Scottish Natural Heritage Commissioned Report No. 879

Climate change impacts on the vegetation of Ben Lawers







COMMISSIONED REPORT

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COMMISSIONED REPORT 必 ふう Summary

Climate change impacts on the vegetation of Ben Lawers

Commissioned Report No. 879 Project No: 14633 Contractor: Louise Ross (Ilex Ecological Services) Year of publication: 2015

Keywords

Climate change; montane vegetation; moss-heath; vegetation change; re-visitation study; Ben Lawers.

Background

A warming climate poses a serious threat to important Scottish montane plant communities, which contain a high proportion of cold-adapted arctic-alpine species. Warming is expected to continue, resulting in changes to species composition, but how this will develop is uncertain. This study compares 1950s plant species data from Ben Lawers NNR, a key stronghold of arctic-alpine vegetation in Scotland, with present day vegetation in order to provide an indication of future change, and inform management and mitigation strategies. It analyses changes in plant diversity, cover of plant functional groups, abundance of individual species and vegetation height. We also examine the climatic preferences of the species that have undergone the greatest change, and establish indicator species of climate warming for the three habitat types studied.

Main findings

- Vegetation change on Ben Lawers shows the influence of climate change since 1952.
- Species composition has changed most dramatically in montane habitats.
- Montane habitats and acid grasslands have become more homogeneous. Upland fens, marshes and swamps have retained more of their original character.
- The number of species has not declined significantly, but competitive generalist species previously more common at lower elevations have increased in montane habitats.
- Cover of bryophytes, forbs and lichens has declined significantly, while graminoid (grass, sedge and rush) cover and vegetation height have increased significantly.
- The majority of "winning" species have a temperate distribution, whereas many of the "losing" species have a (boreo) arctic-montane element to their distribution.
- "Winning" species prefer significantly higher mean January and July temperatures, and significantly lower precipitation than "losing" species.
- The mean thermophilization (climate warming) score is greatest for plots in montane habitats and lowest for upland fens, marshes & swamps.
- The majority of indicator species of climate warming are grasses, sedges and rushes.

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1. INTRODUCTION

1.1 Climate change trends in Scotland

Between 1961 and 2004, Scotland's climate has undergone considerable change. Mean temperatures have increased by at least 1°C in spring, summer and winter, in all areas of Scotland. Winter rainfall has increased by up to 60% over the same period, particularly in the north and west, whereas summer rainfall has either not changed significantly or has slightly declined (Barnett *et al.* 2006). The number of frost and snow days has declined by more than 25%, while at the same time the growing season now starts around three weeks earlier and ends two weeks later than was typical in the 1960s (Barnett *et al.* 2006). This trend towards warmer, wetter and less snowy conditions reflects a global trend (IPCC 2007).

At Environmental Change Network (ECN) sites across the UK, warming between 1993 and 2007 was more rapid in upland/ montane sites (1-2 °C) than lowland sites (0.7 °C) (Morecroft *et al.* 2009). Winter (as opposed to summer) warming had also dominated at the upland ECN site Moor House in the North Pennines (Holden & Rose 2010). Even a rise in mean temperature of 1.8 °C by 2100 would equate to an annual altitudinal isotherm ascent of 300 m for an area such as the Cairngorms (Hill *et al.* 1999). Projected temperature changes are expected to be greater in mountains at higher northern latitudes than in those in temperate and tropical zones, with the rate of warming in mountain systems projected to be two to three times higher than that recorded during the 20th century (Nogués-Bravo *et al.* 2007). In view of these projected climate changes, the outlook for Scottish montane plant communities, which contain a high proportion of cold-adapted arctic-alpine species, is of great concern.

1.2 Importance of montane plant communities

In Scotland, montane areas are generally defined as being above the potential tree line, which occurs up to around 600 m in more continental areas in the east, but can be as low as 300 m in the north-west (Horsfield and Thompson 1996). However, the widespread loss of natural treeline scrub in Scotland means that it is difficult to fix the altitudinal limits of vegetation zones. The term "montane" here is therefore equivalent to the European term "alpine", i.e. areas above the tree line (Horsfield and Thompson 1996). Montane areas have high topographic diversity, caused by high spatial variability in slope and aspect, giving rise to a high diversity of microhabitats with a range of microclimatic and soil conditions, facilitating in turn high levels of biodiversity. Montane areas therefore represent important areas for the detection of climate change and the assessment of climate-related impacts (Beniston 2003). Montane vegetation may be particularly sensitive to climate change, as species in such communities are adapted to cold conditions and/or are intolerant of more intense competition at lower altitudes (Körner 1999). Upward migration of alpine plant species has been recorded in Scandinavia (Klanderud & Birks 2003) and the Alps (Grabherr et al. 1994). Altered temperature and precipitation regimes may allow the expansion of competitive species from lower altitudes into the montane zone, potentially resulting in a reduction in the area of montane habitat and local extinction of alpine species (Harrison et al. 2001). A wider understanding of the effects of climate change on Scottish montane vegetation is desirable due to the rarity and international importance of many of the communities (Thompson & Brown 1992), yet the evidence base for responses in these habitats and species to climate change is skeletal (Brooker 2011). Studies must necessarily be on a decadal time-scale, as most component species are long-lived and slow-growing (Körner 1999).

1.3 Changes in montane plant communities

Montane plant communities in Scotland are composed of a diverse mix of Atlantic, northern, arctic and arctic-alpine species, with many on the edge of their global range (Averis *et al.*

2004). This diversity, combined with a highly spatially and temporally variable maritime upland climate, means that predicting changes in plant communities is difficult. However, studies carried out to date have begun to reveal the impact of climate change on Scottish montane plant communities. A decline of cold-adapted northern and alpine plant species previously characteristic of montane ecosystems, with a concurrent increase in the frequency and abundance of warm-adapted species, particularly generalist graminoids, has been detected in the Cairnoorms (Britton et al. 2009) and the North-West Highlands (Ross et al. 2012). On Ben Lawers itself, Geddes & Miller (2012) recorded a spread of graminoids and bryophytes in calcareous grasslands between 1996 and 2010, which may be the result of an increasingly warm and prevailingly wet climate, as grazing pressure did not change. Important alpine communities are predicted to lose climate space, even under a conservative climate change scenario, in a study that included the Ben Lawers range (Trivedi et al. 2008). Climate change is also expected to drive substantial changes in mountain summit phenology, especially by prolonging the growing season, which may facilitate colonisation and competitive exclusion by species currently restricted to lower elevations (Chapman 2013). The increase in warm-adapted species and the concurrent decline of cold-adapted species is a process described by Gottfried et al. (2012) as thermophilization.

However, although plant species composition is expected to change following climate change, there are still many unknowns in predicting future change. Archived botanical data on montane plant communities can be exploited to allow comparisons of species composition over a longer time period than can be achieved through most monitoring schemes to date (Ross *et al.* 2010; Stöckli *et al.* 2011). A retrospective study comparing historical data with that from the present day can provide a more probable indication of future change, potentially improving the suitability of management and mitigation strategies.

