Increasing Vascular Plant Richness on 13 High Mountain Summits in Southern Norway since the Early 1970s

Authors: Odland, Arvid, Høitomt, Torbjørn, and Olsen, Siri Lie

Increasing Vascular Plant Richness on 13 High Mountain Summits in Southern Norway since the Early 1970s

Arvid Odland*

Torbjørn Høitomt† and

Siri Lie Olsen‡

*Corresponding author: Telemark University College, N-3800 Bø, Norway arvid.odland@hit.no
†Biofokus, Gaustadalleen 21, Oslo, Oslo 0349, Norway
‡The Norwegian University of Life Sciences, Plant and Environmental Sciences, P.O. Box 5003, Ås, Ås 1432, Norway

Abstract

We describe changes in vascular plant richness on 13 high mountain summits based on a historical study performed approximately 40 years ago. A summit is defined as the uppermost 30 m of the mountain tops. The altitudes of the summits range from 1512 to 1814 m. Data from neighboring climatologic stations showed higher mean values for July temperature (+0.7 °C) and January temperature (+1.5 °C), and mean annual precipitation had increased from 714 to 764.7 mm (7.1%) for the period from 1970 until 2009 compared with average data for the normal period (1961–1990). The total "top flora" had during this period increased by 19 taxa. On average, the increase in taxa richness was 18.9 ± 8.4 per summit, representing an average increase of 90.2%. Woody species had an average upward movement of 7.3 m during the study period. The ongoing upward shift of common, ubiquitous alpine species has resulted in a floristic homogenization of the mountain summits, and thus increasing α-diversity was accompanied by decreasing β-diversity. The use of recorded plants as temperature indicators showed that average summer temperatures had increased by approximately 1.3 °C during this period. Several of the newly established species indicate that the climate has become more humid. We assume that the recorded floristic changes are the result of ongoing climatic changes.

Introduction

Summits with old records of their flora can be considered as permanent plots (Grabherr et al., 2001), and resampling of such mountain summits have given opportunities to study long-term changes in the vascular plant flora. Several such sites have now been resampled, and most have shown major floristic changes. In most cases these changes have been explained as results of ongoing global warming (e.g. Parmesan, 2005; Pauli et al., 2007). According to Vittoz et al. (2009), alpine-nival summits in the Swiss Alps have experienced an average increase in species richness of 86% in the 20th century. In central Sweden, Kullman (2007a) resampled the uppermost 20 m of two mountain summits after five decades. These summits had experienced a major increase in plant species richness (58% and 67%, respectively), and in another study Kullman (2007b) found an increase of 156% at one mountain and 88% at another. In both cases, the increases were compatible with a warming climate. Some mountains have also been recorded repeatedly since the early 1800s, and studies on 30 high summits of the Eastern Alps indicate an accelerating trend in species richness. The increase in species richness per decade increased from 1.3 species per decade during 1905–1985, to 3.7 species per decade in 1985–2003 (Walther et al., 2005a). Holzinger et al. (2008) described an average increase in species richness of 11% per decade on summits in the alpine-nival ecotone.

Another predicted consequence of climate warming is the extinction of high-alpine species due to increased competition on the decreasing summit space with the passage of time, i.e. more species are forced to share a smaller area (Grabherr et al., 1994; Sætersdal et al., 1998; Thuiller et al., 2005). Holzinger et al. (2008) found that 13% of the historical species occurrences on their investigated summits could not be reconfirmed.

Study of upward migration trends of vascular plants is another study approach related to climate changes. In central Norway, Klanderud and Birks (2003a, 2003b) reanalyzed data from 23 mountain slopes within the Jotunheimen Mountain massif collected 68 years earlier. Here species richness had increased on 19 of 23 mountains by an average of 10 species, 53.5% of the species were found at higher elevations than in the historical study, and the mean elevational advance was 1.2 m per year. Vascular plant upward shifts have also been shown by other studies (e.g. Kullman, 2002, 2007a, 2007b; Lenoir et al., 2008; Moen and Lagerström, 2008). Upward migration rates of alpine and nival plant species have been estimated at 8–10 m per decade (Grabherr et al., 1994), and new studies from the Alps also indicate an accelerating trend in upward shift (Walther et al., 2005a). All these changes have been assumed to be results of recent climatic changes.

So far, studies on floristic changes have focused on quantity (number of plants and their altitudinal limit) and not biological traits (e.g. indicator species, functional types, and life-forms). The process of competition and upward migration depend on the potential expansion rates of particular species-specific plant populations, which are unknown for the vast majority of alpine plants (Grabherr et al., 1995). Klanderud and Birks (2003b) found that dwarf shrubs occurred at a much higher frequency in 1998 than in the 1930s at all studied altitudinal bands (1500–2000 m) on 25 high mountains in central Norway, and similar trends were also found by Kullman (2007a) on mountains in central Sweden. Sturm et al. (2001) presented evidence for a widespread increase in shrub abundance in an Arctic landscape during the past 50 years, and Cannone et al. (2007) showed that shrubs had rapid expansion rates of 5.6% per decade at altitudes of 2400–2500 m in the Alps.
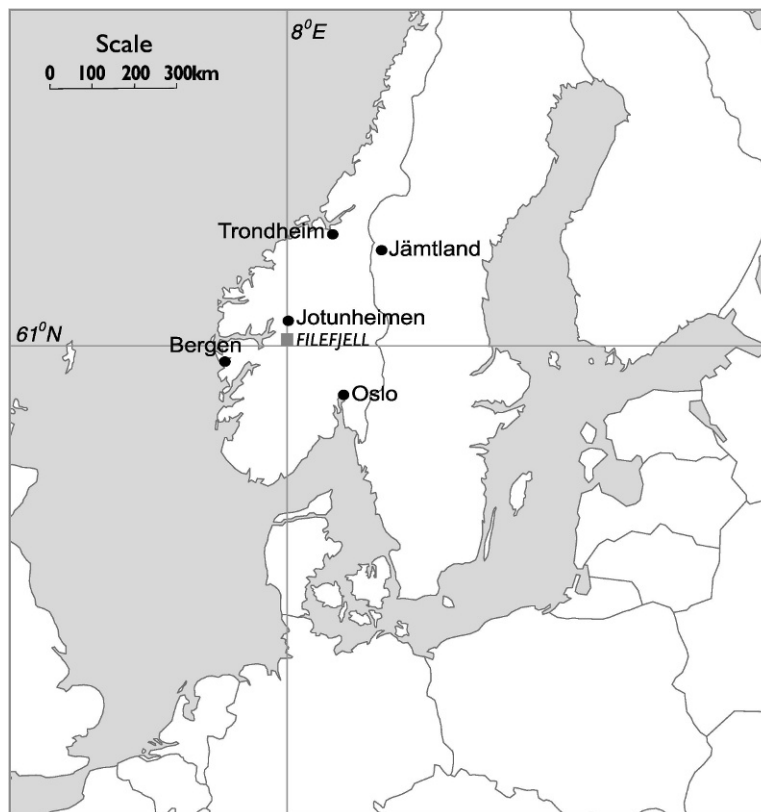
FIGURE 1. The geographic location of the study area at Filefjell; see also Table 1. Locations where studies on effects of climatic changes were carried out in Scandinavia previously are also shown: Jotunheimen (Klanderud and Birks, 2003a, 2003b), and Jämtland, Sweden (Kullman, 2007a; Moen and Lagerström, 2008).

In a recent study of upward shift in plant species optima, Lenoir et al. (2008) found that most shifting species tended to have life-forms (herbs, ferns, and mosses) involving faster life history traits (shorter life cycle, faster maturation, and smaller sizes at maturity) than species showing a reduced shift.

The use of vascular plant species as indicators potentially offers very high-resolution data on local climate where instrumentation is unavailable, and they may also provide information regarding the biological impact of changing climate (e.g. Lewis Smith, 1994; Vittoz et al., 2009; Brady et al., 2010). Calculation of mean indicator values for the summits "before" and "after," by the use of the occurring plants as environmental indicators, may indicate potential environmental changes during the actual period. Floristic and vegetation changes induced by climatic variations were explored by Pignatti et al. (2001) using Ellenberg's indicator values, and Vittoz et al. (2009) used Landolt's values.

Differences in the total floral composition on mountain summits between two study periods can also be quantified using multivariate methods (Walther et al., 2005b). Jurasinski and Kreyling (2007) noticed that an upward shift of flora was taking place as a result of climate change, and this had resulted in an increasing number of species on the mountain summits studied. In addition, they showed an increasing homogenization of species composition of the alpine summit vegetation, resulting in increasing species diversity within individual areas (α-diversity), and also decreasing species diversity across ecosystems (β-diversity).

Based on resampling of 13 mountain summits at Filefjell, previously investigated by Lye (1973) and climatic data from neighboring meteorological stations, we try to answer the following main questions:

- Have there been any trends in temperature and precipitation during the study period?

- Have there been any changes in species richness (α-diversity), and total species composition (ß-diversity) on the summits?
- How important are summit altitude and summit area for the variation in vascular plant richness?
- Can vascular plants as climatic indicators indicate changes in climatic conditions between the historical and the present study?

