

The influence of terrain age on the species composition of alpine "climax" heath communities in southern Norway*

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Abstract. This paper assesses the relationship of terrain age to vegetation diversity and the frequency of individual species, in low- and mid-alpine plant communities in Jotunheimen, southern Norway. It focuses on changes in the composition of vegetation at the boundaries of 15 glacier forelands (where sharp discontinuities exist in terrain age from <250 years to c. 9,000 years) to determine whether the vegetation on the terminal moraine has yet reached a "climax" state.

Statistically significant differences exist in the frequency of several taxa at the glacier foreland boundary: *Vaccinium vitis-idaea*, *Vaccinium* spp., Ericales, *Carex* spp., Cyperaceae/Juncaceae, *Festuca ovina* and Gramineae. Diversity indices indicate higher diversity and lower dominance outside the foreland boundary. The length of time available for succession is considered the primary reason for the discontinuity in vegetation. Alternative hypotheses relating to the influence of local-scale differences in biotic and abiotic factors are considered. Variations in the substrate, historical events and grazing pressure probably contribute to differences in species composition. It is inferred that succession is still proceeding on the terminal moraine, that vegetation within the terminal moraine has not reached equilibrium with its environment, and that it has not achieved a "climax" state.

Keywords: climax, alpine plant communities, diversity, primary succession, glacier forelands, chronosequences

Introduction

Primary vegetation succession has been studied on many glacier forelands (e.g. Faegri 1933; Cooper 1923b, 1926; Crocker and Major 1955; Palmer and Miller 1961; Stork 1963; Worsley and Ward 1974; Birks 1980a; Matthews 1992). Glacier forelands are particularly well suited to such studies since they provide a good chronological framework, whilst factors other than time, such as lithology and aspect, are relatively constant. A series of plant communities in a chronological sequence (chronosequence)

can usually be recognised. The succession at Storbreen glacier foreland, southern Norway, has been extremely well documented (Matthews 1978a, 1979a, b, c, d, 1992; Whittaker 1985, 1987, 1989; Matthews and Whittaker 1987; Crouch 1993). At Storbreen, Matthews (1978a, 1979a) observed a marked spatial discontinuity in species occurrence and abundance at the foreland boundary and interpreted this as indicating that a dynamic equilibrium (the "climax" state) is still to be reached after 220 years of development. However, until now, such contrasts in vegetation have only been observed at individual forelands. They may, therefore, be site specific and determined by local conditions. This paper extends this approach to a sample of 15 forelands in the Jotunheimen region of southern Norway (Fig. 1) to test whether the occurrence of a spatial discontinuity in the vegetation at the terminal moraine is a characteristic feature of forelands in this region and hence to determine whether the "climax" state has been reached after 250 years of succession. Strictly, the term equilibrium should only be used to refer to closed systems. However, in many studies of plant succession it has been applied more widely to include ecosystems where there are fluxes of matter and energy and it is in this sense that the term is used here.

This paper concerns low- and mid-alpine plant communities (as defined by Dahl, 1956). It focuses on differences in the frequency of individual species and species diversity and discusses the implications of the results in the context of vegetation succession. Within the study area, the nature of the "climax" vegetation is relatively consistent; at the majority of forelands there is a heath-type community beyond the glacier foreland boundary, dominated by taxa such as *Empetrum nigrum*, *Vaccinium vitis-idaea*, *V. uliginosum*, *V. myrtillus*, *Phyllodoce caerulea*, *Arctostaphylos uva-ursi*, *Betula nana*, *Salix herbacea* and *Juncus trifidus*. A clear terminal moraine defining the extent of the foreland can usually be identified (Fig. 2). Dating of such moraines indicates that they were deposited during the maximum glacial advance of the "Little Ice Age". The outermost terminal moraine has been lichenometrically dated to approximately A.D. 1750 at Storbreen (Matthews 1975a, 1977b) and a similar date is consistent with radiocarbon dating and other evidence relating to the terminal moraines of other glaciers in the region (Matthews and Shakesby 1984; Matthews 1987, 1991) although they may be up to 40 years younger (Erikstad and Sollid 1986; Matthews 1987). The ground outside the terminal moraine at Storbreen is thought to have been deglaciated about 9,000 years