2. OBJECTIVES

In this study, we carry out a botanical re-survey of plots first surveyed in the 1950s to examine the impact of climate change on the vegetation of the Ben Lawers range and surrounding hills in Perthshire. We aim to analyse changes in the following areas: plant species diversity; how change varies between habitats; cover of plant functional groups; vegetation height; cover of individual species; and plant species' climatic preferences. Finally, indicator species of climatic warming are to be derived from the calculation of thermophilization indicator scores.

3. METHODS

3.1 Study area

The study area (Figure 1) is situated in the southern Scottish Highlands (lat: 56°34' and long: 4°19' approx.). It covers the Ben Lawers summit area, Coire Fionn Lairige and Meall nan Tarmachan to the south-west, Meall a' Choire Leith and Meall Corranaich to the west, the corrie above Lochan nan Cat and Meall Garbh to the north, Coire Cireineach to the east and Creag nan Gabhar and Creag Dhubh to the south. The altitude of the plots varies between 484 m and 1145 m a.s.l, with a mean altitude of 839 m a.s.l.. The area has been designated as a National Nature Reserve, Site of Special Scientific Interest, Special Area of Conservation and a National Scenic Area. Unusually for the mainly acidic Scottish Highlands, the geology consists of soft Dalriadan calcareous mica schists, which give rise to basic soils (Lusby & Wright 2001). Meteorological data for the study area itself is not available, but at 130 m a.s.l. at Ardtalnaig on the banks of Loch Tay, approximately 7 km distant and 900 m lower in altitude than the summit of Ben Lawers, the annual mean

maximum temperature is 11.6°C, mean minimum temperature is 4.7°C and precipitation 1252 mm per annum (Geddes & Miller 2012). The vegetation on Ben Lawers includes elements of both arctic and alpine floras, but is also subject to an oceanic influence. Floristically richer vegetation is found where the soil is enriched through deposits of weathered rock (e.g. at cliff bases) or flushing with water which has run through or over the bedrock (Poore 1993). Sheep are the main grazing animals, hefted onto the area from June to September at a density of around 2.5-3 ha⁻¹ (Miller *et al.* 2010). An appropriate level of grazing is essential to the maintenance of calcareous grasslands and dwarf-herb communities. The Ben Lawers range is also grazed by red deer (*Cervus elaphus*), mountain hares (*Lepus timidus* ssp. *scoticus*), field voles (*Microtus agrestis*) and ptarmigan (*Lagopus mutus*) (Geddes & Miller 2012).



Figure 1. Ben Lawers National Nature Reserve and the surrounding area. Circles represent the location of re-survey plots.

3.2 Original survey of 1952-1958

Fifty of the original vegetation records used in this re-survey study were collected in 1952 by Duncan Poore (Poore 1955), with seven plots recorded by Derek Ratcliffe in 1958 and one by Donald McVean in 1957. In 1962, these records were incorporated into the monograph "Plant Communities of the Scottish Highlands" (McVean & Ratcliffe 1962). The aim of this work was to describe and classify, for the first time, the upland plant communities of the Scottish Highlands, based on the presence and cover of the dominant and abundant species. These historic records provide rare documentation of vegetation composition five decades ago. Poore's survey concentrated on the Breadalbane area, particularly Ben Lawers and the surrounding hills. Representative samples of a range of vegetation types were recorded. The original dataset includes information on locality, geographical coordinates (British National Grid to nearest 100 m x 100 m), altitude, aspect, slope, vegetation height and overall vegetation cover, but the plots were not permanently marked. Plots were usually 4 m² (2 m x 2 m) in size, occasionally 0.3 m², 0.5 m², 1 m², 1.5 m², 2 m², 5 m², 6 m², and 10 m². Smaller plots were used in habitat types that are rather limited in extent, such as flushes, and larger plots used in more homogeneous, species-poor vegetation. All plant species including bryophytes and terricolous macrolichens in the plots were recorded using percentage cover values that were subsequently converted to the Domin scale of cover abundance (1 = one or two individuals; 2 = sparsely distributed; 3 = frequent but low cover (<5%); 4 = 5%-19%; 5 = 20%-25%; 6 = 26%-33%; 7 = 34%-50%; 8 = 51%-75%; 9 = 76%-90%; 10 = 91%-100%).

3.3 Re-survey of 2013

The re-survey was carried out in August 2013, when 58 plots were surveyed. This includes fifteen plots which were in acid grassland (Plate 1), 21 in upland fen, marsh and swamp habitats (Plate 2) and 20 in montane habitats (Plate 3). The plant communities re-surveyed are shown in Table 1, below. More plot details are shown in Annex 1. A further 14 plots originally recorded in the area were not re-surveyed as part of this study. This was because some plots could not be satisfactorily relocated from the original plot information (396, 534, 685, 882), incomplete or inaccurate information in the original data (379, 381, 479, 534, 617) or because time constraints prevented the re-survey of more distant plots (266, 363, 426, 494, 618). There are some more original plots in the Breadalbane area to the north of Ben Lawers, principally on Carn Mairg, Schiehallion and Rannoch Forest.

UK BAP broad habitat type	NVC Community type	Number of plots
	U5 Nardus stricta - Galium saxatile grassland	8
Acia grassiana	U6 Juncus squarrosus-Festuca ovina grassland	7
Calcareous grassland	CG11 <i>Festuca ovina-Agrostis capillaris-Alchemilla alpina</i> grass-heath	1
Dwarf-shrub heath	H18 Vaccinium myrtillus-Deschampsia flexuosa heath	1
	M9 Carex rostrata-Calliergonella cuspidata mire	1
	M12 Carex saxatilis mire	9
Upland fen,	M21 <i>Narthecium ossifragum - Sphagnum papillosum</i> valley mire	2
marsh &	M23 Juncus effusus - Galium palustre rush-pasture	1
swamp	M37 Palustriella commutata - Festuca rubra spring	1
	M38 Palustriella commutata - Carex nigra spring	3
	unclassified	4
	U7 Nardus stricta - Carex bigelowii grass-heath	6
	U8 Carex bigelowii - Polytrichum alpinum sedge-heath	7
Montane	U10 Carex bigelowii - Racomitrium lanuginosum moss-heath	4
nabilals	U12 Salix herbacea - Racomitrium heterostichum snow bed	2
	U15 Saxifraga aizoides-Alchemilla glabra banks	1

Table 1. Classification and sample size of re-survey plots, according to UKBAP Broad Habitat type and NVC community type (Rodwell 1991, 1992, 1995).



