01
<i>Deschampsia flexuosa</i>	11	0.01
<i>Rubus idaeus</i>	10	0.01
<i>Rumex acetosa</i>	10	0.01
<i>Veronica serpyllifolia</i>	10	0.01
GROUP 3		
<i>Salix herbacea</i>	67	0.00
<i>Luzula arcuata</i>	51	0.00
<i>Harrimanella hypnoides</i>	50	0.00
<i>Luzula spicata</i>	46	0.00
<i>Silene acaulis</i>	30	0.00
<i>Veronica alpinum</i>	23	0.00
<i>Omalotheca supina</i>	18	0.02
<i>Huperzia selago</i>	15	0.01
GROUP 4		
<i>Juncus trifidus</i>	59	0.00
<i>Hieracium alpinum</i>	54	0.00
<i>Betula nana</i>	49	0.00
<i>Bartsia alpina</i>	44	0.00
<i>Empetrum nigrum</i>	43	0.00
<i>Campanula rotundifolia</i>	38	0.00
<i>Arctostaphylos alpinus</i>	37	0.00
<i>Vaccinium vitis-idaea</i>	37	0.00
<i>Vaccinium uliginosum</i>	33	0.00
<i>Antennaria dioica</i>	32	0.00
<i>Arctostaphylos uva-ursi</i>	30	0.00

TABLE 3

Continued.

Species	Indicator Value	p-value
<i>Pulsatilla vernalis</i>	30	0.00
<i>Phyllodoce caerulea</i>	28	0.00
<i>Anthoxanthum odoratum</i>	27	0.00
<i>Carex bigelowii</i>	26	0.01
<i>Polygonum viviparum</i>	24	0.01
<i>Diphysastrum alpinum</i>	20	0.00
<i>Pedicularis lapponica</i>	19	0.00
<i>Euphrasia frigida</i>	18	0.00
<i>Loiseleuria procumbens</i>	17	0.00
<i>Salix lanata</i>	14	0.05
<i>Saussurea alpina</i>	14	0.01
<i>Astragalus alpinus</i>	13	0.01
<i>Juniperus communis</i>	12	0.02
<i>Salix reticulata</i>	9	0.05
<i>Viscaria alpina</i>	9	0.05
<i>Pyrola norvegica</i>	8	0.04

Vaccinium unit (characterized by *Betula pubescens* and *Vaccinium myrtillus*); the Salix-Luzula unit (characterized by *Salix herbacea* and *Luzula arcuata*); and the Juncus-Hieracium unit (characterized by *Juncus trifidus* and *Hieracium alpinum*). Additional indicator species for the Juncus-Hieracium vegetation unit include characteristic shrubs of the low-alpine belt, e.g. *Betula nana*, *Empetrum nigrum*, and *Vaccinium vitis-idaea* (Fig. 2d).

Arranging the four vegetation units along successional trajectories (Table 4) reveals the pattern of development in relation to altitude. Below 1000 m, early development to birch woodland (*Betula-Vaccinium*) occurs within 70 years. Between 1100 and 1600 m, vegetation at the 70-year stage is predominantly characterized as either *Poa-Oxyria* or *Salix-Luzula*, while at the 250-year and mature stages the vegetation is either characterized by the *Salix-Luzula* or the *Juncus-Hieracium* units, with the latter being more common by the mature stage. At sites above 1600 m, *Salix-Luzula* vegetation does not develop before the 250-year stage, with pioneer vegetation persisting into the mature stage on the three highest forelands. Figure 5, a schematic summary of the successional trajectories and rates, illustrates the tendency for the early-successional stage in the low-alpine belt to form a later stage in the mid-alpine belt, and for faster attainment of relatively mature vegetation at lower altitudes within an overall divergent framework.

Variation partitioning of each of the four stages (Table 5) shows that the relative contributions of altitude and continentality (distance east) to the total variation in the data set is substantial. The results confirm that the overall variation in the data increases as succession proceeds (from 2.9 in the pioneer stage to 4.1 in mature vegetation). Furthermore, the influence of altitude increased consistently from 0.09 to 0.24 between the pioneer and mature stages, whereas the influence of continentality showed little change during succession (0.12 to 0.16). The relatively high component shared between altitude and continentality (0.21–0.39) reflects the regional topography.