Methods

STUDY AREA

The study area lies on the watershed between western and eastern Norway. The bedrock in the area consists mainly of Caledonian gneisses, and only one (summit 10) is made up of gabbro.

The mountains investigated are situated within 61°06′–61°14′N and 7°52′–8°15′E (Fig. 1), with summits ranging from 1512 to 1814 m. Summit area was estimated by the use of a digital map area calculator (Table 1). Climatic measurements and trends during the last years were studied based on two data from two neighboring meteorological stations (provided by The Norwegian Meteorological Institute). Temperature data are taken from station 23160 (Åbjørsbråten), operational from 1922 and onward. This station is situated at 60°91′N and 9°29′E, at 639 m, approximately 60 km southeast of the study area. Precipitation data are taken from station 54600 (Maristova), operational from 1895 and onward, situated at 61°10′N and 8°03′E, at 806 m, approximately 10 km west of the study area. Mean July and January temperatures (for 1961–1990 normal period) for station 23160 were 12.1 and −9.1 °C, respectively, and mean annual precipitation was 604 mm for station 54600. Climatic trends

A. ODLAND ET AL. / 459

TABLE 1

Summit number, name, and geographic positions. Altitude in m a.s.l., Area = summit area in ha.

No	Summit name	Coordinates	Altitude	Area
1	Berdalseken	61°12.169′N, 7°54.993′E	1814	10.0
2	Suletinden	61°07.362′N, 8°07.582′E	1791	3.1
3	Unnamed peak	61°11.393′N, 7°55.847′E	1653	9.2
4	Storeknippa	61°06.162′N, 8°15.137′E	1649	14.0
5	Grånosi	61°12.679′N, 7°57.720′E	1615	3.3
6	Loppenosi	61°10.225′N, 7°53.839′E	1612	5.4
7	Graveggi	61°10.145′N, 7°51.107′E	1564	9.0
8	Rjupeskareggen	61°07.892′N, 7°55.330′E	1555	7.2
9	Krekanosi	61°13.771′N, 7°56.832′E	1554	12.1
10	Frostdalsnosi	61°11.765′N, 7°59.435′E	1536	9.7
11	Krekanosi S	61°13.144′N, 7°56.750′E	1533	6.7
12	Slettningseggi	61°13.907′N, 8°06.567′E	1524	2.0
13	Krekahøgdi	61°14.134′N, 7°58.711′E	1512	5.5

during the past 80 years were inferred from data from the same two stations.

The altitudinal position of the climatic birch forest limit within the study area varied between 1150 and 1200 m on south-facing slopes, and the upper limit of the low alpine zone (LA) was approximately at 1400 m. According to criteria presented in Moen (1999), summit 1 and 2 (Table 1) lie in the high alpine zone (HA), while the others lie within the mid-alpine zone (MA). The vegetation on all summits was, however, very sparse, and mostly scattered individuals and small stands of vascular plants were found. Only on the lower summits (<1600 m) were small patches with a closed vegetation cover found. The MA zone is characterized by vegetation stands dominated by graminoids (especially *Juncus trifidus*, *Carex bigelowii*, *Festuca vivipara*, *Deschampsia alpina*, and *Luzula* spp.) and late snow-beds (characterized by *Salix herbacea*, *Sibbaldia procumbens*, and *Omalotheca supina*). In the LA zone, *Salix glauca*, *S. lapponum*, *Juniperus communis*, *Betula nana*, and *Vaccinium myrtillus* are the most common species. The summits are mostly covered by bare rock, frost-eroded boulders, and stones. Late-lying snow patches are frequent in a zone below the summits.

We consider the effects of hikers to be very small, as the summits are situated relatively long distances from roads and tourist route networks. An exception is summit 2, which is popular for day trips along a marked route. Sheep and semi-domestic reindeer may graze on some of the lowest mountains, but we consider the effect of grazing in the study areas to be very small. We observed only a few sheep in the area, and reindeer are mostly grazing in more productive areas during the summer.

METHODS

In the historical study, Lye (1973) started recording vascular plants at mountain tops (during the summer of 1972), and the uppermost occurrences of all species were measured by leveling meter by meter down to 32 m below the summits. We applied a similar procedure and measured the altitudinal distribution limits of all recorded vascular plants on all 13 summits. In the final analysis we used all plants growing <30 m below the summit, a frequently used altitudinal span for similar studies in the Alps (Grabherr et al., 2001; Walther et al., 2005b).

Species and taxa names are according to Lid and Lid (2005). Lye (1973) followed the taxonomy of an earlier edition of the flora, and thus some adjustments were required. We had problems distinguishing *Poa arctica* (Coll.) and *Poa pratensis* ssp. *alpigena*, and therefore these were grouped together. Both *Luzula arcuata*

and *L. confusa* were common in the area, but these were also grouped because only *L. arcuata* appeared in Lye's data. The species (taxa) were divided into four growth forms: herbs and forbs; graminoids; woody species (shrubs); and pteridophytes.

Floristic similarities between the two study periods were calculated according to the Sørensen (1948) similarity index (SSI). Floristic differences between all summits were quantified by use of Detrended Correspondence Analysis (DCA) within the CANOCO program package (ter Braak and Šmilauer, 2002). The ordination was based on the historical data (nominal data) with the present data as supplementary variables (passified). Otherwise default settings were used.

Possible changes in summer temperature on the different summits were tested using the Dahl-R values for vascular plants in northern Europe (Dahl, 1998). Plant respiration is a function of temperature, but the relationship is not linear. Temperatures are therefore weighted according to their effect on the respiration sum. Scandinavian plants are given values from 0.0 (high mountain plants) to 2.0 (lowland, southern plants). The Dahl-R values are closely related to the Ellenberg T-value, but the Dahl-R values appear to perform better to describe the decreasing temperature conditions along the altitudinal gradient (Odland, 2009). Sætersdal et al. (1998) used the annual accumulated respiration equivalents for grid squares in Fennoscandia to predict possible changes of climate change for plant distribution and diversity.

Statistical analyses (correlation, regression, and paired *t*-tests) were performed by the Minitab 15 program (Microsoft Corporation).

Results

CLIMATIC TRENDS DURING THE LAST 80 YEARS

Mean July temperature, mean January temperature, and annual precipitation from the neighboring climatic stations all show considerable variation during the past 80 years (Fig. 2). High summer temperatures during the 1930s and low temperatures during the 1960s are in accordance with more broad-scale patterns, and so are the low winter temperatures during the early 1940s. There are, however, no significant linear trends in the mean July and January temperatures during the period from 1929 to 2009. Mean July temperature for the whole study period (1970–2009) had increased from 12.1 °C (the normal period 1961–1990) to 12.8 °C, and mean January temperature had increased from −9.1 °C to −7.6 °C. The data indicates an increasing trend in mean July temperatures during the study period, but the
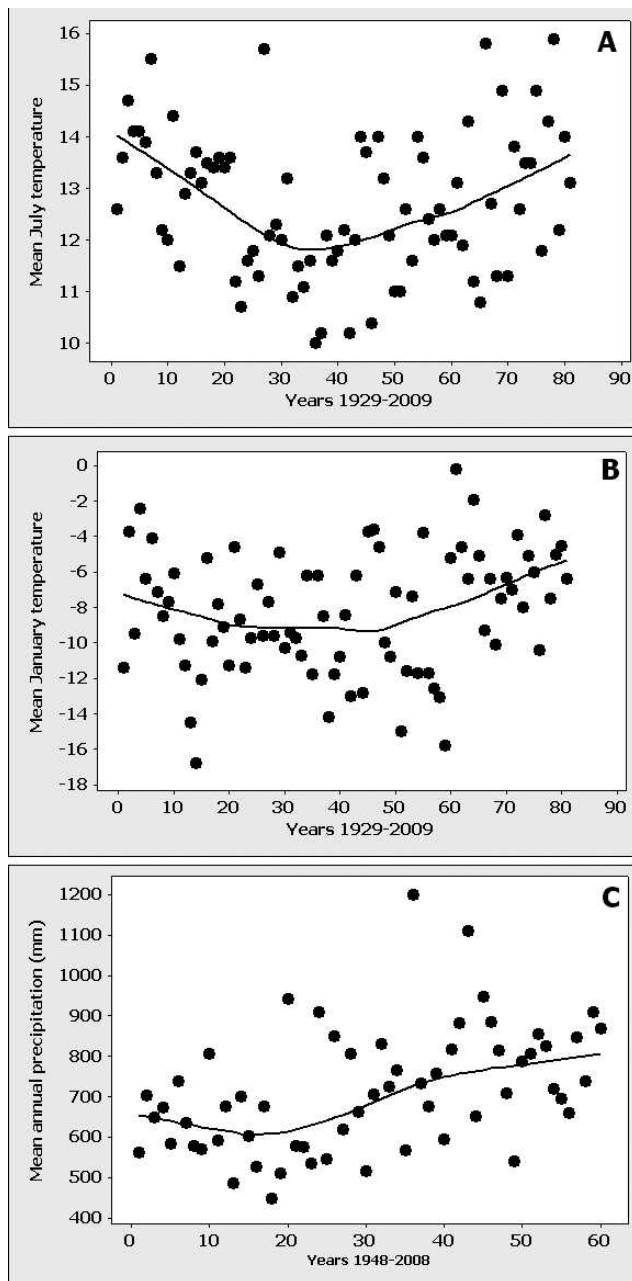
FIGURE 2. Climate measurements from neighboring meteorological stations. Actual values and lowess trend lines (degree of smoothing = 0.5, number of steps = 4) are shown. (A) Variation in mean July temperature from 1929–2009 compiled from data from the nearest meteorological station (23160, 639 m a.s.l.). Actual values and moving averages (length 4) are shown. (B) Variation in mean January temperature from 1929–2009 compiled from data from the nearest meteorological station (23160, 639 m a.s.l.). (C) Variation in mean annual precipitation from 1948 to 2008 based on data from the nearest meteorological station (54600, 806 m a.s.l.).

temperatures have, however, not (yet) reached the values measured during the warm 1930s.