Plate 1. Re-survey plot in an acid grassland habitat (U6 Juncus squarrosus – Festuca ovina grassland)



Plate 2. Re-survey plot in an upland fen, marsh and swamp habitat (M12 Carex saxatilis mire)



Plate 3. Re-survey plot in a montane habitat (U10 Carex bigelowii – Racomitrium lanuginosum *moss-heath)*

The survey method described by McVean and Ratcliffe (1962) was followed as closely as possible in the re-survey. Sampling areas were re-located by the original geographical coordinates (British National Grid to nearest 100 m x 100 m) using a hand-held GPS unit, and the exact location of the plot selected using information on slope, aspect and vegetation from the original survey. Where possible, plots for re-survey were located in a homogenous stand of vegetation (as McVean and Ratcliffe did) within the sampling area. Again where possible, their composition was generally similar to that of the original plot, ensuring that estimates of change were conservative. This method of placing plots in cases where their precise original location is uncertain has been shown to be suitable for detecting temporal change with confidence (Ross et al. 2010). The re-survey plots were recorded using the same size of plots as in the original survey, in most cases 4 m². For each plot, the ten-figure grid reference, GPS error, altitude, number of groups of dung, abundance of hoof prints and signs of grazing were recorded. The grazing intensity measurements were not analysed in this report, but banked for future comparisons. Five vegetation height measurements and five moss height measurements were taken in the plot, by placing a ruler vertically on the surface of the soil or litter at five random locations in the plot, from which means were later calculated. All plant species including bryophytes and terricolous macro-lichens in the plots were recorded using percentage cover values, except where cover was <5%, when Domin categories were also recorded. This ensured that the re-survey data are backwardly compatible with the original McVean and Ratcliffe Domin data, yet retain a high level of accuracy for future use. Nomenclature follows Stace (2010) for vascular plants, Hill et al. (2008) for bryophytes and Smith et al. (2009) for lichens. Species names that have changed since the original survey are listed on the synonyms tab of the species data file and in Annex. 3, with their 2013 equivalent as used in this study. Up to five photos were taken of each plot, to provide landscape context and to aid relocation in future re-surveys.

3.4 Data analysis

All statistical tests were carried out using the *vegan* package (Oksanen *et al.* 2013) in R version 3.0.2 (R Development Core Team 2013), except the Detrended Correspondence Analysis (DCA), where CANOCO 4.5 (ter Braak & Šmilauer 2002) was used. Records of species from either survey that only occurred once or twice and at $\leq 1\%$ cover were removed from the analysis, as they are more likely to be overlooked. As the original records were made using Domin categories, all the new percentage cover data were converted to the Domin scale, and both datasets were subsequently back-transformed to percentage cover using the midpoint of each Domin category in the "Domin 2.6" transformation (Currall 1987), where

% cover = $(Domin value)^{2.6}/4$

The transformation provides a convenient and robust transformation of Domin ordinal values to quasi-continuous variables that are directly comparable for use in numerical analysis (Rothero *et al.* 2007).

3.4.1 Diversity changes

Four types of test were carried out for each of the three broad habitat types for which there were multiple plots, and for all the plots combined (including the single dwarf-shrub heath and calcareous grassland plots). First, we calculated the mean species richness (number of species) per plot for both surveys using the function *specnumber*, then tested for significant differences using paired t-tests. Second, the mean Shannon-Weaver diversity indices were calculated using the *diversity* function and tested using Wilcoxon rank sum tests for non-parametric (not normally distributed) data. Third, a heterogeneity index based on the distance from a plot to the centroid (central point of species composition in ordination space) was calculated using the function *betadiver*, and tested using analysis of variance. This is a

test of the equality of variances. A high value of this index shows high heterogeneity (Oksanen *et al.* 2013). Finally, multivariate analysis of variance was carried out to check for significant difference in species composition between the original survey and re-survey, using the *adonis* function, which is based on differences in group means (Oksanen *et al.* 2013).

3.4.2 Patterns of change

To reveal the patterns of compositional change, detrended correspondence analysis (DCA) was carried out on all species data to give two points (original survey and re-survey) in ordination space for each plot. Rare species were down-weighted, detrending was by segments, non-linear re-scaling was applied, and the data were log-transformed to stabilise the variances. An ordination diagram was produced. For each of the three broad habitat types, and for all the plots combined (including the single dwarf-shrub heath and calcareous grassland plots), the Bray-Curtis distance (in ordination space) between the original and resurvey plots was calculated using the function *vegdist*.

3.4.3 Plant functional groups

For the six plant functional groups found in the plots (bryophytes, dwarf-shrubs, forbs, graminoids (grasses, sedges and rushes), lichens and pteridophytes), we calculated the mean cover per plot in the original and re-survey for all the plots combined, and tested these for significant differences using paired t-tests.

3.4.4 Vegetation height

For all the plots combined, where data were available for the original plot (n = 36), the mean vegetation height was calculated for the original and re-survey plots, and tested for significant differences using paired t-tests.

3.4.5 "Winners" and "losers"

For all the plots combined, the difference in total percentage cover points between the original survey and re-survey was calculated for each species. Each species was also tested for significant differences in cover between the two surveys. The 15 species that had undergone the greatest increases in cover, and the 15 species where the greatest declines were recorded, were listed with their biogeographic distribution, taken from Hill *et al.* (2004, 2007). The species used in this analysis and in that described in Section 3.4.6, with the greatest cover changes between the two surveys, have the strongest influence on the compositional change. There were many species that did not show any or much change, but such species were not included in the analysis as they could obscure any patterns of environmental change (Ross *et al.* 2012).

3.4.6 *Climatic preferences*

For the winning and losing species, the unweighted mean values of mean January temperature (°C), mean July temperature (°C) and annual precipitation (mm) were calculated, and tested for significant differences using paired t-tests. These climate variables are based on the mean values across all the 10 km squares in which these species occur in the British Isles, and were obtained from PLANTATT (Hill *et al.* 2004) and BRYOATT (Hill *et al.* 2007). The two "losing" lichen species were not included in this analysis as the climatic preference values are not available for lichen species, but are still included in the table for information.

3.4.7 Thermophilization scores

A thermic indicator score (S) was calculated for each plot in both surveys, from which a thermophilization score (D) for the change in each plot was derived. This was based on the method described in Gottfried *et al.* (2012), except mean January temperature was used here, as changes in this value are likely to reflect climatic warming more accurately than the altitudinal rank of species used in that study. Moreover, the rise in temperature was greater in winter than in summer at UK upland weather stations between 1961 and 2000 (Burt and Holden 2010), so impacts are more likely to be driven by changes in winter rather than summer temperatures.

The formula used for the thermic indicator scores (Gottfried et al. 2012) was:

$S = (\sum \text{mean January temperature (species_i)} \times \text{cover (species_i)}) / \sum \text{cover (species_i)})$

The thermophilization score (D) for each plot was then calculated by:

$D = (S_{2013} - S_{1952})$

The thermophilization scores for each broad habitat type were then tested for significant differences using t-tests.

3.4.8 Indicator species of climate warming

For each of these habitat types, the three plots with the highest thermophilization scores were selected. The top 25% of species in these plots that had undergone positive change in D were then derived, and listed as indicators of climate warming.

4. RESULTS

The original and re-survey species data, with information on location, plot details, community, and vegetation measurements, have been lodged in a data archive (Ross & Flagmeier 2015). This contains all the original data compiled by McVean and Ratcliffe (1962) and re-survey data from several studies. Data relevant to this study can be found using the plot references given in Annex 1.