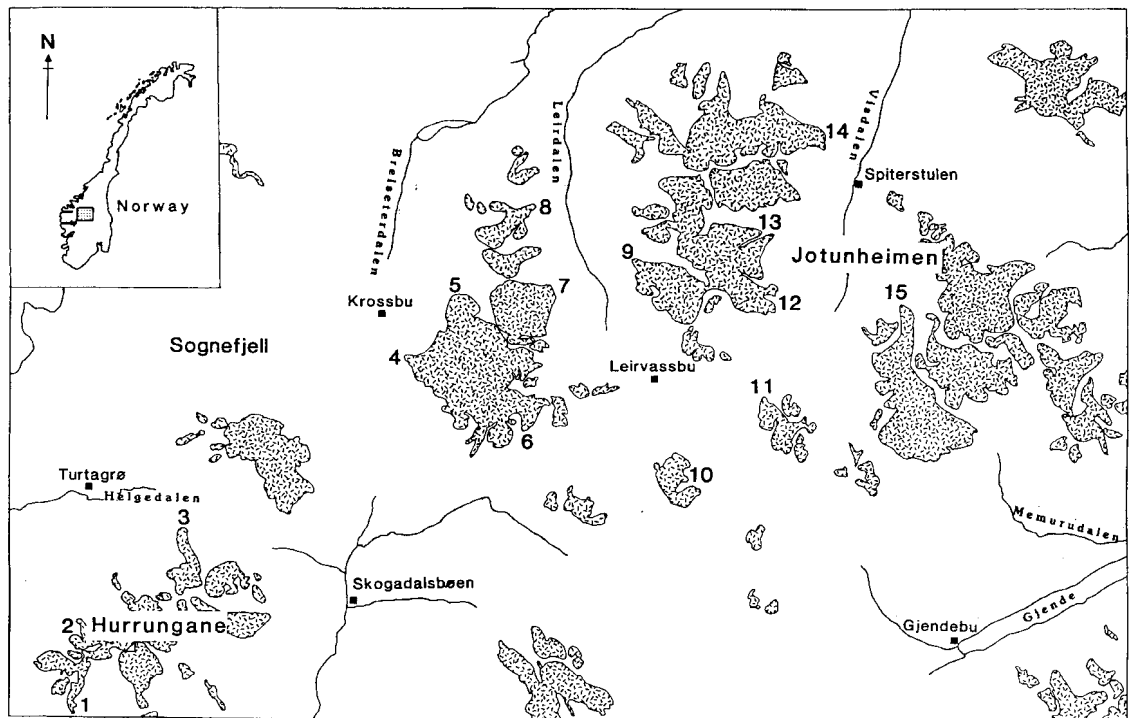


Fig. 1 The location of the study area. Key: 1. Austabotnbreen, 2. Ringsbreen, 3. Styggedalsbreen, 4. Boverbreen, 5. Leirbreen, 6. Sandelvbreen, 7. Storbreen, 8. Hurrbreen, 9. South Illabreen, 10. Mognvaglbreen, 11. Visbreen, 12. Bukkeholsbreen, 13. Tverrabreen, 14. Styggebreen, 15. Hellstugubreen.



Fig. 2 The discontinuity in vegetation can be seen here at the terminal moraine of Bukkeholsbreen.

ago (Matthews 1991). Previous studies show that both terrain age and altitude are strongly correlated with factors associated with stability such as disturbances, including frost churning and soil depth, indicating that the old, low-altitude sites outside the foreland are relatively inactive and more stable (Whittaker 1989).

Methods

As part of a larger project (Pardoe 1992) a vegetation survey was conducted at the fifteen numbered glacier forelands (Fig.1), using a modified version of the method used previously by Matthews and Whittaker (1987). The results discussed here relate to paired sampling sites: the first on the proximal side of the terminal moraine, close to the crest; and the second, comparable site, from approximately 20 m outside the terminal moraine. At three of the forelands, replicate sites were sampled (Styggedalsbreen, Bøverbreen and Storbreen). At each sampling site, a 4 m² quadrat, divided into 100 subdivisions, each measuring 20 cm x 20 cm, was used. All species rooted within each quadrat were recorded, with a possible maximum frequency of 100 if the species was present in all subdivisions. This approach allowed consideration of differences in both species composition and frequency.

The mean frequencies of individual taxa, together with associated 95% confidence intervals, were calculated, and matched-pairs t-tests were used to determine whether the difference in vegetation at the terminal moraine is statistically significant. For each taxon, the null hypothesis being tested was that there is no difference in the taxon frequency between the sites on the terminal moraine and those outside the terminal moraine. Only those taxa which occurred in five or more quadrats were included in the statistical analysis. Certain species were grouped into larger, broadly taxonomically-based, groups, since several occur only at a few forelands or at low frequencies. Grouping such species increased the sample size, increasing the likelihood of the identification of clear trends. The groups employed were *Salix* spp. (including *Salix herbacea*, *S. glauca*, *S. phylicifolia*, and *S. reticulata*), *Vaccinium* spp. (including *Vaccinium uliginosum*, *V. myrtillus* and *Vaccinium vitis-idaea*), Ericales (including *Empetrum nigrum*, *Empetrum hermaphroditum*, *Loiseleuria procumbens*, *Phyllococe caerulea*, *Arctostaphylos alpinus*, *A. uva-ursi*, *Cassiope hypnoides*, *Calluna vulgaris*, *Vaccinium uliginosum*, *V. myrtillus* and *V. vitis-idaea*), Gramineae (including *Festuca ovina*, *Poa alpina*, *Trisetum spicatum*, *Anthoxanthum odoratum*, *Phleum alpinum* and *Deschampsia alpina*), and Cyperaceae/Juncaceae (including *Carex* spp., *Eriophorum* spp., *Luzula spicata* and *Juncus* spp.).

Four indices of diversity were calculated:

- (1) species number (richness);
- (2) the Berger-Parker index

$$d = N_{\max}/N$$

where N = total number of individuals and N_{\max} = number of individuals of the most abundant species

- (3) the Shannon index

$$H' = -\sum p_i \ln p_i$$

where p_i is the proportional abundance of the i th species = (n_i/N)

- (4) Simpson's index

$$D = \sum \left[\frac{n_i(n_i-1)}{N(N-1)} \right]$$

where n_i = the number of individuals in the i th species, and N = the total number of individuals. In this paper the reciprocal form of Simpson's index is adopted to ensure that the value of the index increases with increasing diversity.