Discussion

REGIONAL VARIATION IN THE TRAJECTORY OF SUCCESSION

In the lowest altitudinal group, below 1000 m (corresponding approximately with the boreal and sub-alpine birch belt in the

TABLE 4

The distribution of the four vegetation units (cluster analysis groups) in relation to altitude and successional stage: 1 = *Poa-Oxyria*; 2 = *Betula-Vaccinium*; 3 = *Salix-Luzula*; 4 = *Juncus-Hieracium*.

Altitude (m)	Pioneer	70 years	250 years	Mature
80	1	2	2	2
100	2	2	2	2
400	1	2	2	2
420	1	2	2	2
580	1	2	2	2
700	1	2	2	2
780	1	2	2	2
880	1	2	2	2
900	1	2	2	2
1100	1	1	3	3
1280	1	1	3	3
1280	1	3	4	4
1300	1	2	3	3
1380	1	3	3	2
1380	1	3	4	4
1380	1	3	4	4
1400	1	3	3	4
1420	1	1	3	3
1420	1	3	3	4
1440	1	1	2	4
1460	1	1	4	4
1480	1	3	4	4
1500	1	1	3	3
1520	1	1	3	3
1530	1	3	4	4
1540	1	1	3	4
1580	1	1	3	4
1580	1	3	3	4
1600	1	3	3	4
1600	1	3	4	4
1600	1	1	3	3
1600	1	3	4	4
1620	1	1	3	3
1700	1	1	3	3
1700	1	1	3	3
1770	1	1	3	3
1780	1	1	1	3
1780	1	1	1	3
1860	1	1	1	3

TABLE 5

The relative contributions of altitude and continentality to compositional variation at each successional stage. All values are significant at $p < 0.02$.

	Pioneer	70 years	250 years	Mature
Altitude (A C)	0.09	0.16	0.21	0.24
Continentality (C A)	0.12	0.14	0.13	0.16
Shared (A∩C)	0.21	0.39	0.30	0.28
Variation explained (VE)	0.42	0.69	0.64	0.69
Total Variation (TV)	2.90	3.64	4.38	4.06
VE as proportion of TV	0.15	0.19	0.15	0.17

Jostedalsbreen area), mean Sørensen dissimilarity indicates that the mature vegetation is significantly more variable than the pioneer stage, suggesting appreciable successional divergence. A divergent pathway due to the presence of woody species, which can establish early and gain dominance, is consistent with the interpretation of successional processes at Glacier Bay, Alaska (Fastie, 1995). However, convergence has also been identified on sub-alpine glacier forelands (Faegri, 1933), and successional convergence between 70-year-old and 250-year-old moraines on a foreland at 700 m a.s.l. (Vetaas, 1994) was attributed to the establishment of *B. pubescens*. If variability is measured in terms of the number of standard deviations from the mean, however, the pattern in Figure 4a could be interpreted as evidence of later convergence. The picture within this altitudinal zone is therefore somewhat ambiguous. Divergence clearly occurs within the chronosequence but evidence for the exact stage at which it occurs is not clear, and the broad confidence intervals for the Sørensen dissimilarity within the first three successional stages suggest a lack of consistency in the patterns observed at individual forelands.

In the literature there are two conflicting views regarding the effects of altitudinal influences on successional pathways. For example, Walker and del Moral (2003) found that convergence is likely where there are few dispersal limitations and homogeneous initial conditions. Convergence would therefore tend to occur below the tree-line, supported by the effects of canopy development and competitive dominance by trees and shrubs. Recent research (Anthelme et al., 2007) supports this view, identifying a convergent trajectory in sub-alpine vegetation due to the effect of