4.1 Diversity changes

Overall, 49 species were lost from the original survey, and 16 were gained in the re-survey. The species present in either or both surveys are listed in Annex 2. The results of the analyses on changes in diversity are shown in Figures 2a, b and c, and in tabular form in Annex 4. None of the habitats showed significant changes in species richness, although the decline recorded in acid grasslands was marginally significant (P = 0.068). However, the diversity index increased significantly in montane habitats (P < 0.001) and in the overall analysis (P = 0.007), but not in acid grasslands (P = 0.131) or upland fens, marshes & swamps (P = 0.338). Acid grasslands and montane habitats had undergone significant declines in heterogeneity (P = 0.019, P = 0.022), which was also the case for the re-survey plots as a whole (P = 0.005). The decline of heterogeneity in acid grasslands was particularly marked (-0.102 ordination units).



Figure 2a. Mean species richness per plot in the original survey (1952) and re-survey (2013).



Figure 2b. Mean Shannon-Weaver diversity index per plot in the original survey (1952) and re-survey (2013). Asterisks show significant differences between surveys: ** = P<0.01, *** = P<0.001



Figure 2c. Mean heterogeneity index per plot in the original survey (1952) and re-survey (2013). Asterisks show significant differences between surveys: * = P < 0.05, ** = P < 0.01

4.2 Patterns of change

The ordination diagram of the DCA of all the plot data is shown in Figure 3. The polygon of re-survey plots lies more or less within that of the original survey plots, showing that species composition is more similar in the re-survey.



Figure 3. Detrended Correspondence Analysis (DCA) ordination diagram for plant species composition data from the original survey plots (squares) and the re-survey plots (circles). Polygons are envelopes around samples from the original survey and re-survey.

The Bray-Curtis distances, i.e. the magnitude of change in species composition between the original and re-survey plots, is shown in Figure 4. Montane habitats had changed to the greatest extent, and upland fen, marsh & swamp habitats the least. There are no significant differences between the scores for the different habitat types. This is corroborated by the results of the *adonis* tests, which reported significant changes in species composition for acid grasslands (P<0.001), montane habitats (P=0.002) and all the plots combined (P=0.005), but not for fens, marshes & swamps (P=0.915). The full results of the *adonis* tests are shown in Annex 5.



Figure 4. Mean (± standard error) Bray-Curtis Distance (through ordination space) between the species composition of plots of the original and re-survey.

4.3 Plant functional groups

Table 2 shows how the cover of plant functional groups has changed between the two surveys. In both surveys, bryophytes and graminoids are the most important components of the vegetation. There has been a significant decline in the cover of bryophytes, forbs and lichens since the original survey, and a very highly significant increase of large magnitude in graminoid cover. The cover of dwarf-shrubs and pteridophytes was relatively low in both surveys, and showed little change.

Table 2. Percentage cover of key plant functional groups in both surveys. P values are derived from paired t-tests, and those in bold are significant below the 5% level.

	Original survey (1952)		Re-su	ırvey (2013)	Change	Р
	Mean	Standard error	Mean	Standard error		
Bryophytes	52.7	4.1	43.9	2.8	-8.8	0.038
Dwarf-shrubs	6.3	2.1	8.2	1.8	1.9	0.2
Forbs	22.6	3.2	16.6	1.8	-6	0.029
Graminoids	46.4	4.3	69.1	3.7	22.7	<0.001
Lichens	5.1	2.1	0.7	0.2	-4.4	0.037
Pteridophytes	1.2	0.3	0.7	0.2	-0.5	0.06

4.4 Vegetation height

The mean vegetation heights recorded in the original survey and in the re-survey are shown in Figure 5. The height in 2013 was significantly greater than that in 1952 (P<0.001).



Figure 5. Mean (\pm standard error) vegetation height in plots of the original survey (n=36) and the re-survey (n=36).

4.5 "Winners" and "Losers"

The species that have undergone the greatest increases and decreases in plot mean percentage cover between the original survey and the re-survey are shown in Table 3, although not all of them have changed significantly. Of the winning species, *Hylocomium splendens, Carex demissa, Carex bigelowii* and *Nardus stricta* have increased significantly. Of the losing species, only *Carex saxatilis, Cladonia arbuscula* and *Pleurozium schreberi* have declined significantly. *Carex saxatilis* is an important species which characterises the M12 *Carex saxatilis* mire community.

Table 3. "Winners" and "Losers": plant species that have undergone the greatest increases and decreases in plot mean percentage cover between the original survey and the resurvey. P values are derived from paired t-tests, and those in bold are significant below 5%. n/a=not applicable, as there were insufficient records of those species to perform a t-test. The biogeographic distribution data is taken from Hill et al. (2004, 2007).

		Mean change in abundance (% cover)	P value	Biogeographic distribution
	Juncus effusus	38	n/a	European southern temperate
	Carex rostrata	15	0.215	Circumpolar boreo-temperate
	Rhytidiadelphus triquetrus	11	0.444	Circumpolar boreo-temperate
	Hylocomium splendens	9	0.008	Circumpolar wide-boreal
	Ditrichum heteromallum	9	n/a	European boreo-temperate
	Carex demissa	8	0.006	Sub-oceanic boreo-temperate
ers	Racomitrium lanuginosum	8	0.525	Circumpolar boreo-arctic montane
un	Empetrum nigrum	8	n/a	Circumpolar boreo-arctic montane
Ň	Carex bigelowii	7	<0.001	Circumpolar arctic-montane
	Nardus stricta	6	0.034	European boreo-temperate
	Salix herbacea	6	0.241	European arctic-montane
	Carex binervis	6	n/a	Oceanic temperate
	Warnstorfia exannulata	6	n/a	Circumpolar boreo-temperate
	Carex nigra	6	0.23	Eurosiberian boreo-temperate
	Juncus articulatus	5	0.25	Eurosiberian southern-temperate
	Gymnomitrion concinnatum	-42	n/a	Circumpolar arctic-montane
	Dichodontium palustre	-28	0.19	European boreal-montane
	Sphagnum papillosum	-18	0.471	European boreo-temperate
	Dicranum fuscescens	-17	n/a	Circumpolar boreo-arctic montane
	Juncus squarrosus	-15	0.977	Suboceanic temperate
ers	Carex saxatilis	-15	0.004	Circumpolar arctic-montane
ose	Warnstorfia sarmentosa	-11	0.341	Circumpolar boreo-arctic montane
Ľ.	Cladonia arbuscula	-9	0.057	
	Epilobium alsinifolium	-8	n/a	European arctic-montane
	Cladonia rangiferina	-8	n/a	
	Alchemilla filicaulis	-7	n/a	European boreal-montane
	Sphagnum girgensohnii	-7	n/a	Circumpolar boreo-arctic montane
	Pleurozium schreberi	-6	0.035	Circumpolar boreo-temperate

Festuca ovina agg.	-6	0.073	Circumpolar Wide-boreal
Saxifraga aizoides	-6	0.625	European arctic-montane
Scorpidium scorpioides	-5	0.271	Circumpolar boreo-arctic montane
Sphagnum cuspidatum	-5	n/a	European boreo-temperate

Figure 6 shows that amongst the winning species, 11 had a temperate element to their distribution, which was the case for only five of the losing species. However, 10 of the losing species had a boreo arctic-montane or arctic montane distribution, compared with only four of the winning species.