Details of these indices are described in Magurran (1988). Species number is simply the number of species per 4m² quadrat. The Shannon index, which was derived from information theory, takes into account the evenness of the abundances of species but emphasises species richness. In contrast, the Berger-Parker and Simpson's indices are both dominance measures since they are weighted towards the abundances of the commonest species rather than providing a measure of species richness. Similar matched-pairs t-tests were conducted using each of these indices. This approach has the advantage that all the constituent taxa in the vegetation are included in the analysis simultaneously, and thereby overall differences in vegetational complexity are measured.

Nomenclature: Lid (1985)

Results

The results of the statistical analyses are presented in Tables 1 and 2 and Figures 3 and 4. The matched-pairs t-tests show statistically significant differences in frequency at the foreland boundary for the following taxa: *Vaccinium vitis-idaea*, *Vaccinium* spp., Ericales, *Festuca ovina*, Gramineae, *Carex* spp., and Cyperaceae (Table 1). Many of the other taxa show interpretable differences in mean frequency, although these changes are not statistically significant: in all, 23 taxa (85%) exhibit an increase in frequency, whereas 4 taxa (15%) show a decrease; an outcome unlikely to be the result of chance.

The matched-pairs t-tests of the diversity indices (Table 2, Fig. 4) show that species number, the Berger-Parker index (which indicates dominance), and the Shannon index exhibit highly significant differences at the terminal moraine, while Simpson's index is marginally significant ($p < 0.06$).

Discussion

The concept of "climax" has undergone radical change since the earliest theories of succession to climax were postulated at the end of the nineteenth century by Hult and Cowles (Burrows 1990). Clements,

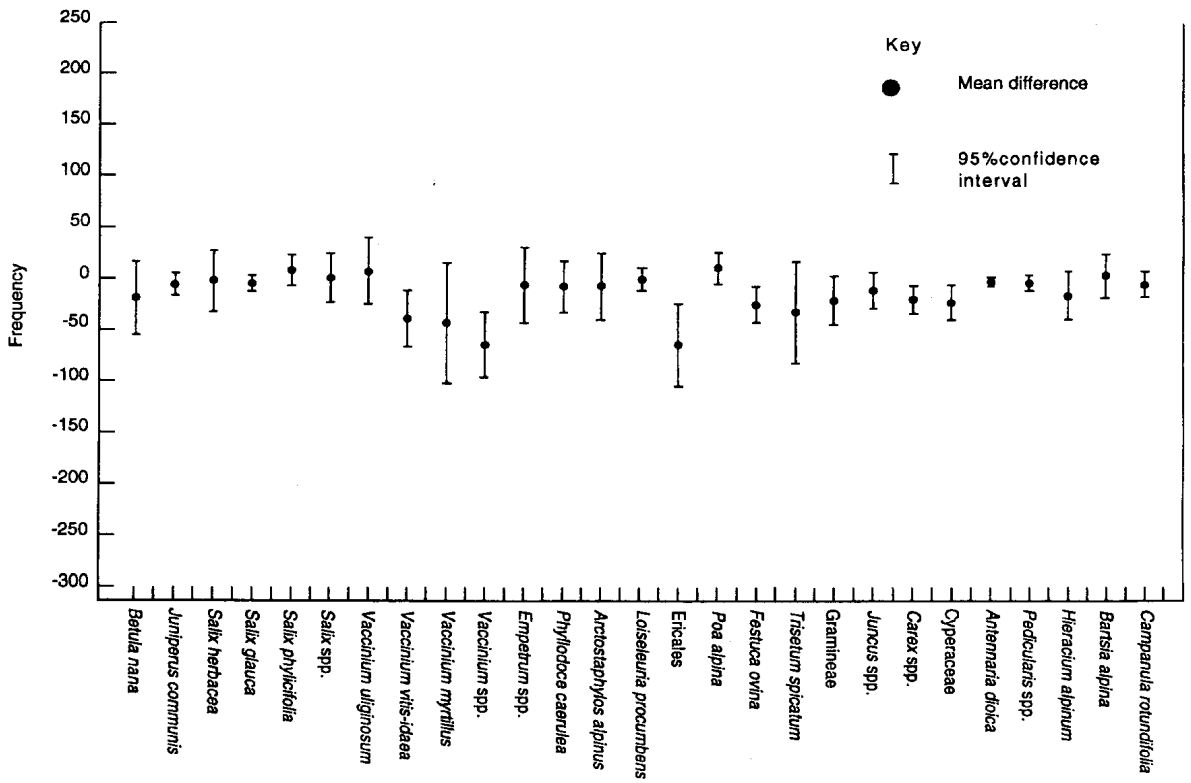


Fig. 3 A diagram to show the difference in mean frequency of selected taxa between sites on the terminal moraine and sites outside the glacier foreland. 95% confidence intervals are shown.