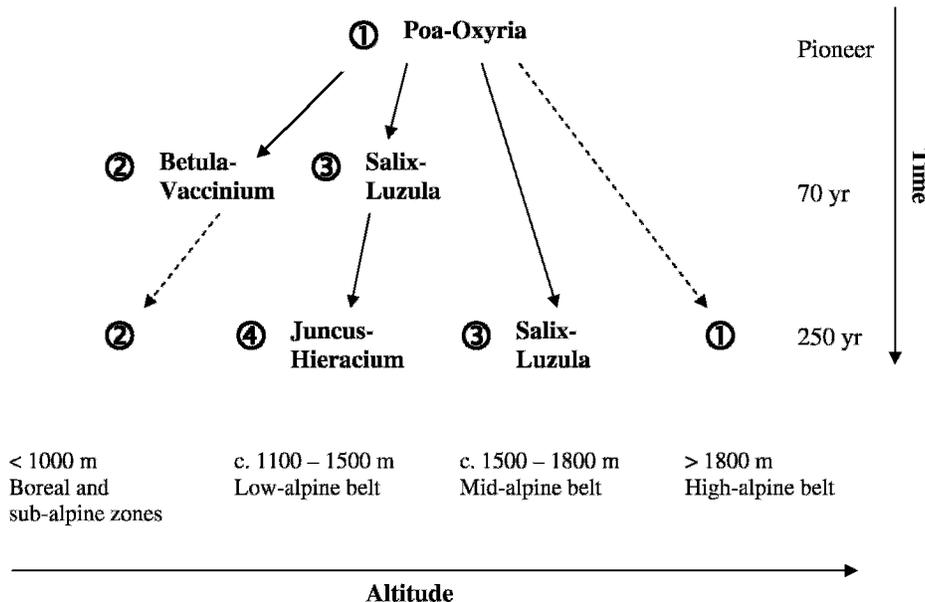


FIGURE 5. Schematic summary of regional successional trajectories and rates in relation to altitude: full arrows indicate directional change; dashed arrows indicate no further directional change. Note that numerical values for altitude and time are approximate and that low- and mid-alpine trajectories in particular are affected by small-scale topographic variation and associated habitats, such as snowbed distribution and exposure. Successional stages along each trajectory approximate to the numbered vegetation units defined in this paper.

a single dominant species. However, Matthews (1979a, 1979b) hypothesized that divergence could occur at relatively low altitudes due to lower environmental stress, which is partially consistent with the findings of this study. It is possible that human impact on some of the low-altitude forelands could be contributing to these patterns.

In the 1100–1480 m and 1500–1600 m zones, both analytical methods (using Sørensen dissimilarity and standard deviation) show a significant increase in variability between the pioneer and the 250-year stages, which does not subsequently increase further (Fig. 3 and Figs. 4b and 4c). This provides a clear indication of divergence between these two stages in the low- and mid-alpine zones. Matthews' (1979a) use of multiple discriminant analysis to assess the relationship between within-group and between-group variability on Storbreen foreland (1380 m) also found evidence of successional divergence within this altitudinal zone. The position of centroids along NMS axis 1 (Figs. 4b and 4c) suggests, moreover, slower successional development than in the sub-alpine zone.

In the highest altitudinal zone (1620–1860 m), mean within-stage Sørensen dissimilarity shows no significant change with increasing terrain age (Fig. 3), suggesting a parallel trajectory or little successional change. The latter is supported by less of an increase in NMS axis 1 scores between pioneer and mature stages than at lower altitudes (Fig. 4d). Previous research has found that the effect of adverse environmental factors at high altitudes can result in vegetation failing to progress beyond the pioneer stage (Svoboda and Henry, 1987). This is attributed to environmental conditions acting in opposition to the biological forces and relatively low species richness weakening interactions. Stress tolerance therefore becomes the major factor influencing survival. The concept of autosuccession (Muller, 1952; Matthews, 1979b), whereby additional species colonize during succession but are not replaced, may also be applicable here. If there is little or no replacement change, then species composition and Sørensen dissimilarity will show no significant change with increasing terrain age.

The general pattern suggests that divergent succession occurs on glacier forelands in all but the highest altitudinal zone where there is no clear tendency to either convergence or divergence. Within the lower three altitudinal zones, within-stage variability is fairly constant. However, pioneer-stage variability is greater in the highest altitude zone than at 1100 to 1600 m, possibly linked to the effects of disturbance associated with the freezing and thawing of the active layer above permafrost.

The overall findings are consistent with a geoeological model of primary succession (Matthews, 1992), characterized by relatively homogeneous pioneer vegetation limited by the availability of 'safe sites' for establishment of seedlings (Harper et al., 1961) in the generally harsh environment with intense disturbance adjacent to glaciers (Robbins and Matthews, 2009). Subsequent divergence of vegetation occurs with increasing distance from the glacier due to topographic variation (Cutler et al., 2008), decreasing intensity and frequency of disturbance, and generally more favorable conditions for establishment despite greater competition. The fact that later colonizing species are more sensitive to environmental factors may mean that their narrower niche width results in increasing heterogeneity (Lepš and Rejmanek, 1991). At higher altitudes, there is less difference between pioneer and mature vegetation zones due to less of a change in environmental conditions with distance from the glacier and the smaller species pool. The tendency for vegetation to diverge can be due to weak biotic interactions in early succession, so that abiotic and chance effects have relatively greater influence (del Moral, 2007).