Figure 6. The three broad categories of biogeographic distribution and the number of winning and losing species in each category

4.6 Climatic preferences

In Figures 7a and 7b, we can see that the winning species preferred January and July temperatures of 3.1 °C and 13.7 °C, significantly higher than those of the losing species (2.4 °C and 13.0 °C; P = 0.017, 0.032). Figure 7c shows that the mean annual precipitation was significantly higher (P = 0.028) for the losing species (1569 mm) than for the winning species (1333 mm).



Figure 7a. Mean +/- SE score for mean January temperature preferred by winning and losing species



Figure 7b. Mean +/- SE score for mean July temperature preferred by winning and losing species



Figure 7c. Mean +/- SE score for mean annual precipitation preferred by winning and losing species

4.7 Thermophilization scores

The mean thermophilization scores for the three broad habitat types are shown in Figure 8. Montane habitats have the highest score, followed by acid grassland, while the fen, marsh & swamp category has the lowest thermophilization score. The scores for montane habitats and upland fen, marsh and swamp are significantly different (P = 0.014), but there are no other significant differences between thermophilization scores of these habitat types.



Figure 8. Mean +/- SE thermophilization scores for each broad habitat type.

4.8 Indicator species of climate warming

The indicator species of climate warming, or thermophilization, for each habitat type are shown in Table 4. *Nardus stricta* indicates warming in all three habitat types, as do *Trichophorum germanicum* and *Carex echinata* for upland fen, marsh & swamps and montane habitats. The indicator species are dominated by graminoids, with only five bryophyte species, one forb species and a single dwarf-shrub species.

Table 4. Indicator species of climate warming for each of the three broad habitat types, based on the highest 25% of species with positive changes in percentage cover in those three plots (for each habitat type) with the highest thermophilization scores.

Broad habitat type	Indicator species	Change in %
		cover
	Hylocomium spiendens	121
Acid grasslands	Juncus squarrosus	50
Acia gracolariao	Nardus stricta	27
	Anthoxanthum odoratum	22
	Juncus effusus	83
	Trichophorum germanicum	26
Upland fen,	Nardus stricta	16
marsn &	Palustriella commutata	16
Swamps	Carex nigra	12
	Carex echinata	11
	Nardus stricta	58
	Trichophorum germanicum	18
	Carex demissa	18
Mantana	Galium saxatile	9
Montane	Carex bigelowii	9
nabitats	Carex echinata	9
	Carex lepidocarpa	9
	Carex panicea	9
	Dicranum scoparium	9
	Polytrichastrum alpinum	9
	Salix herbacea	9

4.9 Plot photos

There are up to five photos available for each re-survey plot, showing the plot from different angles in order to provide landscape context and aid future relocation. These are numbered using the format 478 1, 478 2 etc., where 478 is the plot number. The photos may be obtained from SNH if required.

5. DISCUSSION

5.1 Diversity changes

Diversity within and between plant communities has changed since the original survey in the 1950s. The decline in heterogeneity (variability in species composition), significant change in species composition and increased similarity of species composition shown in the ordination diagram suggest that the vegetation has undergone a process of homogenisation, whereby species composition becomes more similar over time (McKinney & Lockwood 1999). The decline in species richness (number of species) was not significant, but this is not necessary for homogenisation to have occurred (Ross et al. 2012). Diversity indices, which take into account species' abundances as well as number, increased because of the increased abundance of generalist species, previously more common at lower altitudes, in plots in montane habitats. The trend towards the homogenisation of plant communities has been reported in other studies on Scottish montane vegetation (Britton et al. 2009, Ross et al. 2012), and in similar vegetation in the Alps (Jurasinski & Kreyling 2007) and Norway (Odland et al. 2010). It is difficult to determine whether climate change has driven this process of homogenisation, as the latter is still an understudied phenomenon. However, the loss of cold-adapted species through climate warming and the increase in more competitive, generalist species, at least partly facilitated by warming, is likely to have played a large part in the homogenisation process.

5.2 Indications of climate warming in changes in the vegetation

The significant increase in graminoid cover across the study area was also recorded in similar vegetation in studies by Pearce & van der Wal (2002), Klanderud & Birks (2003), Britton et al. (2009), Ross et al. (2012) and Geddes and Miller (2012). Warming has been shown to favour the growth and spread of graminoids (van der Wal & Brooker 2004; Gornall et al. 2009), and experimental warming of tundra vegetation caused an increase in the height and cover of graminoids (Walker et al. 2006; Natali et al. 2011). Increased nitrogen deposition is also known to encourage the spread of graminoids in arctic-alpine vegetation (Britton & Fisher 2008), so the impact of this driver cannot be ruled out, although the changes in species composition in this study did not suggest acidification or eutrophication. Grazing (by sheep but also by deer) is also likely to have affected the vegetation on Ben Lawers, and is causing several features to remain in unfavourable condition (Anon. 2011). Grazing has also been associated with the homogenisation of plant communities, as grazing-sensitive species are lost (Speed et al. 2013), so it may be difficult to fully disentangle the impacts of climate change and grazing. However, sheep numbers were relatively stable over the first 40 years of the inter-survey period, and actually declined from the 1990s onwards (Helen Cole, personal communication), so given the magnitude of vegetation change recorded here, it seems likely that climate change must also have been an important driver of change. Indeed, changes in climate appeared to be impacting on vegetation to a greater extent than the regional effects of grazing and nitrogen deposition in the North-West Highlands and East Central Highlands (Ross 2011).

Despite the possible effects of nitrogen deposition and grazing, changes in the vegetation do indicate a strong climate change signal. The decline of bryophytes also implies that warming has taken place. Generally, bryophyte cover in acidophilous tundra has been found to decrease as a consequence of experimental warming (Hollister *et al.* 2005, Jonsdottir *et al.* 2005, Wahren *et al.* 2005, Walker *et al.* 2006, Klanderud & Totland 2008). However, the cover of the feather moss *Hylocomium splendens* increased significantly in this study. In contrast to the drier arctic regions where the above experimental studies took place, the oceanic montane climate on Ben Lawers, coupled with increasingly wet and humid conditions, may have favoured a positive response by this species (Geddes & Miller 2012). In contrast to our findings, the latter study found an increase in forb and bryophyte cover; however, those changes were recorded on calcareous grassland, which has a different

ecology to the habitats studied here. Lichen cover, which significantly declined in this study, has also been shown to be adversely affected by climate warming (Cornelissen *et al.* 2001). The decline of northern and alpine species was also recorded by Preston *et al.* 2002, Britton *et al.* 2009 and Ross *et al.* 2012.

The increase in vegetation height again suggests that warming has taken place. In a study on tundra vegetation, Elmendorf et al. (2012) recorded an increase in the height of the plant canopy, and an increase in the abundance of rushes with warming. The climatic preferences of the "winning" and "losing" species also suggest the impact of warming, with winning species preferring warmer and drier conditions. Although this does not at first glance fit with the pattern of wetter conditions over the inter-survey period in this study, a closer examination of seasonal patterns shows that although there has been a considerable increase in rainfall over the winter months, summers have become drier in some areas (Barnett et al. 2006). The resulting lack of water during critical periods of the growing season may have been sufficient to confer a competitive advantage on species tolerant of drier conditions. The change to warmer and drier summer conditions is echoed by Matteodo et al. (2013), who reported that the most successful colonisers on alpine summits preferred warmer temperatures, and Callaghan et al. (2011), who found that changes in species composition in sub-arctic vegetation in Greenland since the 1960s indicated a change to drier conditions. The appearance of Juncus squarrosus as a "losing" species is somewhat surprising, as it has been known to have spread in other montane areas (Ross et al. 2012). However, this is a result of a decrease in its cover in just three plots where it was the dominant species in the original survey.