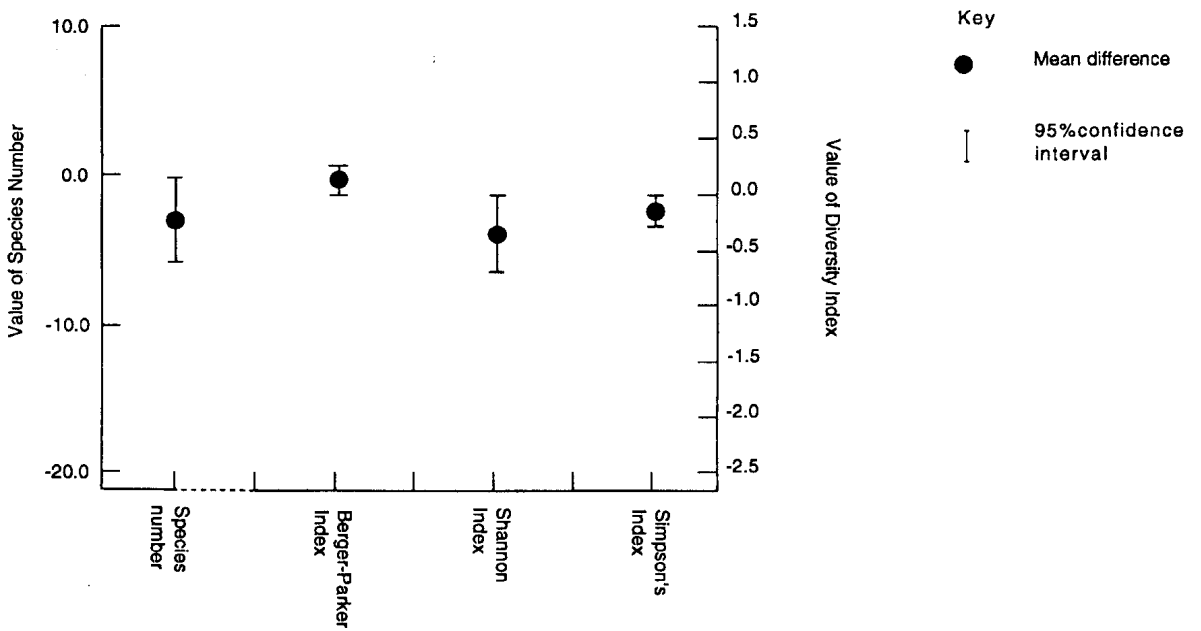


Fig. 4 A diagram to show the difference in mean values of four diversity indices between sites on the terminal moraine and sites outside the glacier foreland. 95% confidence intervals are shown. (Note that the left-hand vertical axis corresponds to Species number only, while the right-hand axis corresponds to the remaining three diversity indices).

Taxon	Terminal moraine			Outside foreland			Difference between the two sites			Matched-pair t-test		
	n	\bar{x}	$\hat{\sigma}$	CI	\bar{x}	$\hat{\sigma}$	CI	\bar{x}	$\hat{\sigma}$	CI	t_{calc}	Prob.
<i>Betula nana</i>	8	19.88	28.00	23.46	38.00	24.18	20.26	-18.13	41.91	35.12	-1.22	0.26
<i>Juniperus communis</i>	5	0.40	0.89	1.11	4.60	7.02	8.73	-4.20	7.40	9.20	-1.27	0.27
<i>Salix herbacea</i>	14	36.07	35.36	20.41	36.36	37.58	21.69	-0.29	49.36	28.49	-0.02	0.98
<i>Salix glauca</i>	10	4.60	5.56	3.98	8.10	9.68	6.92	-3.50	12.00	8.59	-0.92	0.38
<i>Salix phylicifolia</i>	5	8.80	8.41	10.45	1.80	4.03	10.45	7.00	11.25	13.98	1.39	0.24
<i>Salix</i> spp.	17	35.24	32.77	16.85	35.35	34.18	17.58	-0.12	42.78	22.01	-0.01	0.99
<i>Vaccinium uliginosum</i>	9	34.67	32.66	25.16	26.78	32.50	25.02	7.89	44.73	34.44	0.53	0.61
<i>Vaccinium vitis-idaea</i>	13	16.00	32.94	19.93	56.54	40.77	24.66	-40.54	47.96	28.99	-3.05	0.01
<i>Vaccinium myrtillus</i>	5	5.80	8.61	10.70	49.00	42.39	52.71	-43.20	46.98	58.38	-2.06	0.11
<i>Vaccinium</i> spp.	15	36.73	47.43	26.34	97.47	33.23	18.45	-60.73	52.97	29.41	-4.44	<0.01
<i>Empetrum</i> spp.	12	40.33	45.76	29.06	48.92	40.25	25.56	-8.58	59.02	37.49	-0.50	0.62
<i>Phylodoce caerulea</i>	11	21.00	29.79	20.03	26.46	40.66	27.34	-5.45	34.25	23.04	-0.53	0.61
<i>Arctostaphylos alpinus</i>	5	7.40	11.13	13.84	15.20	16.65	20.71	-7.80	25.18	31.30	-0.69	0.53
<i>Loiseleuria procumbens</i>	6	4.00	7.51	7.89	4.33	6.53	6.89	-0.33	11.86	12.44	-0.07	0.95
Ericales	17	83.47	89.24	45.88	150.77	74.54	38.33	-67.29	85.78	44.12	3.23	<0.01
<i>Poa alpina</i>	8	9.88	16.31	13.68	0.25	0.71	0.59	9.63	16.50	13.82	1.65	0.14
<i>Festuca ovina</i>	13	7.54	12.67	7.65	32.85	27.22	16.46	-25.31	29.12	17.61	-3.13	0.01
<i>Trisetum spicatum</i>	5	2.80	3.90	4.84	37.00	38.19	47.48	-34.20	40.11	49.87	-1.91	0.13
Gramineae	17	11.29	14.77	7.59	38.18	34.46	17.72	-26.88	37.46	19.27	2.96	<0.01
<i>Juncus</i> spp.	11	14.73	29.00	19.49	26.18	28.62	19.24	-11.45	28.41	19.11	-1.34	0.21
<i>Carex</i> spp.	12	7.67	12.91	8.21	28.33	20.13	12.78	-20.67	20.59	13.09	-3.48	<0.01
Cyperaceae	17	13.94	29.57	15.20	38.00	26.40	13.57	-24.06	31.58	16.24	-3.14	<0.01
<i>Antennaria dioica</i>	9	2.44	3.47	2.68	4.33	7.42	5.94	-1.89	6.25	4.83	-0.91	0.39
<i>Pedicularis</i> spp.	6	2.83	6.94	7.27	5.50	3.15	3.32	-2.67	7.39	7.76	-0.88	0.42
<i>Hieracium alpinum</i>	6	4.33	8.80	9.23	19.67	18.84	19.76	-15.33	23.35	24.49	-1.61	0.17
<i>Bartsia alpina</i>	5	9.60	10.24	12.73	4.40	8.76	10.90	5.20	16.65	20.71	0.70	0.52
<i>Campanula rotundifolia</i>	5	1.60	1.52	1.89	6.40	11.06	13.76	-4.80	12.13	15.10	-0.88	0.43