RATES OF SUCCESSION

The results of NMS ordination and cluster analysis show rapid successional development within the lowest altitudinal zone from pioneer vegetation to birch woodland, with little subsequent change. Similar, relatively rapid rates of succession at low altitudes have been identified in a variety of other habitats (Prach et al., 2007).

In the 1100–1480 m and 1500–1600 m zones, examination of the distances between successional stage centroids on the NMS diagrams (Fig. 4) confirms that the greatest differences in centroid scores along axis 1 (interpreted as successional change) occurs between the 70- and 250-year stages. Examination of the differences between vegetation units also confirms this (Table 4). The vegetation units identified suggest succession from pioneer species towards mature vegetation typical of areas of late-lying snow, with subsequent development to dwarf shrubs or grassy heaths (cf. Matthews, 1978a, 1978b; Dahl, 1986, 1987).

Cluster and indicator species analyses of sites in the highest altitudinal zone show a relatively late development from pioneer *Poa-Oxyria* vegetation to *Salix-Luzula* vegetation (Table 4). An early study of mature arctic tundra vegetation (Griggs, 1934) concluded that it most closely resembles that of the pioneer stage in temperate zones, the extreme climate with its associated physical disturbances preventing the vegetation from reaching a stable equilibrium. The "problem of Arctic vegetation" that Griggs refers to is whether the concept of succession is applicable at all, especially in the High Arctic, which is the latitudinal equivalent to the high-alpine belt. However, it is also clear that, within the low- to mid-alpine belts, vegetation on a number of glacier forelands has not reached the composition of mature vegetation within 250 years of succession.

Patterns identified in relation to successional rate and trajectory on glacier forelands point to the influence of regional factors on primary successional processes. However, while it was possible to identify consistent patterns in successional rate and trajectory in relation to altitude, the results of variation partitioning suggest that continentality is also a significant factor. The influence of fine-scale meso- and micro-environmental factors must also be important (Löffler, 2003). Although data collection attempted to minimize variation in local environmental factors, these are also an important component of the geoeological model of succession and will be assessed in future work.

Conclusions

- (1) This study provides the first analysis of successional patterns at a regional scale using species data from a large number of glacier forelands at a range of altitudes. It has therefore revealed new insights that were not possible from previous site-specific studies.
- (2) On glacier forelands up to approximately 1600 m, transformation of the pioneer plant community generally follows divergent successional trajectories. This is reflected in the increase in mean dissimilarity between sites during the transition from a single pioneer community to more variable mature vegetation. This general finding suggests that the physical environmental characteristics of recently deglaciated terrain are prevalent over the biotic interactions necessary for successional convergence to occur.
- (3) Above 1600 m, successional pathways are neither convergent nor divergent. On the three highest forelands sampled, there is little change in the pioneer vegetation after 250 years, and it is arguable whether succession is occurring.

- (4) Relatively slow rates of successional change on the highest altitude forelands contrast with the rapid changes in species composition that occur within the first 70 years below 1000 m. At altitudes of 1100–1600 m the greatest change in vegetation composition tends to occur between the 70- and 250-year stages.
- (5) Assessment of the respective contributions of altitude and continentality to the variation in the data indicates the increasing influence of altitude as a regional-scale environmental factor on the vegetation as succession proceeds. It also reflects their covariance within the study area and points to the importance of micro- and meso-scale factors in determining successional patterns.
- (6) The unique combination of analytical techniques applied in this study provides a useful means of measuring and assessing relative variability in vegetation composition during succession. Sørensen dissimilarity provided a method of quantifying the relative variability within each successional stage. NMS ordination of the sites enabled visualization of relative variability in relation to altitudinal belts and successional stages. The general patterns observed were confirmed by cluster analysis of the sites which, when combined with indicator species analysis, provided an objective method of characterizing each stage in terms of key species. Finally, variation partitioning enabled quantification of the relative influence of regional environmental factors—altitude and continentality—on the successional patterns detected.

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