5.3 Change in the three broad habitat types

The magnitude of change in species composition and the thermophilization score is greatest in montane habitats, followed by acid grasslands, and least in upland fens, marshes and swamps. This is in line with other studies that have shown that montane communities have been most heavily impacted by climate change (Beniston 2003, Rammig et al. 2010), due to the short growing season and low temperatures conferring low resistance and resilience. However, this is the first time that this has been shown to be the case for Scottish montane vegetation. The lesser degree of change in the wettest habitat type is echoed by results from the North-West Highlands (Ross et al. 2012) and in tundra vegetation by Speed et al. (2010), who showed that plant communities with higher soil moisture and higher moss cover were most resilient to disturbance. This resilience may be due to rhizomes being protected by the moss cover, and the fact that rhizomes extend deep into the organic soil layers found in wetter communities (Speed et al. 2010). The relative stability of these wet habitats is despite the significant decline of Carex saxatilis, as many of the other characteristic species have maintained their distribution. These differences between the three key habitats are echoed by the site condition monitoring that has been carried out in the study area: features relating to montane habitats and acid grasslands have been classified as "unfavourable, no change", whereas those relating to upland fens, marshes and swamps were classified as "favourable, recovered" (Anon. 2011).

5.4 Implications of vegetation change

It is essential to consider if the vegetation change recorded in this study should be regarded as problematic. Changes in plant community composition can represent a decline in the conservation value of habitats, either through the decline of typical, rare or valuable species, or increases in atypical or undesirable plant species. The acid grassland habitats, U5 *Nardus stricta - Galium saxatile* grassland and U6 *Juncus squarrosus – Festuca ovina* grassland, are considered to be a conservation problem rather than asset (Averis *et al.* 2004), and as they are already dominated by generalist graminoids, are unlikely to reduce further in conservation value. However, the upland fen, marsh and swamp habitats, such as M12

Carex saxatilis mire, which is one of the rarest mire types in Great Britain and a valuable example of a near-natural vegetation type (Averis *et al.* 2004), has been invaded by species such as *Carex demissa*, *C. echinata*, *Hylocomium splendens* and *Nardus stricta*, which increases the risk of conversion to another as yet undefined vegetation type of lower conservation value. Similarly, montane communities such as U8 *Carex bigelowii* – *Polytrichum alpinum* sedge heath and U10 *Carex bigelowii* – *Racomitrium lanuginosum* moss heath are of high value for nature conservation yet have increased in graminoid cover, threatening less competitive species such as alpine forbs and lichens and therefore risking the decline in condition or even the loss of the original habitat.

The effect of vegetation change on ecosystem processes and function is also an important consequence. Changes in plant community composition can affect decomposition rate (Garnier *et al.* 2007), nutrient cycling (Fortunel *et al.* 2009) and biogeochemistry (Cornelissen *et al.* 2007). One of the major changes in vegetation composition since the original survey has been the marked increase in graminoid cover. Such a shift has been found to reduce the carbon sequestration potential in peatlands by Ward *et al.* (2009) and in Arctic tundra by Woodin *et al.* (2009). The reduction in diversity through homogenisation is also likely to have impacts on ecosystem function, knock-on effects on other trophic levels, and a decline in ecosystem services to humans (van der Wal *et al.* 2012).

5.5 Further work

This study has identified some of the impacts of climate change on the vegetation of Ben Lawers between the 1950s and 2013. Further monitoring is clearly essential in order to track the impacts of climate change and other factors such as management on montane vegetation. Although this study has made use of unmarked plots, permanent plots would remove the relocation error implicit in any re-survey study, improving the level of confidence with which the results could be interpreted. This would be best achieved by the involvement of research or conservation organisations, as multi-decade studies are beyond the scope of most individuals. More work is needed to extend the evidence base on the impacts of climate change in order to inform the policy sphere, such as the Scottish Government's Climate Change and Adaptation Framework (Anon. 2009). It would be enlightening to disentangle the impacts of climate change from those of other drivers, particularly nitrogen deposition and grazing. This could include experimental studies on species and communities, and modelling studies using interpolated values from existing climate, deposition and stocking density data to quantify the impacts of these drivers at a finer spatial scale and link them with vegetation change. Furthermore, integrated models of environmental change, using ecological, hydrological and land-use data could provide a more comprehensive analysis of climate-induced change. Another factor that has not been considered here and is worthy of more attention is the effect of wind speed, which is particularly important in Scotland, where increasingly higher wind speeds could possibly offset the expansion of generalist species facilitated by warmer temperatures.

6. CONCLUSIONS

The impacts of climate change are manifested in most of the ways in which the vegetation of Ben Lawers has changed since the original survey in the 1950s: the decline of northern and boreal species, the spread of temperate species and the increase in species with a preference for warmer and drier conditions. In addition, the decline in bryophyte and lichen cover, increased vegetation height, considerable spread of graminoids and the homogenisation of plant communities (in this case the loss of variability within and between habitats) may well also be effects of climate change, although these changes could also be influenced by additive or interacting effects of nitrogen deposition and grazing.

Montane habitats, including U7 *Nardus stricta - Carex bigelowii* grass-heath, U8 *Carex bigelowii - Polytrichum alpinum* sedge-heath and U10 *Carex bigelowii - Racomitrium lanuginosum* moss-heath, have undergone the most dramatic changes and the greatest degree of thermophilization, or impact of warming, since the 1950s. Acid grasslands, composed here of U5 *Nardus stricta - Galium saxatile* grasslands and U6 *Juncus squarrosus-Festuca ovina* grasslands, have also undergone change, but to a lesser extent. The decline of heterogeneity has been particularly marked in this habitat type. Upland fen, marsh and swamp communities, including M12 *Carex saxatilis* mires, have changed least since the original survey, and have undergone the smallest degree of thermophilization, perhaps because wet habitats are, at least to some extent, buffered from the most severe impacts of warmer, drier conditions.

Species with an arctic-montane or boreo-arctic montane distribution, including *Gymnomitrion concinnatum*, *Dicranum fuscescens* and *Carex saxatilis*, and those that prefer cooler, wetter conditions, such as Scorpidium *scorpioides*, *Saxifraga aizoides* and *Epilobium alsinifolium*, have been identified as being vulnerable to climate change. The majority of species that have fared well since the original survey are graminoids, notably *Nardus stricta*, *Carex bigelowii* and *Carex demissa*. Conversely, the cover of bryophytes (with the clear exception of *Hylocomium splendens*), forbs and lichens have all significantly declined.