Precipitation data for the period from 1948 until 2008 indicate a significant linear increase in annual precipitation ($r = 0.448$). Mean annual precipitation had increased from 714 mm for the normal period (1961–1990) to an average of 764.7 mm for the study period (1970–2009), representing an average increase of 7.1%.

CHANGES IN SPECIES RICHNESS AND PLANT TURNOVER

Taxa names and their highest records are given for the 13 summits, both for the historic and the present study (Appendix). Numbers of recorded taxa on all summits are given in Table 2. The number of taxa increased on all summits (Fig. 3.), in total from 85 to 104 (Table 2). The number of "new taxa" on the different summits varied from 8 to 31, representing an average increase of 42.9% of the present average taxa number. Number of "lost taxa" varied from 0 to 5, representing an average of 5.3% of the original average taxa number. Only two species (2.35%) were not recorded at present: *Petasites frigidus* and *Coeloglossum viride*. The average number of "lost taxa" on all different summits was 1.5, and "new taxa" average was 20.3, representing an average increase of 90.2%.

There was a linear decreasing trend in species richness with increasing summit altitude, and trends were significant for both periods (Fig. 4), but the slope coefficient was larger for the present data. The percentage increases in species richness was, however, not significantly related to summit altitude ($P > 0.142$). Neither historical species richness, present species richness, nor the increase in species richness was significantly correlated with the estimated summit area ($P > 0.700$ for all).

The number of species in the different life-form groups had increased on most summits, and the increases were significant for all groups as calculated by paired *t*-tests (Table 2). Largest increases (as percentages) were among pteridophytes (128.6%), herbs (80.7%), and woody species (69.0%), while the increase of graminoids was lower (40.0%). The only frequent pteridophyte recorded by Lye was *Huperzia selago*, while we also found relatively high frequencies of *Athyrium disentifolium*, *Cryptogramma crispa*, and *Diphasiastrum alpinum* (Appendix). *Eriophorum angustifolium*, *Saxifraga stellaris* and *Cryptogramma crispa* showed the highest increase in frequency. They were found on 8 more summits in the present study compared with the historic study. The number of woody plants (shrubs and small trees) had increased on all summits, except one. Woody species with the highest increase in frequency were *Betula pubescens*, *Juniperus communis*, *Phyllodoce caerulea*, *Salix lapponum*, *Vaccinium myrtillus*, and *V. uliginosum*. Several herbs (forbs), very common at lower altitudes, had increased in frequency on the summits (Appendix).

ALTITUDINAL DISTRIBUTION CHANGES

Many species had moved upward, but there were major variations between summits. There were significant differences in altitudinal position for taxa recorded both in the historical and the present study only on four summits, with significant upward shifts on three (Table 3). The species on these summits showed an average shift upward of approximately 1 m per decade. Several taxa were found at almost the same altitude (m below the top) in both periods, indicating that the plants had survived on the same site since the historic study.

Differences in altitudinal position for the different life-forms were only significant for woody plants (Table 4). In the historical study they had an average distance from the tops of 17.0 m, while at present the average distance was 9.7 m, an average upward movement of almost 2 m per decade. The largest changes were for *V. myrtillus* (on average 12.0 m higher), *Harrimanella hypnoides* (10.3 m higher), and *Phyllodoce caerulea* (9.3 m higher).

A. ODLAND ET AL. / 461

TABLE 2

Results from the 13 studied summits. A = data from the historic investigation and B from the present investigation. Inc% = increase in taxa richness. Joint = taxa recorded both times. SSI% = Sørensen similarity index. Lost = no. of species not recorded during the present investigation. New = no. of species not recorded during the historic investigation. Dahl-R = mean Respiration coefficient (Dahl, 1998). Number of taxa belonging to different physiognomic groups recorded during the two study periods. P = significance level as calculated by paired t-tests.

	No taxa							Dahl-R		Gram.		Herbs		Pterid.		Woody	
	A	B	Inc%	Joint	SSI%	Lost	New	A	B	A	B	A	B	A	B	A	B
1	4	12	200.0	4	50	0	8	0.00	0.13	3	8	1	2	0	1	0	1
2	20	32	60.0	19	73	1	12	0.12	0.15	6	11	12	18	1	1	1	2
3	9	27	200.0	8	44	1	18	0.19	0.24	5	13	1	7	1	3	2	4
4	38	66	73.7	37	71	1	29	0.15	0.22	13	23	21	35	1	3	3	5
5	23	36	56.5	22	75	1	14	0.15	0.23	11	13	8	13	1	2	3	8
6	35	63	80.0	34	69	1	22	0.18	0.27	12	16	17	33	1	2	5	12
7	22	45	104.5	21	63	1	31	0.21	0.25	12	13	5	20	2	4	3	8
8	30	51	70.0	28	69	2	23	0.21	0.28	10	17	13	22	2	5	5	7
9	34	42	23.5	31	82	3	12	0.18	0.22	11	13	16	20	1	3	6	6
10	64	71	10.9	58	86	5	13	0.27	0.29	19	18	33	36	3	5	9	12
11	21	51	142.9	21	58	0	30	0.19	0.29	10	14	7	26	1	4	3	7
12	26	51	96.2	25	65	1	26	0.20	0.27	13	17	7	23	2	4	4	7
13	44	68	54.5	42	75	2	26	0.28	0.30	11	14	20	36	2	4	11	14
Mean	28.5	47.3	90.2	26.9	67.7	1.5	20.3	0.178	0.241	10.5	14.6	12.4	22.4	1.4	3.2	4.2	7.2
Diff.	18.9							0.063		4.2		10		1.8		2.9	
± SD	8.4							0.033		3.0		6.2		0.8		1.9	
P	<0.0001							<0.0001		<0.0001		<0.0001		<0.0001		<0.0001	

QUALITATIVE FLORISTIC CHANGES

Floristic similarities between the two study periods as expressed by SSI are shown in Table 2. The data show that summits with lowest initial diversity had changed most. Linear regression analyses showed that the variation in SSI was best explained when the historical summit taxa richness (noA) was used as the independent variable ($r = 0.829$; $P < 0.0001$).

The DCA ordination of the summit floristic composition gave three relatively short gradients with almost the same length (2.07, 1.75, and 1.98 SD units, respectively, with Eigenvalues of 0.294, 0.146, and 0.057). Species distribution along DCA axis 1 indicates a gradient from species characteristic of exposed, dry sites at high altitudes to the left (*Draba fladnizensis*, *Saxifraga nivalis*, *Saxifraga cernua*, *Carex rupestris*, and *Silene acaulis*) to species indicating more sheltered conditions at lower altitudes to the right (*Salix lapponum*, *Salix glauca*, *Salix lanata*, *Saxifraga stellaris*, *Carex atrata*, *Juniperus communis*, *Ranunculus acris*, *Solidago virgaurea*, *Phleum alpinum*, and *Potentilla crantzii*). DCA axis 2 indicates a gradient from relatively dry, snow protected sites

(*Carex brunnescens*, *V. myrtillus*, *Bistorta vivipara*, and *Avenula flexuosa*) in the upper part, to species indicating moist snow-bed conditions (*Saxifraga rivularis*, *Athyrium distentifolium*, *Ranunculus pygmaeus*, *Oxyria digyna*, and *Eriophorum* spp.) in the lower part.

The DCA ordination showed a greater floristic gradient between summits in the historical data compared with the present data. (Fig. 5). The total floristic gradient along DCA axis 1 based on the historical data was 2.07 SD units (range 0.0–2.07), and 1.25 SD units based on the present data (range 0.53–1.78). Along DCA axis 2, gradient length in the historical data was 1.74 SD units (range 0.0–1.74) and 0.56 SD units for the present data (range 0.51–1.07). There was a much smaller difference between summits in the present data, 0.82 and 1.18 SD units along DCA axes 1 and 2, respectively. The general trend was that most summits had "moved" toward the ordination centroid, resulting in a lower total floristic gradient in the present situation.