Table 1. Mean frequency (\bar{x}), standard deviation ($\hat{\sigma}$), and 95% confidence intervals (CI) of individual taxa a) on the terminal moraine and b) outside the foreland. The mean difference in frequency between the two sites, the standard deviation and 95% confidence interval of that difference are shown. Also, the results of matched t-tests to test the hypothesis that there is a change in the frequency of individual taxa in the vegetation at the terminal moraine are shown, together with the corresponding two-tailed probability value. (Taxa which exhibit statistically significant t-tests at the 5% probability level are emboldened).

Diversity index	Terminal moraine			Outside foreland			Difference between the two sites			Matched-pair t-test		
	n	\bar{x}	$\hat{\sigma}$	CI	\bar{x}	$\hat{\sigma}$	CI	\bar{x}	$\hat{\sigma}$	CI	t_{calc}	Prob.
Species number	18	7.83	4.30	2.13	7.80	6.04	3.02	-2.94	5.81	2.89	-2.15	0.05
Berger-Parker Index	18	0.48	0.21	0.11	0.34	0.16	0.08	0.14	0.24	0.13	2.44	0.03
Shannon's Index	18	1.38	0.53	0.27	1.75	0.52	0.25	-0.36	0.66	0.34	-2.35	0.03
Simpson's Index	18	0.65	0.21	0.11	0.76	0.14	0.06	-0.11	0.24	0.13	-1.98	0.06

Table 2. Mean frequency (\bar{x}), standard deviation ($\hat{\sigma}$), and 95% confidence intervals (CI) of diversity indices a) on the terminal moraine and b) outside the foreland. The mean difference in frequency between the two sites, the standard deviation and 95% confidence interval of that difference are shown. Also, the results of matched t-tests to test the hypothesis that there is a change in the diversity of the vegetation at the terminal moraine are shown, together with the corresponding probability value. (Diversity indices which exhibit statistically significant t-tests at the 5% probability level are emboldened).

one of the most influential proponents of the theory of succession, conceived the final stage of plant succession as a stable monoclimate characteristic of a climatic region, towards which all plant communities in the region eventually converged (Clements 1936). A more realistic concept of the "climax" developed, as it was recognised that several climaxes could coexist within a climatic region, reflecting environmental variables such as soil and aspect, producing a mosaic of communities at the local-scale. According to Tansley (1935:300), 'the "climax" represents the highest stage of integration and the nearest approach to perfect dynamic equilibrium that can be attained in a system developed under the given conditions and with the available components.' Tansley (1935) defined a "climax" as a permanent or apparently permanent condition reached when vegetation is in equilibrium with all the incident factors. He recognised that a relatively stable "climax" community is a complex whole with a more or less definite structure, i.e., inter-relation of parts adjusted to exist in the given habitat and to co-exist with one another, which has developed through a series of stages which have approximated more and more to dynamic equilibrium in these relations.

In contrast, Gleason considered that any vegetation units that can be recognised are temporary and fluctuating phenomena and he stressed the importance of stochastic processes in succession (Gleason, 1939; see also Glenn-Lewin, Peet and Veblen 1992). He believed that species behave as unique individuals, responding each in their own way to environmental factors, including interactions with other species, and that no fixed species composition exists. He suggested that succession is not an orderly process leading to the establishment of any definite climax, because change is universal and constant. He viewed communities as resulting from the fortuitous overlap of distributions of species with similar environmental tolerances rather than the highly integrated organic entities visualised by Clements (Glenn-Lewin, Peet and Veblen 1992).

Whittaker (1953, 1974) proposed that, rather than the "climax" community occurring as a discrete entity, in fact there exists a coherent pattern of climax communities, reflecting continuous gradients in environmental variables and subtle changes in plant populations and species composition. He stated that "the final condition of the community is determined by the interaction of populations and their organisation into a self-maintaining balance, in partial independence of original environment and populations" (Whittaker 1953:48). This view, although realistic, makes it difficult to produce an objective definition of the term "climax". Whittaker emphasised that the "climax" is dynamic, yet relatively stable, with change fluctuating about an average. Recently, disturbance and extreme events are increasingly seen as important. As the patch dynamics paradigm achieved widespread acceptance, the concept of the climax was considered less significant (Glenn-Lewin, Peet and Veblen 1992).