As climate change trends are set to continue in future, a warming climate is likely to remove former limiting factors on the distribution of species and allow generalist species to colonise areas that were previously unsuitable, reducing the area suitable for cold-adapted arcticalpine species. Despite this, the fact that observed trends over the last c. 60 years are comparable with projected future trends should mean that we are in an informed position to plan appropriate adaptation measures for the future. The management of sites with nature conservation designations (which applies throughout this study area) must take account of the changing climate, so that the management of vulnerable species and habitats can be prioritised accordingly, increasing their population size and resilience. In the context of SNH's Climate Change Action Plan (2012), where adaptation principles include improving habitat management and enhancing habitat diversity, it may be possible to buffer the effects of homogenisation (and perhaps also thermophilization) by implementing appropriate grazing regimes to maintain the open nature and diversity of montane systems, as has been demonstrated in Norway by Speed et al. (2010). Neither is the increased dominance of Nardus stricta irreversible, as cessation of grazing can result in a decline in the cover of this species and an increase in the cover of Deschampsia flexuosa (Austrheim et al. 2007), which should promote greater diversity.

The indicator plant species of climate change should be applicable to most montane areas with the habitat types examined here, particularly widespread species such as *Nardus stricta* and *Carex bigelowii*. However, in areas with rather different bioclimatic conditions, such as the hyper-oceanic North-West Highlands, species composition may be sufficiently different that *some* of the indicator species listed here may not be appropriate in every case. Thermophilization scores could also be calculated and tracked over time to monitor the

impact of warming in a range of habitat types. In summary, the analyses and information in this report should help to identify, quantify and monitor the impacts of climate change on Scottish montane vegetation, and to inform strategies to increase resilience and adaptation.

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ANNEX 1: PLOT INFORMATION: RE-SURVEY PLOTS

Plot number	Locality	Grid reference	GPS error (m)	Altitude (m)	Aspect (°)	Slope (°)	Plot size (m)	Date of re-survey
247	Ben Lawers	NN 63208 39566	8	808	190	30	2 x 2	05/08/2013
248	Ben Lawers	NN 63132 39711	14	902	90	15	2 x 2	05/08/2013
249	Ben Lawers	NN 61467 43661	6	873	150	15	2 x 2	29/08/2013
255	Ben Lawers	NN 65150 40825	6	761	170	5	2.5 x 2.5	16/08/2013
256	Ben Lawers	NN 65052 40845	5	788	170	5	2 x 1	16/08/2013
257	Ben Lawers	NN 65065 40895	6	802	170	3	2.5 x 2.5	07/08/2013
335	Meall nan Tarmachan	NN 58142 37979	5	790	70	10	2 x 2	27/08/2013
376	Ben Lawers	NN 63749 38853	13	484	140	10	2 x 2	01/08/2013
377	Ben Lawers	NN 63597 39063	6	577	140	3	2 x 2	01/08/2013
378	Ben Lawers	NN 63586 39217	10	629	180	4	2 x 2	01/08/2013
390	Ben Lawers	NN 65349 40999	9	728	180	4	5 x 2	16/08/2013
391	Ben Lawers	NN 64956 40933	5	821	170	2	2 x 2	07/08/2013
392	Ben Lawers	NN 63399 39360	7	683	150	8	2 x 2	01/08/2013
394	Ben Lawers	NN 65375 40422	11	583	150	3	2 x 1	16/08/2013
395	Ben Lawers	NN 65437 40348	6	567	120	3	2 x 1	16/08/2013
418	Meall nan Tarmachan	NN 56589 37844	14	776	135	10	2 x 2	27/08/2013
423	Meall Garbh	NN 64559 44156	6	986	360	7	2 x 2	27/08/2013
464	Ben Lawers	NN 61408 42341	5	946	50	2	2 x 1	29/08/2013
477	Ben Lawers	NN 64026 41782	9	901	0	0	2 x 2	13/08/2013
478	Ben Lawers	NN 64281 41477	5	1020	350	5	2 x 2	06/08/2013
480	Ben Lawers	NN 64289 41536	5	1000	350	10	2 x 2	06/08/2013
481	Ben Lawers	NN 63191 41108	8	982	120	8	2 x 2	08/08/2013
497	Ben Lawers	NN 63591 41620	15	1145	100	12	1 x 1	31/07/2013
498	Ben Lawers	NN 64756 41133	6	862	60	4	2 x 2	07/08/2013
499	Ben Lawers	NN 64609 41148	6	914	60	4	2 x1	07/08/2013
500	Ben Lawers	NN 64607 41119	9	914	120	1	2 x 2	07/08/2013

Plot number	Locality	Grid reference	GPS error (m)	Altitude (m)	Aspect (°)	Slope (°)	Plot size (m)	Date of re-survey
533	Ben Lawers	NN 63309 41301	12	1130	250	15	2 x 1	31/07/2013
577	Ben Lawers	NN 63240 41103	9	983	150	8	2 x 2	08/08/2013
578	Ben Lawers	NN 63235 41137	18	987	150	5	2 x 2	08/08/2013
579	Ben Lawers	NN 63136 41175	34	1008	150	8	2 x 2	08/08/2013
580	Ben Lawers	NN 63105 40945	8	933	160	12	2 x 2	26/08/2013
581	Ben Lawers	NN 62906 40715	23	985	110	15	2 x 1	26/08/2013
582	Ben Lawers	NN 63239 41067	8	963	200	15	2 x 2	30/07/2013
583	Meall Corranaich	NN 61189 41679	12	830	310	12	2 x 2	29/08/2013
605	Meall nan Tarmachan	NN 56552 37383	10	723	90	45	2 x 2	27/08/2013
616	Ben Lawers	NN 63004 39788	7	933	0	0	2 x 1	05/08/2013
684	Ben Lawers	NN 64268 41465	7	1020	350	15	2 x 2	06/08/2013
686	Ben Lawers	NN 64223 41512	5	998	350	10	2 x 2	06/08/2013
687	Ben Lawers	NN 64159 41524	6	993	320	10	2 x 2	06/08/2013
784	Ben Lawers	NN 64419 39511	6	567	270	3	2 x 2	05/08/2013
804	Meall Garbh	NN 64608 44317	8	938	360	15	2 x 2	28/08/2013
812	Meall nan Tarmachan	NN 57383 37504	5	720	0	0	2 x 2	27/08/2013
834	Meall nan Tarmachan	NN 57232 37929	6	796	0	0	2 x 2	27/08/2013
859	Meall nan Tarmachan	NN 57222 37913	5	795	0	0	2 x 2	27/08/2013
860	Ben Lawers	NN 63215 40913	7	901	210	1	2.5 x 2.5	14/08/2013
861	Ben Lawers	NN 63176 40896	20	884	120	1	2.5 x 2.5	14/08/2013
862	Ben Lawers	NN 63113 40864	14	881	150	3	2 x 3	26/08/2013
863	Ben Lawers	NN 63133 40869	8	884	150	3	2 x 2	26/08/2013
864	Ben Lawers	NN 63483 40739	9	862	220	4	2 x 2	14/08/2013
865	Ben Lawers	NN 64195 42160	15	756	220	3	2 x 2	13/08/2013
866	Ben Lawers	NN 64140 42147	6	782	0	5	2 x 2	13/08/2013
867	Ben Lawers	NN 64166 42108	11	780	0	5	2 x 1	13/08/2013
868	Ben Lawers	NN 64055 41883	14	868	350	2	1 x 1	13/08/2013