The mean Dahl-R value for the summits was 0.178 for historical and 0.241 for the present data, a difference of −0.063
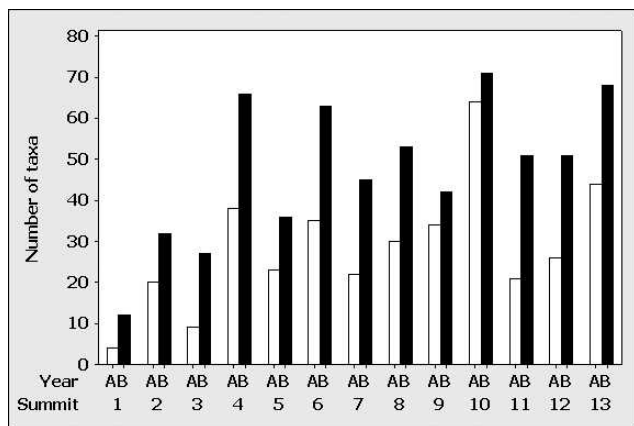

FIGURE 3. Differences in taxa richness between the different summits, and between the two study periods (A = historical data, B = present data).
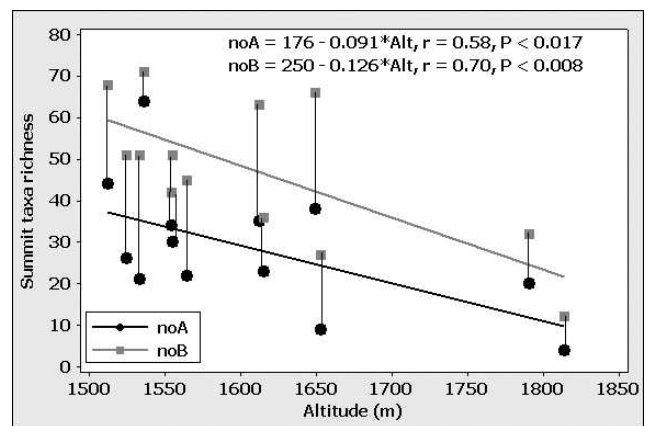

FIGURE 4. Relationships between summit taxa richness and summit altitude (noA = historical richness data, noB = present richness data).

TABLE 3

Average variations in plant upper limit in relation to the top. Number of taxa found both times, their average distance below the summit measured in the historic survey (Am) and the present survey (Bm), and the average difference (Diff). Positive differences indicate that the species are in general found at higher elevations on the top at present. The significance level (*P*) shows that there has been a small, but significant general taxa upward movement on summits 4, 12, and 13 as calculated by paired *t*-tests.

Sum.	No	Am	Bm	Diff.m	P
1	4	5.8	5.8	0.0	1.000
2	19	9.8	8.8	1.0	0.600
3	8	7.1	9.0	−1.9	0.282
4	37	9.9	5.9	4.0	0.004
5	22	8.8	6.9	1.9	0.310
6	34	5.2	7.5	−2.4	0.039
7	21	5.6	5.0	0.7	0.418
8	28	6.7	8.6	−1.9	0.081
9	31	4.1	3.8	0.3	0.533
10	58	11.4	11.8	−0.4	0.667
11	21	4.7	4.7	0.0	1.000
12	25	8.3	4.3	4.0	0.034
13	42	13.1	8.7	4.5	0.000

(±0.033) and highly significant according to a paired *t*-test (Table 2). The average Dahl-R values for all summits, calculated for both periods, were plotted against the summit altitude (Fig. 6). For both periods, there was a decreasing mean Dahl-R value with increasing summit height, and the trends were strongly significant.

Discussion

Most studies on changes in summit floras show increasing trends in species richness and upslope migration compared with the historical studies, but the rates of change are variable. Such differences may be explained by several factors, but especially summit altitude, altitudinal span, and time range are frequently emphasized (Pauli et al., 2001; Grabherr et al., 2001). Our comparisons focus on average changes in data from 13 summits, often as percentage increase compared to the historical study.

CHANGES IN TAXA RICHNESS AND UPSLOPE MIGRATION

The average increase in summit vascular taxa richness (on average 90.2% during four decades) found in the present study is in accordance with similar studies in both Scandinavia and southern Europe (e.g. Kullman, 2007a, 2007b; Parmesan, 2005; Pauli et al., 2007), but a 200% increase in taxa richness found on two summits is exceptional. Kullman (2007a, 2007b) found variations between 58% and 156%, an average increase of 92.3% in central Sweden, which is close to our result.

The positions of the uppermost occurrences of plants are given in the Appendix. This shows that most of the species are found more or less at the same distances from the summits in the historic and the present study. Some deviations (probably within the range of 1–3 m) between the studies should be expected due to measurement error, especially at the longest distances from the summits. The data show that most of the new taxa are mostly found more than 20 m below the summits, but some have also been established close to the top (e.g. *Empetrum*). Some taxa appear to have experienced a turnover, i.e. that they have disappeared from their historic site, and have been re-established

TABLE 4

Differences in the altitudinal positions of physiognomic groups in relation to the summit. No. = number of taxa, Am = mean distance for the taxa below the summit in the historic data, and Bm = mean distance for the taxa below the summit in the present data. Diffm = average difference between Am and Bm, SD = Standard deviation, and *P* = significance level as calculated by a paired *t*-test.

	No.	Am	Bm	Diffm	SD	P
Graminoids	21	10.1	10.3	−0.2	5.9	0.884
Herbs	40	11.2	10.8	+0.4	5.5	0.658
Pteridophytes	4	11.2	13.2	−2.0	5.4	0.507
Woody plants	13	17.0	9.7	+7.3	6.4	<0.001

(or survived) at a lower site, but most taxa were found closer to the summit during the present study. Three species showed an average upward movement of 9–12 m between investigation periods. In the present study only woody plants increased their altitudinal distribution limit within the studied summit area.

The shifts at the upper edge of the altitudinal range agree with the hypothesis of an upward trend to escape rising temperatures (Klanderud and Birks, 2003a; Kullman, 2007a, 2007b; Lenoir et al., 2008; Holzinger et al., 2008). The rate of upward shifting of plants is highly dependent on the studied time scale, and it could be assumed to be smaller close to the mountain top than at lower altitudes. We found significant overall species shift upward of approximately 4 m on only three summits, and the woody plants showed a significant upward trend during the investigated period. The significant trends are in accordance with other similar studies. Pauli et al. (1996) found that the observed upward movements showed maximum migration rates of at least 4 m per decade for two species, whereas most values were within 0–1.5 m for other common species. Grabherr et al. (1995) found the range in observed upward movement for eight of the most common species was 2–4 m per decade.

Recent vegetation dynamics observations across the Arctic show that, in general, shrubs have become more abundant and taller. A study in northern Alaska (Tape et al., 2006) showed that both larger and smaller shrub species increased in size, abundance, and extent over the last 50 years. Sturm et al. (2001) found a widespread increase in shrub abundance over >320 km^2 in the arctic landscape.

Floristic changes are frequently given as decade averages (e.g. Walther et al., 2005a). In this area the climate conditions during the actual study period are highly variable, even if both temperatures and precipitation show increasing trends (Fig. 2). In the first part of the 1970s, summer temperatures increased for a period, and then decreased again in the first part of the 1980s. In this area it is therefore not valid to assume linear increases in taxa richness and report a decadal increase in richness and species upward shift.

CHANGES IN SUMMIT FLORISTIC COMPOSITION

The relatively short gradient lengths resulting from the DCA analysis (Fig. 5) is partly a result of the relatively high number of species occurring on all the summits both in the historic data and in the present data (Appendix), and the low Eigenvalues mainly reflect the heterogeneity within the sample plots (the summits).

The SSIs showed substantial changes in total floristic composition of the summits during the past four decades, and the summits with the lowest initial taxa richness experienced the largest changes (Table 2). Establishment of common and wide-
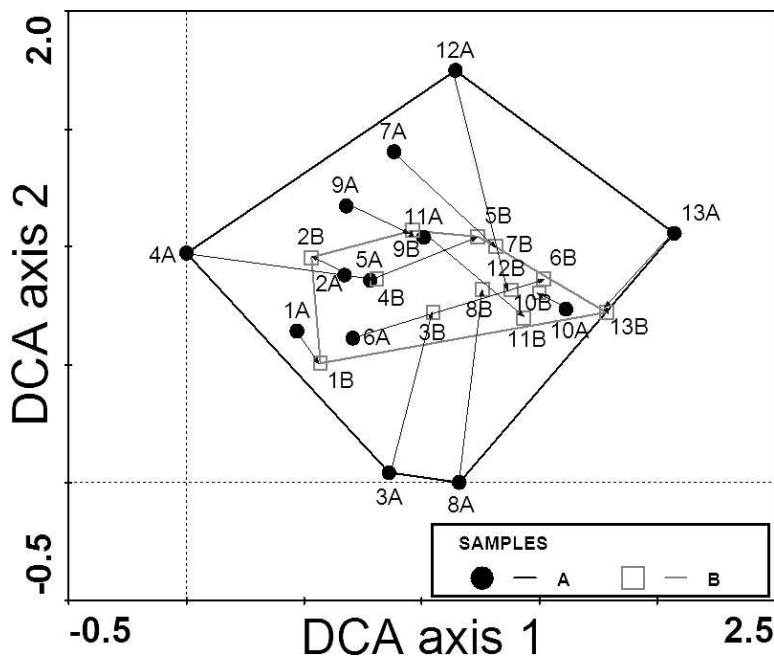
A. Odland et al. / 463

FIGURE 5. Position of the 13 summits calculated on the basis of the historical floristic data (A), and with the present summit floristic data as supplementary data (B). Envelopes show the spatial distribution of the A-summits and the B-summits, and lines show the separation of the summits in relation to sampling period.

spread species since the historical study indicates that the new summit colonizations were not random processes since some species (Appendix) appeared to have much higher colonization rates than others (cf. Vittoz et al., 2009). This has also resulted in smaller floristic gradients along the main DCA axes. Thus, we conclude that as α-diversity (number of taxa on summits) increased, the β-diversity (total floristic variation on all summits) decreased. This is consistent with the reduced β-diversity observed by Jurasinski and Kreyling (2007). They noticed that the increased biodiversity on alpine-nival summits resulted in a higher similarity of species composition. Since a limited number of species are responsible for a large proportion of the colonization events, summit biodiversity tended toward similar floristic compositions. Continued homogenization may in turn lead to a reduction of spatial biotic diversity as specialized species can be replaced by ubiquitous species.