With specific reference to glacier forelands, Matthews (1992) recognised an apparent tendency for progression towards relative stability of commu-

nity structure and function in the latest stages of succession. He envisaged a relatively mature ("climax") community that could be self-perpetuating and in a steady-state equilibrium under prevailing environmental conditions. It is implicit in the theory of primary succession that the final stage of the succession is a relatively stable "climax" vegetation and previous studies have inferred that, given sufficient time, the vegetation on the foreland would eventually become identical to the vegetation outside the terminal moraine.

The present study indicates that a discontinuity exists at the terminal moraine characterised by a change in the species composition and an increase in diversity of the vegetation (Tables 1 and 2, Figs. 3 and 4). Both the frequency of individual taxa and the diversity indices (which reflect gross trends) exhibit this discontinuity. Detailed examination of the vegetation data reveals three groups of taxa (Table 1): the first, the largest group, consists of taxa that are absent (or are present only at relatively low frequencies) within the foreland but that are substantially more abundant outside the terminal moraine, for example, *Carex* spp., *Vaccinium vitis-idaea*, *V. myrtillus*, *Festuca ovina*, *Juniperus communis*, *Arctostaphylos alpinus*, *Trisetum spicatum*, *Juncus* spp., *Campanula rotundifolia*, *Pedicularis* spp., *Gnaphalium supinum*, *Leontodon autumnalis*, *Hieracium alpinum*, *Polygonum viviparum*, *Saussurea alpina*, *Antennaria dioica*, *Vaccinium* spp., Gramineae, Cyperaceae and Ericales. Many of these taxa are relatively late colonisers and characteristic of comparatively undisturbed heath and snowbed communities in the late-successional and "climax" stages (Matthews 1978a). Several of the taxa in this group show statistically significant differences at the terminal moraine. For example, the mean frequency of *Vaccinium vitis-idaea* increases from 16 on the terminal moraine to 56 outside the foreland (Table 1). This species was also distinguished by Matthews (1978a) as being a good indicator of the glacier foreland boundary at Storbreen. Similar trends are shown by *Vaccinium myrtillus* and *Pedicularis lapponica*.

Members of the second group exhibit significantly higher frequencies on the foreland. This group includes *Poa alpina*, *Cardaminopsis petraea*, *Ranunculus glacialis* and *Bartsia alpina*. For example, the mean frequency of *Poa alpina* falls from 10 on the terminal moraine to less than 1 outside the foreland (Table 1). Taxa within this group are characteristic of the early or intermediate stages of vegetation succession and may indicate localised disturbance or other environmental characteristics of the immature communities. In previous studies of species distribution at Storbreen glacier foreland, Matthews (1978a) classified many of the species in this group as transitional, showing characteristics of more than one plant group, or outlying, having characteristics that are not a feature of any group.

The final group consists of taxa which exhibit little or no evidence of a difference in frequency at the terminal moraine. Many of these taxa, including *Empetrum* spp., *Salix herbacea*, *Phyllodoce caerulea* and *Vaccinium uliginosum*, are the characteristic dominants of heath or snowbed communities (Matthews 1978a). Others, including *Loiseleuria procumbens*,

Arctostaphylos uva-ursi, *Cassiope hypnoides* and *Salix reticulata*, have more localised distributions that may be related to factors such as length of snowlie or degree of exposure. Factors such as the dispersal mechanism and reproductive strategy of individual taxa also influence the contrast in vegetation composition at the foreland boundary but this study is primarily concerned with patterns shown by the entire plant community rather than by individual taxa.

The diversity indices clearly indicate that the diversity of vegetation increases beyond the foreland boundary while, conversely, dominance decreases. This is largely a consequence of there being little change in the frequency of the dominant taxa (notably *Empetrum nigrum*, *Salix herbacea*, *Phylodoce caerulea* and *Vaccinium uliginosum*) at the foreland boundary. Matthews and Whittaker (1987) also found that the greatest variety of assemblages is found on the relatively old vegetation landscape outside the glacier foreland boundary. This association of high diversity with stability outside the foreland contrasts with trends earlier in the succession, where increasing dominance is associated with decreasing disturbance (Matthews 1978a; Pardoe 1992). Peet (1990) notes that a number of different patterns in diversity through succession have been reported and concludes that change in diversity during succession depends on the environmental context. Peet observes that part of the explanation for the conflicting observations and predictions is that diversity does not exhibit a simple or consistent response to any one factor.

There is a high degree of variation within the data, indicated by high standard deviations and relatively broad confidence intervals (Tables 1 and 2, Figs. 3 and 4). This is thought to be a consequence of several factors including differences in environmental factors on the local and regional scale, the existence of a mosaic of plant communities on a local scale, localised population fluctuations, the low frequencies and localised distribution of several of the species, and the relatively small sample sizes. Nevertheless, there are reproducible, consistent trends at the 15 forelands. The statistical significance of many of the differences in both species' frequencies and diversity indices suggests that the sample sizes are adequate, that the differences are biologically meaningful and that any local differences are overridden by one or more general factor.

Three interpretations of the results are proposed. The first, preferred, interpretation is that the vegetation on the terminal moraine has not yet reached a "climax" state and is not in equilibrium with its environment. The difference at the foreland boundary is attributed primarily to the greater length of time available for plant succession beyond the terminal moraine. Autogenic succession continues on the terminal moraine and, in addition, the vegetation may still be adjusting to climatic amelioration following the "Little Ice Age", although the rate of change is now relatively slow. This interpretation implies that eventually the vegetation on the terminal moraine will be indistinguishable from the vegetation outside the foreland and will exist in a state of dynamic equilibrium with the environment.