FIGURE 6. Results of linear regression analyses between summit altitude (Alt) and the mean Dahl-R values calculated on the basis of the floristic composition of the historical data (A) and the present data (B).

CLIMATE INDICATORS AND CLIMATE CHANGE

Biodiversity is continually transformed by changing climate; therefore, the ranges of individual species shift and novel species associations should be expected (Hughes, 2000; Walther, 2003; Lee et al., 2005). The global warming trend is most frequently given on a mean annual temperature basis, but the distribution of vascular plants is mainly determined by the heat-sum or the mean temperature of the warmest month (July in the northern hemisphere) (Dahl, 1998). Data from neighboring meteorological stations showed significant regional climatic changes during the study period, and the changes were greater than described by Kullman (2007a) from central Sweden, where mean summer temperatures (June–August) had increased by about 1 °C since 1950, and annual precipitation had increased by 10–15%.

The use of plants as temperature indicators showed an average increase in the mean Dahl-R value of 0.063 during the study period. Data from two mountain areas not far from our study area showed that within 1400–2400 m a.s.l., there was a significant linear decrease of Dahl-R of 0.0302 units per 100 m increase in altitude (Odland, 2009). If a general lapse rate of 0.67 °C per 100 m (Laaksonen, 1979) is assumed, the calculated increase in Dahl-R (0.063 units) indicates an increase in mean July temperature of 1.3 °C, as verified by data from meteorological stations (Fig. 2).

Betula pubescens, which may here be characterized as a lowland plant, was found on five summits in the present study, and it was not recorded earlier. On summit 6 it was found at 1610 m a.s.l., higher than previously reported (Lid and Lid, 2005). The specimens were small, and they will probably not survive at such extreme sites, but the seeds have obviously been able to germinate. The observed increase in pteridophytes and woody dwarf-shrub species may be interpreted as results of increased precipitation and temperatures on the summits. Similar trends were reported by Kullman (2007a) and Cannone et al. (2007). Increasing precipitation and decreasing winter temperatures will result in a more oceanic climate, and this may explain the higher frequency of species associated with moist growth conditions: e.g. *Eriophorum angustifolium*, *Saxifraga stellaris*, *Cryptogramma crispa*, *Athyrium distentifolium*, and *Ranunculus pygmaeus*.
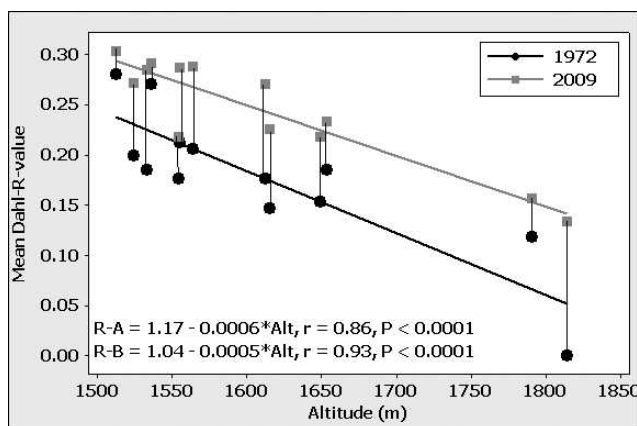
ALTITUDE, AREA, HABITATS, AND DISTURBANCE

The number of species that can inhabit a summit is highly correlated with summit height. According to Körner (2003), the general decrease of species richness with altitude varies mostly within 30–40 species per 100 m increase in altitude (based on all species within 100 m elevation bands), but the absolute decrease also depends on total species richness in the data set.

The present study also shows that the number of new species decreased with increasing summit height, a pattern that supports earlier findings (Vittoz et al., 2009). When the species increase is considered as a proportion of initial species richness, the trend is, however, not significant (cf. Holzinger et al., 2008; Vittoz et al., 2009).

Variation in floristic change between the summits in the present study was also significantly related to summit height (Fig. 4). The average decreases in summit species richness per 100 m was 11.5 species (or 11.1%) at present while it was 8.2 species (9.6%) in the historical data. The linear decrease in species richness is almost parallel between the two study periods. However, the variation was quite large so other variables were obviously also important (e.g. Gottfried et al. [1998] stated: "Descriptors of relief curvature and roughness explained more of the variability than "essential" terrain attributes, such as elevation or exposure.") In the present study area, bedrock quality may have resulted in higher diversity on summit 10 compared with the others. Variation in growth substrate was not studied here, but this may be an important factor for variation in taxa richness. On average, the difference between the two periods was almost as large as the general differences between summits.

The accessibility of mountain summits influences the grazing pressure as well as hiker activity. Hiker visits may increase seed dispersal by functioning as vectors, and trampling and grazing pressure may also influence species richness (Walther et al., 2005a; Moen and Lagerström, 2008). Most of the plants recorded on the summits (Appendix) are common and typical for Scandinavian alpine areas, and none of them are generally associated with cultural activities (e.g. Wistrand, 1962). An exception may be *Achillea millefolium*, which appears to have survived on the same site on the same summit (No 6) since the historic study. In the present study there may be some effects of grazing sheep and reindeer on the lower summits (especially summits 4, 12, and 13), but in general the vegetation stands on the summits were small and we have no reason to assume that grazing has contributed significantly to the observed floristic changes. Grazing animals most likely use the wide surrounding lower altitudinal areas.

Effects of grazing animals (domestic as well as rodents) may contribute to floristic changes in mountain areas, but this effect is difficult to quantify. In some studies it has been assumed that pasturing has remained nearly constant (Cannone et al., 2007), while floristic changes on summits in central Sweden were assumed to be highly influenced by grazing (Moen and Lagerström, 2008). The nine summits (uppermost 50 m) resampled by Moen and Lagerström (2008) showed results that strongly deviated from the results of Kullman (2007a, 2007b) and the present results. They found that species richness had declined on eight of the nine summits. Five species were new, while 17 were lost from the summits. Species turnover was even higher; 57 of recorded species occurrences had established on at least one mountain since the 1950s, while 132 of the occurrences from 1950 were not found. This major change in flora and net decline in species richness on the summits were explained as a result of increased temperatures, increased hiker visits, and a strong increase in reindeer population. These findings have resulted in

some discussion on the importance of grazing, climate change, and methodological aspects for studies on changes in summit vascular plant species richness (Kullman, 2009; Moen and Lagerström, 2009).

HOLOCENE HISTORY AND PREDICTIONS FOR THE FUTURE

Kammer et al. (2007) maintained that the recent increase in summit diversity in the Alps is mainly a result of a natural dispersion process triggered by the temperature increase at the end of the Little Ice Age (LIA), which is still in progress mostly due to the dispersal limitation of the species involved. Suitable habitats occurred on nival summits under the mesoclimatic conditions prevailing at the beginning of the 20th century, and these habitats were, at least in part, occupied by plant species. According to this, they maintained that there is no need for a further increase in temperature for plant species to be able to colonize these areas. There is, however, an important difference between the Alps, where LIA had its optimum around 1850, and in Scandinavia where the LIA optimum has often been dated to approximately 100 years earlier (Nesje and Dahl, 2003). It is therefore hard to believe that the strong increase in vascular plant richness during the last four decades is mainly a result of natural dispersion processes, because vascular plants have probably had a period of >200 years for potential recolonization after the LIA in Scandinavia, and during the 1930s (Fig. 2) there was a period of high temperatures during which the plants could have been established (cf. also Kullman, 2007a). We therefore conclude that the present increase in species richness is mainly a result of recent climatic change. How species richness on the summits responded to the warm summer during the 1930s, we do not know, but the forest limits increased significantly during this period (Kullman, 2007a).

Global models for the change in climate during the next four decades predict continuous increases in temperatures and precipitation, and this will probably result in an even warmer and more oceanic climatic within the study area. An important question is then how fast vascular plants may respond with changed distribution patterns to changing climatic conditions. Kullman (2007b) showed that vascular plants are capable of tracking climate change with only minor time lag. During repeated investigations he found decreasing altitudinal limits for several species and decreased vascular plant species from 1974 to 1994 as a response to deteriorated climatic conditions, and then strong increases from 1994 to 2006 with increasing temperatures. Consequently, we may assume that the main increase in species richness on the summits studied here is primarily a result of the July temperature increases during the last two centuries (cf. Fig. 2), and that the future annual increases in vascular plant richness will be much higher than the average changes predicted by the studied four decades. This is in accordance with Cannone et al. (2007) who suggested that alpine and nival vegetation may respond faster to climate change than previously thought possible. We assume that the strongest increases in species richness will occur at the highest summits where more growth sites may become available with increasing temperatures and earlier melting of snow patches. Future floristic changes with increased species richness will also depend on changes in snow melt-out dates. According to Jonas et al. (2008), models predict earlier snowmelt even at high elevations (between 2000 and 3000 m in the Alps) despite higher precipitation rates and more snow. The poor soil conditions on the summits will, however, represent a barrier for establishment of

many species until more organic matter has accumulated (e.g. Frak and Ponge, 2002).

Acknowledgments

References Cited

Brady, T. J., Monleon, V. J., and Gray, A. N., 2010: Calibrating vascular plant abundance for detecting future climate changes in Oregon and Washington, USA. *Ecological Indicators*, 10: 657–667.

Cannone, N., Sgorbati, S., and Guglielmin, M., 2007: Unexpected impacts of climate change on alpine vegetation. *Frontiers in Ecology and the Environment*, 5: 360–364.

Dahl, E., 1998: *The Phytogeography of Northern Europe*. Cambridge: Cambridge University Press.

Frak, E., and Ponge, J.-F., 2002: The influence of altitude on the distribution of subterranean organs and humus components in *Vaccinium myrtillus* carpets. *Journal of Vegetation Science*, 13: 17–26.

Gottfried, M., Pauli, H., and Grabherr, G., 1998: Prediction of vegetation patterns at the limits of plant life: a new view of the alpine-nival ecotone. *Arctic and Alpine Research*, 30: 207–221.

Grabherr, G., Gotfried, M., Gruber, A., and Pauli, H., 1994: Climate effects on mountain plants. *Nature*, 369: 448.

Grabherr, G., Gotfried, M., Gruber, A., and Pauli, H., 1995: Patterns and current changes in alpine plant diversity. *In* Chapin, F. S., III, and Körner, Ch. (eds.), *Arctic and Alpine Biodiversity*. Berlin: Springer, 167–181.

Grabherr, G., Gotfried, M., and Pauli, H., 2001: Aspects of global change in the Alps and in the high arctic region. *In* Burga, C. A., and Kratochwil, A. (eds.), *Biomonitoring—General and Applied Aspects on a Regional and Global Scale.* Tasks for Vegetation Science, vol. 35. Dordrecht: Kluwer Academic Publishers, 153–175.

Holzinger, B., Hüllber, K., Camendisch, M., and Grabherr, G., 2008: Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. *Plant Ecology*, 195: 179–196.

Hughes, L., 2000: Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution*, 15: 56–61.

Jonas, T., Rixen, C., Sturm, M., and Stoeckli, V., 2008: How alpine plant growth is linked to snow cover and climate variability. *Journal of Geophysical research*, 113: article G03013, doi:10.1029/2007/JG000680.

Jurasinski, G., and Kreyling, J., 2007: Upward shift of alpine plants increases floristic similarity of mountain summits. *Journal of Vegetation science*, 18: 711–718.

Kammer, P. M., Schöb, C., and Choler, P., 2007: Increasing species richness on mountain summits: upward migration due to anthropogenic climatic change or re-colonization? *Journal of Vegetation Science*, 18: 301–306.

Klanderud, K., and Birks, H. J. B., 2003a: Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene*, 13: 1–6.

Klanderud, K., and Birks, H. J. B., 2003b: Nylige endringer i Jotunheimens flora – et resultat av klimaforandring? *Naturen*, 127: 61–69.

Körner, Ch., 2003: *Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems.* 2nd edition. Berlin: Springer.

Kullman, L., 2002: Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, 90: 68–77.

Kullman, L., 2007a: Long-term geobotanical observations of climate change impacts in the Scandes of west-central Sweden. *Nordic Journal of Botany*, 24: 445–467.

Kullman, L., 2007b: Modern climate change and shifting ecological states of the subalpine/alpine landscape in the Swedish Scandes. *Geoöko*, 28: 187–221.

Kullman, L., 2009: High species turnover and decreasing plant species richness on mountain summits in Sweden: reindeer grazing overrides climate change? Comment. Arctic, *Antarctic, and Alpine Research*, 41: 151.

Laaksonen, K., 1979: Areal distribution of monthly mean air temperatures in Fennoscandia 1921–1959. *Fennia*, 157: 89–124.

Lee, H., Lovejoy, T. E., and Schneider, S. H., 2005: Biodiversity and climate change in context. *In* Lovejoy, T. E., and Lee, H. (eds.), *Climate Change and Biodiversity*. New Haven & London: Yale University Press, 3–14.

Lenoir, J., Gègout, J. C., Marquet, P. A., de Ruffray, P., and Brisse, H., 2008: A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 27: 1768–1771.

Lewis Smith, R. I., 1994: Vascular plants as bioindicators of regional warming in Antarctica. *Oecologia*, 99: 322–328.

Lid, J., and Lid, D. T., 2005: *Norsk Flora.* 7th edition. Oslo: Elven, R. Det Norske samlaget.

Lye, K. A., 1973: The vascular plants on alpine peaks at Filefjell, south Norway. *Norwegian Journal of Botany*, 20: 51–55.

Moen, A., 1999: *National Atlas of Norway: Vegetation*. Hønefoss, Norway: Norwegian Mapping Authority.

Moen, J., and Lagerström, A., 2008: High species turnover and decreasing plant species richness on mountain summits in Sweden: reindeer grazing overrides climate change? *Arctic, Antarctic, and Alpine Research*, 40: 382–395.

Moen, J., and Lagerström, A., 2009: High species turnover and decreasing plant species richness on mountain summits in Sweden: reindeer grazing overrides climate change? Reply. *Arctic, Antarctic, and Alpine Research*, 41: 152.

Nesje, A., and Dahl, S. O., 2003: The "Little Ice Age"—Only temperature? *The Holocene*, 13: 139–145.

Odland, A., 2009: Interpretation of altitudinal gradients in south central Norway based on vascular plants as environmental indicators. *Ecological Indicators*, 9: 409–421.

Parmesan, C., 2005: Biotic response: range and abundance changes. *In* Lovejoy, T. E., and Lee, H. (eds.), *Climate Change and Biodiversity*. New Haven & London: Yale University Press, 41–55.

Pauli, H., Gottfried, M., and Grabherr, G., 1996: Effects of climate change on mountain ecosystems—Upward shifting of alpine plants. *World Resource Review*, 8: 382–390.

Pauli, H., Gottfried, M., and Grabherr, G., 2001: High summits of the Alps in a changing climate. *In* Walther, G.-R., Burga, C. A., and Edwards, P. J. (eds.), *"Fingerprints" of Climatic Change*. New York: Kluwer Academic/Plenum Publishers, 139–149.

Pauli, H., Gottfried, M., Reiter, K., and Grabherr, G., 2007: Signals of range expansions and contractions of vascular plants in the high Alps: observations 1994–2004 at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology*, 13: 147–156.

Pignatti, S., Bianco, P., Fanelli, G., Guarina, R., Petersen, J., and Tescarollo, P., 2001: Reliability and effectiveness of Ellenberg's indices in checking flora and vegetation changes induced by climatic variations. *In* Walther, G.-R., Burga, C. A., and Edwards, P. J. (eds.), *"Fingerprints" of Climatic Change*. New York: Kluwer Academic/Plenum Publishers, 281–304.

Sætersdal, M., Birks, H. J. B., and Peglar, S. M., 1998: Predicting changes in Fennoscandian vascular-plant species richness as a result of future climatic change. *Journal of Biogeography*, 25: 111–122.

Sturm, M., McFadden, J. P., Liston, G. E., Chapin, F. S., III, Racine, C., and Holmgren, J., 2001: Snow-shrub interactions in arctic tundra: a hypothesis with climate implications. *Journal of Climate*, 14: 336–344.

Sørensen, T., 1948: A method of establishing groups of equal amplitude in plant sociology based on similarity of species

content. *Kongelige Danske Videnskabernes Selskab Bioloiske Skrifter*, 5: 1–34.

Tape, K., Sturm, M., and Racine, R., 2006: The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology*, 12: 686–702.

ter Braak, C. J. F., and Šmilauer, P., 2002: *CANOCO Reference Manual and CanoDraw for Windows. Users Guide: Software for Canonical Community Ordination.* Version 4.5. Ithaca, New York: Microcomputer Power.

Thuiller, W., Lavorel, S., Araujo, M. B., Sykes, M. T., and Prentice, I. C., 2005: Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences*, 102: 8245–8250.