Numerous estimates have been made of the

length of time needed for a "climax"-type vegetation to be achieved. For example, Solomina (1989) suggests that 800-1000 years are necessary for the development of a "climax" community within the tundra zone of Eurasia, 1000 - 1500 years for Svalbard and possibly more than 9,000 years for harsher climates. However, it is difficult to compare these estimates since, as Matthews (1992) points out, different definitions of concepts such as "maturity", "climax" or "stability" have been used. This problem is compounded where the vegetation changes are relatively slow and where autogenic succession cannot be distinguished from allogenic succession. Matthews (1992) doubts whether a true steady-state equilibrium is attained, even in the absence of allogenic environmental change. The view that a period of 220 years is insufficient for a "climax" vegetation to develop on glacier forelands in the low- to mid-alpine zones of Norway agrees with previous observations (Elven 1975; Matthews 1978a, b, 1992).

According to the succession to climax theory, as an ecosystem matures, it should become more stable, so that the climax community remains near an equilibrium state and returns to it after disturbance. However, the perception of stability depends on the spatial scale. Species populations of stands may not be very constant or persistent, whereas the species populations of whole land systems or regions, although exhibiting much local temporal variability (fluctuations, cycles and successions), in a mosaic spatial pattern, may be quite constant and persistent. The duration of a relative scale of stability (constancy or persistence) also must be measured on an arbitrary scale. This is because of the different lifespans of the plants which comprise the vegetation (and because of independent behaviour of different species in communities) (Burrows 1990).

A second interpretation of the results is that two relatively mature communities co-exist, each with a slightly different species composition, as a consequence of differences in abiotic factors (such as substrate and edaphic factors) or biotic factors (such as grazing). This would concur with the views of Tansley (1935) and Whittaker (1953, 1974) that there may be several climaxes, in which the vegetation is in equilibrium with all the effective factors present. This interpretation implies that the "climaxes" will never be identical but that each is stable and independently in a state of dynamic equilibrium. The juxtaposed occurrence of two "climaxes" could be a consequence of differences between the last vegetation successions on the terminal moraines and successions that occurred earlier in the Holocene at adjacent sites beyond the glacier foreland boundary. The pattern of succession is determined both by physical factors on the local-scale and by changes in the distribution of individual species on the local- and regional scales through time. Matthews (1979b) questioned whether the successional vegetation on the glacier forelands will ever change into precisely the same "climax" vegetation as today exists outside the glacier foreland. He also emphasised the difficulties of comparing present-day spatial gradients with temporal successional sequences, noting the importance of climatic change and the origin of the parent material. Just as today each glacier

foreland exhibits a unique chronosequence (Pardoe 1992), it is possible that each sequential vegetation succession at a particular foreland also has a unique character in terms of species composition and the frequency of individual species.

A third interpretation of the data is that differences in the vegetation at the foreland boundary are a consequence of historical events. The importance of such events has been recognised in several studies (e.g. Whittaker 1953; McCune and Allen 1985a, b). The effects of historical events seem to be particularly pronounced at insular sites with low environmental variability, where site and vegetation are largely independent. For example, studies of the canyon-bottom forests in the Bitterroot Canyons of Montana suggest that much of the compositional variation arises at stand establishment rather than through a replacement process (McCune and Allen 1985a, b). They conclude that similar sites need not develop similar, relatively stable forests. In the present case, the areas on the terminal moraine and outside the foreland could be equally stable (or unstable) but historical events such as climatic change or changes in the availability of plant propagules, possibly during the early stages of establishment, have left a semi-permanent imprint on the mature vegetation.

Terrain age is considered to be the primary factor responsible for the statistically significant differences in vegetation at the glacier foreland boundary because the sharp discontinuity in terrain age occurs consistently at all fifteen forelands in the 40 km long transect. This consistency between forelands is unlikely to have been the product of the same environmental factor (other than time) or historical event which would have to have been relatively widespread or prolonged. However, a number of related environmental factors such as grazing pressure, nature of the substrate, moisture regime or microtopography, may contribute to the contrast. For example, the area outside the terminal moraine may be more heavily grazed than the foreland, which might favour the growth of certain taxa. The high frequency of grasses and sedges in the vegetation outside the terminal moraine may be caused by grazing and, in turn, may be more attractive to grazing sheep and reindeer than the relatively sparse, shrubby vegetation found on the terminal moraine at the majority of mid-alpine forelands. Selective grazing, trampling and faeces deposition may also contribute to the differences in species composition at the terminal moraine. The impact of grazing is noticeable at certain forelands such as Storbreen and Huribreen which are relatively close to saeters (mountain farms) or former saeters with their sheep and goat populations.