Vittoz, P., Dussex, N., Wassef, J., and Guisan, A., 2009: Diaspore traits discriminate good from weak colonisers on high-elevation summits. *Basic and Applied Ecology*, 10: 508–515.

Walther, G.-R., 2003: Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics*, 6: 169–185.

Walther, G.-R., Breissner, S., and Burga, C. A., 2005a: Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, 16: 541–548.

Walther, G.-R., Breissner, S., and Pott, R., 2005b: Climate change and high mountain shifts. *In* Broll, G., and Keplin, B. (eds.), *Mountain Ecosystems. Studies in Treeline Ecosystems.* Berlin: Springer, 77–95.

Wistrand, G., 1962: Studier i Pite Lappmarks kärlväxtflora. *Acta Phytogeographica Suecica*, 45: 1–211.

MS accepted May 2010

Taxa records from the 13 summits during the historic and the present study. The numbers refer to meters below the summit. 0 indicates that the taxa were found between the top and 1 m below. Records deviating within 1–3 m between the two study periods may lie within the measurement error, especially for records more than 10 m below the summit. L-f = plant life-form: H = herbs and forbs; G = graminoids; W = woody species; and P = pteridophytes. A refers to the historic data and B refers to the present data.

Taxa/Summit code	1A	1B	2A	2B	3A	3B	4A	4B	5A	5B	6A	6B	7A	7B	8A	8B	9A	9B	10A	10B	11A	11B	12A	12B	13A	13B	L-f
Achilla millefolium L.	—	—	—	—	—	—	—	—	—	—	15	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	H
Agrostis mertensii Trin.	—	—	—	—	—	—	30	17	—	—	—	—	—	—	—	—	—	—	22	24	—	—	—	—	—	—	G
Alchemilla alpina L.	—	—	—	—	—	—	—	—	—	—	—	24	—	—	—	—	—	—	—	23	—	—	—	—	10	10	H
Alchemilla glomerulans Buser	—	—	—	—	—	—	—	—	—	—	—	24	—	—	—	—	—	—	30	—	—	—	—	—	—	—	H
Antennaria alpina ssp. alpina Gaertn.	—	—	9	9	—	—	10	17	1	13	5	2	—	30	—	28	1	1	9	8	5	30	4	23	10	8	H
Antennaria dioica (L.) Gaertn.	—	—	—	—	—	18	—	17	—	—	—	—	11	10	—	15	25	28	12	13	4	26	5	3	9	—	H
Anthoxanthum nipponicum Honda	—	—	—	—	—	18	—	17	—	—	—	8	11	10	—	9	—	—	12	13	4	2	5	3	9	5	G
Arabis alpina L.	—	—	—	—	—	—	—	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	H
Arctostaphylos uva-ursi (L.) Spreng.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	27	—	—	—	—	—	29	23	W
Arctous alpinus (L.) Nied.	—	—	—	—	—	—	—	—	—	26	—	—	—	—	—	—	—	—	—	—	—	—	—	12	—	23	W
Athyrium disentifolium Tausch ex Opiz	—	—	—	10	—	26	—	24	—	20	—	28	—	10	10	20	—	—	11	11	—	22	—	12	9	10	P
Avenella flexuosa (L.) Drejer	—	—	8	2	—	—	—	16	—	20	8	11	5	3	—	7	6	4	2	3	7	5	2	3	9	6	G
Bartsia alpina L.	—	5	15	—	—	—	—	16	—	20	8	11	5	3	—	7	—	—	20	22	—	5	15	—	15	15	H
Beckwithia glacialis (L.) A. & D. Löve	4	5	15	18	—	—	0	0	1	1	0	1	0	0	8	13	0	1	4	3	—	2	15	2	1	1	H
Betula pubescens ssp. tortuosa (Ledeb.) Nyman	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	W
Bistorta vivipara (L.) Delabre	—	—	3	3	10	—	—	3	—	13	—	7	—	—	—	30	5	3	15	8	—	15	25	24	29	10	H
Campanula rotundifolia L.	—	—	—	—	—	10	—	7	—	—	—	6	—	—	—	—	—	3	20	14	—	—	—	6	22	12	H
Cardamine bellidifolia (L.) Cranz	—	—	8	2	—	—	0	2	1	—	1	0	0	1	2	6	0	1	2	1	1	3	—	2	—	1	H
Carex atrata L.	—	—	—	—	—	—	—	14	—	—	—	7	—	—	—	—	—	28	19	14	—	—	1	—	—	30	G
Carex bigelowii Torr. Ex Schwein	—	—	3	3	10	22	3	1	1	0	2	2	10	10	3	4	1	1	1	3	3	2	1	2	8	5	G
Carex brunnescens (Pers.) Poir.	—	—	—	22	—	—	—	—	—	—	—	—	12	9	—	30	—	—	—	10	—	7	12	3	—	—	G
Carex lachenalii Schkuhr	—	—	—	29	—	21	25	7	25	18	8	24	14	14	5	8	—	10	11	7	—	17	28	7	—	30	G
Carex rupestris All.	—	—	—	—	—	—	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	G
Carex vaginata Tausch	—	—	9	9	—	—	0	13	—	—	5	13	—	—	—	15	—	—	20	24	—	—	—	3	25	9	G
Cerastium alpinum L.	—	—	—	—	—	20	0	0	10	3	3	21	15	26	7	13	7	7	10	11	4	5	—	16	7	7	H
Cerastium alpinum ssp. lanatum (Lam.) Ces.	—	—	—	—	—	—	25	25	—	—	—	—	—	—	—	—	—	—	—	—	—	29	—	—	—	—	H
Cerastium cerastoides L. Britton	—	—	—	—	—	—	30	27	—	18	—	24	6	14	8	18	11	12	14	28	—	14	—	21	13	26	H
Chamerion angustifolium (L.) Holub	—	—	—	—	5	—	—	—	—	—	—	—	—	—	2	—	—	—	20	—	—	26	—	—	11	11	H
Coeloglossum viride (L.) Hartm.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	—	H
Cryptogramma crispa (L.) R.Br. ex Hook.	—	—	—	—	—	21	—	—	—	—	—	—	—	3	—	13	—	15	—	30	—	12	—	16	—	10	P
Cystopteris fragilis (L.) Bernh.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	—	—	—	—	—	—	—	—	—	—	P
Deschampsia alpina (L.) Roem. & Schult.	10	—	—	2	—	20	30	7	—	3	3	21	15	—	7	13	7	7	10	11	4	5	16	16	7	7	G
Diphasiastrum alpinum (L.) Holub	—	—	—	—	—	—	—	15	—	18	6	7	6	4	—	10	—	1	12	16	—	6	7	3	10	5	P
Draba fladnizensis Wulfen	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	H
Empetrum nigrum L.	—	—	—	3	—	3	—	0	—	5	9	3	1	0	2	3	1	—	1	2	20	1	2	0	1	1	W
Epilobium anagallidifolium Lam.	—	—	30	9	—	—	—	—	—	—	—	22	—	—	—	—	—	—	16	20	—	—	—	—	11	30	H
Erigeron uniflorus L.	—	10	—	9	—	5	—	—	—	—	2	3	—	9	2	3	4	3	20	22	—	—	7	—	—	25	H
Eriophorum angustifolium Honck.	—	10	—	—	5	5	25	10	8	2	6	25	20	30	2	3	—	1	14	29	5	5	2	—	—	30	G
Eriophorum scheuchzeri Hoppe	—	—	—	—	—	26	—	—	—	—	—	—	—	30	—	7	—	—	—	29	—	—	—	—	—	—	G
Eriophorum vaginatum L.	—	23	—	—	8	6	—	4	8	20	15	15	20	—	2	3	—	—	14	—	5	2	—	22	—	—	G
Equisetum arvense L.	—	—	—	—	—	—	—	24	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	P

APPENDIX

Continued.

Taxa/Summit code	1A	1B	2A	2B	3A	3B	4A	4B	5A	5B	6A	6B	7A	7B	8A	8B	9A	9B	10A	10B	11A	11B	12A	12B	13A	13B	L-f
Euphrasia wettsteinii Gussarova	—	—	—	—	—	—	—	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	H
Festuca ovina L.	—	18	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—	G
Festuca vivipara (L.) Sm.	—	—	—	0	6	9	0	0	1	1	0	0	0	0	1	2	0	0	2	2	0	1	0	0	1	1	G
Geranium sylvaticum L.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	32	H
Gymnocarpum dryopteris (L.) Newman	—	—	—	—	—	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	P
Harrimanella hypnoides (L.) Coville	—	—	—	—	—	27	30	10	30	18	6	8	—	—	30	—	6	4	13	19	5	—	—	2	—	10	W
Hieracium sec. *alpina* (Griseb.) Gremli	—	—	—	—	—	3	—	5	—	—	9	4	8	9	8	20	1	1	2	2	—	2	6	2	3	3	H
H. sec. *alpina* grp. *nigrescens*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	—	—	H
Huperzia appressa (Bach. Pyl. Ex Desv.) A.&D. Löve	—	12	1	2	4	5	—	3	0	0	0	2	1	0	8	6	1	0	2	1	1	1	1	1	1	1	P
Juncus biglumis L.	—	—	—	—	—	—	—	11	—	—	—	28	—	—	—	—	—	—	25	27	3	—	—	—	—	1	G
Juncus trifidus L.	—	—	—	—	—	15	—	17	30	10	—	8	12	3	8	6	1	1	2	2	—	3	0	1	1	1	G
Juniperus communis ssp. *alpina* (Sm.) Čelak.	—	—	—	—	—	—	—	—	—	—	—	21	—	—	—	—	—	—	20	11	—	—	—	2	20	8	W
Leontodon autumnalis L.	—	—	—	—	—	—	—	—	—	—	—	23	—	28	—	—	—	—	15	17	—	—	—	—	—	1	H
Luzula arcuata (Wahlenb.) Sw./ *L. confusa* Lindeb.	4	3	1	2	5	8	0	2	0	0	0	0	0	0	2	3	0	1	1	1	1	1	0	0	1	1	G
Luzula multiflora ssp. *frigida* (Buch.) V.I. Krecz.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	G
Luzula spicata (L.) DC.	—	—	9	8	—	15	2	0	1	3	4	4	3	3	—	7	1	1	1	1	9	3	0	0	4	1	G
Minuartia biflora (L.) Schinz & Thell.	—	—	9	29	—	—	15	11	—	—	15	24	—	—	—	27	6	15	12	20	—	—	—	2	—	—	H
Omalotheca norvegica (Gunnerus) Sch.Bip.&F.W.Schulz	—	—	—	—	—	27	—	—	—	30	—	—	—	21	—	—	—	—	—	—	12	—	—	—	11	7	H
Omalotheca supina (L.) DC.	—	—	16	10	—	18	15	8	30	—	3	7	6	1	10	6	10	5	5	5	10	5	25	2	—	7	H
Oxyria digna (L.) Hill	—	—	30	18	—	—	1	7	—	16	15	13	—	26	30	15	—	17	8	5	—	5	—	21	25	14	H
Petasites frigidus (L.) Fr.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25	—	—	—	—	—	—	—	H
Phleum alpinum L.	—	—	—	—	—	—	—	28	23	—	13	—	—	28	—	—	12	—	28	—	—	—	—	29	29	15	G
Phyllodoce caerulea (L.) Bab.	—	—	—	—	—	—	—	23	—	—	2	8	—	4	12	9	4	3	15	28	—	7	—	21	13	8	W
Poa alpina L. var. *alpina*	—	—	—	—	—	—	30	25	—	—	—	21	—	—	—	12	6	—	15	—	—	—	—	—	—	—	G
Poa alpina L. var. *vivipara*	—	—	—	—	—	—	30	28	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	G
Poa arctica R.Br. / *Poa pratensis* L.	—	19	—	—	—	—	0	16	20	10	—	—	—	—	—	22	—	4	14	—	—	—	27	22	27	1	G
Poa flexuosa Sm.	5	5	0	1	4	3	15	0	0	0	0	0	0	0	1	2	0	0	0	0	0	1	—	0	1	—	G
Poa x *jemtlandica* (Almq.) K.Richt.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—	—	—	28	—	—	—	G
Potentilla crantzii (Crantz) Beck ex Fritsch	—	—	—	—	—	—	1	0	—	—	—	19	—	—	—	—	—	4	22	12	—	—	—	—	25	20	H
Pyrola minor L.	—	—	—	—	—	—	—	—	—	—	—	22	—	—	—	—	—	—	—	30	—	26	—	29	—	21	H
Ranunculus acris L.	—	—	—	—	—	—	—	30	1	—	—	21	1	—	—	—	—	—	4	7	—	12	—	—	23	14	H
Ranunculus pygmaeus Wahlenb.	—	—	—	—	—	—	1	7	—	18	2	0	—	21	9	17	0	4	2	6	—	20	—	21	22	26	H
Rhodiola rosea L.	—	—	—	—	—	—	—	1	—	—	—	—	—	—	0	—	—	4	14	30	7	2	—	22	—	10	H
Rubus chamaemorus L.	—	—	—	—	—	—	—	—	—	—	—	15	—	—	6	6	6	—	9	17	7	3	—	26	26	—	H
Rumex acetosa L.	—	30	—	—	—	—	25	13	—	—	—	—	—	13	7	6	7	—	—	—	—	—	28	5	15	5	H
Sagina saginoides (L.) H.Karst.	—	—	—	—	—	—	—	—	—	—	—	24	—	30	—	—	—	1	1	16	—	—	—	5	—	—	H
Salix glauca L.	—	19	—	—	—	—	—	—	—	—	1	1	1	—	—	—	—	1	1	2	—	—	—	—	27	11	W
Salix herbacea L.	—	—	9	2	5	6	0	0	0	0	1	29	1	1	2	3	1	1	2	2	0	1	0	0	1	1	W
Salix lanata L.	—	—	—	—	—	—	—	—	—	—	—	21	—	—	—	—	—	—	—	29	—	—	—	—	26	20	W
Salix lapponum L.	—	—	—	—	—	—	—	—	—	26	—	—	—	—	—	9	—	—	—	—	20	20	—	—	21	14	W

A. ODLAND ET AL. / 469

Taxa/Summit code	1A	1B	2A	2B	3A	3B	4A	4B	5A	5B	6A	6B	7A	7B	8A	8B	9A	9B	10A	10B	11A	11B	12A	12B	13A	13B	L-f
Salix phylicifolia L.	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	W
Saussurea alpina (L.) DC.	—	—	9	9	—	—	2	0	1	2	2	3	—	30	—	7	1	1	18	8	7	24	—	29	25	19	H
Saxifraga cernua L.	—	—	—	14	—	—	1	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	H
Saxifraga cespitosa L.	—	—	—	14	—	—	1	0	—	—	—	7	—	—	—	—	0	—	—	22	—	—	—	—	—	—	H
Saxifraga nivalis L.	—	—	—	14	—	—	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	H
Saxifraga oppositifolia L.	—	—	—	14	—	—	1	0	—	—	—	6	—	—	—	19	—	—	20	27	10	—	—	—	—	8	H
Saxifraga rivularis L.	—	—	—	14	—	—	—	10	—	—	—	—	—	—	9	—	—	—	4	7	—	10	—	21	—	30	H
Saxifraga stellaris L.	—	—	—	10	—	16	—	—	—	—	—	30	—	13	—	15	—	—	14	21	9	—	—	—	8	8	H
Saxifraga tenuis (Wahlenb.) Harry Sm. Ex Lindm.	—	—	—	—	—	—	—	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	H
Selaginella selagioides (L.) P.Beauv.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	24	—	—	—	—	—	—	P
Sibbaldia procumbens L.	—	23	9	9	—	21	15	7	20	5	2	2	6	3	8	7	2	2	2	2	7	3	9	1	8	8	H
Silene acaulis (L.) Jacq.	—	—	—	—	—	—	1	0	1	2	1	1	—	14	1	—	1	1	—	10	—	—	—	—	—	—	H
Silene dioica (L.) Clairv.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	H
Silene wahlbergella Chowdhuri	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	22	—	—	—	—	—	—	H
Solidago virgaurea L.	—	—	—	—	—	—	—	—	—	26	—	21	—	23	—	17	—	—	9	9	—	13	—	—	13	7	H
Taraxacum F.H.Wigg.	—	—	—	22	—	—	30	10	—	26	9	10	—	21	—	18	11	10	10	12	—	14	—	26	—	5	H
Thalictrum alpinum L.	—	—	—	—	—	—	—	18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	H
Trientalis europea L.	—	—	—	—	—	—	—	4	15	10	1	3	—	4	—	—	—	30	—	30	25	25	—	28	—	17	H
Trisetum spicatum (L.) K.Richt.	—	19	9	9	—	30	3	4	15	16	—	22	—	17	8	6	4	2	9	5	5	5	5	3	25	20	G
Vaccinium myrtillus L.	—	—	—	—	—	—	—	—	—	—	—	10	—	29	—	6	25	25	17	17	14	14	5	1	8	5	W
Vaccinium uliginosum L.	—	—	—	—	15	—	—	—	—	—	—	—	—	—	—	—	—	—	22	2	—	—	—	29	20	6	W
Vaccinium vitis-idaea L.	—	—	—	—	—	—	3	0	5	2	1	3	2	1	2	3	1	1	1	1	0	1	0	0	3	1	W
Veronica alpina L.	—	—	—	—	—	—	—	16	—	20	8	8	—	14	—	18	15	5	14	16	—	14	—	—	—	13	H
Viola palustris L.	—	—	—	—	—	29	—	—	—	—	—	23	—	—	—	—	—	—	—	30	—	—	—	—	—	—	H
Viscaria alpina (L.) G.Don	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	13	8	—	13	2	—	7	—	21	—	8	H
No. taxa	**4**	**12**	**20**	**32**	**9**	**27**	**38**	**66**	**23**	**36**	**35**	**63**	**22**	**45**	**30**	**51**	**34**	**42**	**64**	**71**	**21**	**51**	**26**	**51**	**44**	**68**	