The substrate on the foreland consists of a stony till, in the form of arcuate moraines (corresponding to minor re-advances during the period of glacier retreat) separated by till sheets. The substrate is often disturbed and, even on the terminal moraines, soils are relatively thin and immature (Mellor 1985; Messer 1988). The moisture regime may also change at the foreland boundary due to topographic or substrate differences. The frequency of Cyperaceae/Juncaceae is considerably higher outside the foreland indicating that the soils tend to

be wetter, possibly reflecting better drainage on the moraines. Microtopography may contribute to the difference in vegetation at the terminal moraine. For example, at Bukkeholsbreen where there is a large, relatively unstable terminal moraine (Fig. 2). The topography of the terminal moraine, in turn, exerts a considerable influence on the microclimate and, indirectly, on the vegetation. Microtopography also influences the distribution of snowbeds and the duration of snowlie. Both this and the degree of exposure have a profound effect on the composition of the vegetation. Individual local-scale environmental factors or complexes of related environmental factors may produce a habitat which is unsuitable for specific taxa. The greatest impact is on those taxa which have a narrow ecological niche (for example, those with specific temperature requirements), those which are at the limits of their ecological range or those which are particularly sensitive to disturbance. Such constraints may apply to taxa such as *Vaccinium myrtillus*, *Luzula spicata* and *Cassiope hypnoides*. The moisture regime or thin, nutrient-poor soils on the moraines may exclude taxa such as *Saussurea alpina*, *Leontodon autumnalis*, *Polygonum viviparum*, *Antennaria dioica* or *Pedicularis lapponica* which have a relatively narrow ecological range. In consequence, the vegetation on the foreland is unlikely ever to become identical to the "climax" vegetation that exists outside the foreland.

However, the first interpretation is preferred because the pattern of discontinuity at the foreland boundary is consistent at 15 forelands that differ with respect to environmental factors other than time. The three interpretations could be tested further by conducting identical vegetation surveys in the future. This would show whether directional vegetation succession is occurring on the terminal moraine, producing a vegetation with closer affinities to the vegetation outside the foreland or whether the vegetation on the terminal moraine had remained unchanged. The three interpretations are not necessarily mutually exclusive; it is possible that elements of all three interpretations have a role in the explanation of the local differences between forelands.

A crucial point in this argument is whether one allows the term "climax" to include plant communities where succession is still proceeding, albeit at a very slow rate. Modern interpretations of "climax" communities recognise them as dynamic entities (Whittaker 1953; Matthews and Whittaker 1987). Tansley (1935:306) recognises this problem when he states that "change may still be proceeding within a climax, but if it is too slow to appreciate or too small to effect the general nature of the vegetation, the apparently stable phase must still be called a climax." If this view is accepted, the definition of the term "climax" must incorporate the acceptable degree of stability of a plant community and the rate of succession that is consistent with this concept.

Many ecologists consider that the term climax should no longer be used since its use and meaning are fraught with so many problems, preferring less rigid terms such as "most advanced phases" (Selleck 1960), "mature" (Odum 1971) or "steady state" (Bray 1958; Park 1970). Steady state denotes 'a temporary state of dynamic equilibrium in an open system' (Burrows 1990). Burrows (1990) recommends that the

definitions must take into account the spatial scale and relative timescale in relation to disturbance regimes, the dimensions of plants or stands, their regeneration patterns and the turnover time of their generations.

Summary and conclusions

1. A vegetation survey was conducted at paired sampling sites at 15 low-alpine and mid-alpine glacier forelands in southern Norway. The survey was designed to test for changes in the frequency of individual taxa as well as diversity at the glacier foreland boundary. The aims were: first, to test whether observed differences in the vegetation at the terminal moraine (where there is a sharp discontinuity in terrain age) are statistically significant; second, to explain this vegetation pattern; and, third, to examine the implications for vegetation succession theory.
2. This paper shows that in the Jotunheimen region there is repeatedly a distinct change in the vegetation at the glacier foreland boundary, both in terms of the species composition of the vegetation and the frequency of individual taxa. Matched pair t-tests show that there are statistically significant differences at the terminal moraine in the frequency of the following taxa: *Vaccinium vitis-idaea*, *Vaccinium* spp., Ericales, *Festuca ovina*, Gramineae, *Carex* spp., and Cyperaceae/Juncaceae. Three indices of diversity (species number, the Berger-Parker index, and the Shannon index) also exhibit highly significant differences at the terminal moraine while the difference in Simpson's index is marginally significant ($p < 0.06$).
3. Three interpretations of these results are proposed. The first interpretation is that the vegetation on the foreland has not yet reached a "climax" state and is not in equilibrium with its environment. It is suggested that the greater length of time available for plant succession beyond the terminal moraine is primarily responsible for the change in the species composition and frequency of individual species at the terminal moraine. The second interpretation is that two mature communities co-exist, each with a slightly different species composition as a consequence of differences in abiotic factors (such as substrate or edaphic factors) or biotic factors (such as grazing). The third interpretation is that differences in the vegetation at the foreland boundary are a consequence of historical factors, reflecting differences that may have occurred during the early stages of establishment. The first interpretation is preferred because the pattern is consistent at 15 forelands that differ with respect to environmental events other than time.
4. The timescale considered is of fundamental importance. Whittaker (1991) has produced direct evidence that succession has occurred at Storbreen within a period of twelve years. If this foreland is typical of mid-alpine forelands in this region, the evidence supports the view that succession is still proceeding at a very slow rate. The "Little Ice Age" is a relatively recent and brief event on the glacial timescale. Even in this relatively temperate region, the vegetation is probably still responding to the subsequent amelioration in climate and conse-

quent change in environmental conditions. It would seem likely that, on the glacial timescale, the environmental conditions and the vegetation at sites on the terminal moraine would eventually become indistinguishable from the sites outside the foreland. Thus, this paper supports the view that the term "climax" should include relatively stable communities where succession is still proceeding slowly and recommends that use of this term should include a specification of the timescale involved; plant communities that are apparently in a steady state over a period of decades may show significant successional changes over a period of several millennia.

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