Plot number	Locality	Grid reference	GPS error (m)	Altitude (m)	Aspect (°)	Slope (°)	Plot size (m)	Date of re-survey
887	Ben Lawers	NN 64965 40190	5	589	0	0	1 x 0.5	16/08/2013
888	Ben Lawers	NN 64955 40190	9	587	0	0	1 x 0.3	16/08/2013
892	Ben Lawers	NN 64956 40191	9	604	0	0	1 x 1	16/08/2013
920	Ben Lawers	NN 63494 40733	8	861	0	0	1.5 x 1	14/08/2013
941	Ben Lawers	NN 63471 40583	6	827	210	0	1 x 1	14/08/2013

Species name	Present in the	Present in the	Present in
Achillea millefolium	original survey only	re-survey only	both surveys
	^		v
			×
Agrostis capillaris			×
			^
			A V
			X
			A V
			X
Alchemilia vulgaris agg.	X		X
Alchemilia wichurae	X		X
Aneura pinguis			X
Anthoxanthum odoratum		X	X
Armeria maritima.		X	
Aulacomium palustre			Х
Barbilophozia attenuata	Х		
Barbilophozia floerkei			Х
Bartramia ithyphylla	X		
Bellis perennis		Х	
Blindia acuta	Х		
Botrychium Iunaria	Х		
Bryum pseudotriquetrum			Х
Calliergon giganteum	Х		
Calliergonella cuspidata			Х
Calluna vulgaris			Х
Caltha palustris	Х		
Campanula rotundifolia			Х
Campylium stellatum			Х
Cardamine flexuosa		Х	
Cardamine pratensis	Х		
Carex bigelowii			Х
Carex binervis			Х
Carex capillaris			Х
Carex demissa			Х
Carex dioica			Х
Carex echinata			Х
Carex flacca			Х
Carex lepidocarpa		Х	
Carex nigra			Х
Carex panicea			Х
Carex pilulifera			Х
Carex pulicharis			Х

ANNEX 2: SPECIES PRESENCE/ ABSENCE ACROSS BOTH SURVEYS

Species name	Present in the	Present in the	Present in
Carey rostrata	original survey only	re-survey only	both surveys
Carex rostrata			X
Carex vaginata	Y		~
	×		
	^		v
	V		^
	X		X
Cetraria Islandica		X	X
oppositifolium		X	
Cinclidium styaium			X
Cirsium palustre		X	
Cirsium vulgare		X	
Cladonia arbuscula			X
Cladonia bellidiflora			X
Cladonia coccifera s lat			X
Cladonia gracilis	X		Λ
Cladonia macrophylla	X		
Cladonia maciopitylia	Λ		x
Cladonia pyxidata			X
			×
			×
biuncialis			^
Conostomum tetragonum	Х		
Crepis paludosa			Х
Ctenidium molluscum			Х
Danthonia decumbens		Х	
Deschampsia cespitosa			Х
Deschampsia flexuosa			Х
Dichodontium palustre			Х
Dicranella heteromalla	Х		
Dicranum fuscescens			Х
Dicranum scoparium			Х
Diphasiastrum alpinum			Х
Diplophyllum albicans			Х
Ditrichum heteromallum			Х
Draba norvegica	Х		
Drosera rotundifolia		Х	
Eleocharis quinqueflora			Х
Empetrum nigrum			Х
Epilobium alsinifolium			Х
Epilobium anagallidifolium	Х		
Epilobium palustre			Х

Species name	Present in the	Present in the	Present in
Equisetum palustre	oligiliai sulvey olily	re-survey only	X
Equisetum variegatum			X
Eriophorum angustifolium			Х
Eriophorum vaginatum			Х
Euphrasia frigida	Х		
Euphrasia officinalis agg.			Х
Euphrasia scotica			Х
Euphrasia species			Х
Festuca ovina agg.			Х
Festuca rubra			Х
Fissidens adianthoides	Х		
Fissidens osmundoides	Х		
Galium saxatile			Х
Geranium sylvaticum	Х		
Geum rivale	Х		
Gnaphalium supinum			Х
Gymnomitrion concinnatum			Х
Gymnomitrion coralloides	Х		
Hieracium species		Х	
Huperzia selago			Х
Hylocomium splendens			Х
Hypnum cupressiforme			Х
Hypochaeris radicata		Х	
Juncus articulatus			Х
Juncus bulbosus			Х
Juncus castaneus			Х
Juncus effusus			Х
Juncus squarrosus			Х
Juncus triglumis			Х
Kiaeria starkei			Х
Lecidea alpestris	Х		
Leiocolea alpestris	Х		
Linum catharticum	Х		
Lophocolea bidentata			Х
Lophozia ventricosa	Х		
Lotus corniculatus	Х		
Luzula multiflora			Х
Luzula spicata			Х
Luzula sylvatica	X		
Minuartia sedoides			X
Montia lamprosperma			X
Myosotis alpestris	X		

Species name	Present in the	Present in the	Present in
	original survey only	re-survey only	both surveys
Nardia scalaris			X
Nardus stricta			X
Narthecium ossifragum			X
Oligotrichum hercynicum	X		
Oxalis acetosella			Х
Palustriella commutata			Х
Parnassia palustris			Х
Pellia endiviifolia	Х		
Persicaria vivipara			Х
Philonotis calcarea	Х		
Philonotis fontana			Х
Pinguicula vulgaris			Х
Plagiomnium undulatum			Х
Plagiothecium undulatum			Х
Pleurozium schreberi			Х
Poa annua		Х	
Pogonatum urnigerum			Х
Pohlia nutans	Х		
Polygala serpyllifolia			Х
Polytrichastrum alpinum			Х
Polytrichastrum sexangulare	Х		
Polytrichum commune.			Х
Polytrichum piliferum			Х
Polytrichum strictum			Х
Potentilla erecta			Х
Prunella vulgaris		Х	
Pseudocalliergon trifarium			Х
Pseudoleskea incurvata	Х		
Pseudoscleropodium purum			Х
Ptilidium ciliare			Х
Ptilium crista-castrensis		Х	
Racomitrium canescens			Х
Racomitrium fasciculare			Х
Racomitrium heterostichum			Х
Racomitrium lanuginosum			Х
Ranunculus acris			Х
Rhizomnium			Х
pseudopunctatum			
Rhytidiadelphus loreus			X
Rhytidiadelphus squarrosus			X
Rhytidiadelphus triquetrus			X
Riccardia multifida			X
Rumex acetosa			X

Species name	Present in the	Present in the	Present in
	original survey only	re-survey only	both surveys
Sagina saginoides	X		N N
Salix nerbacea			X
Saxifraga aizoides			X
Saxifraga hypnoides	X		
Saxifraga oppositifolia			Х
Saxifraga stellaris			X
Scapania uliginosa	Х		
Scapania undulata			Х
Scorpidium revolvens			Х
Scorpidium scorpioides			Х
Scorzoneroides autumnalis			Х
Selaginella selaginoides			Х
Sibbaldia procumbens			Х
Silene acaulis			Х
Solidago virgaurea	Х		
Solorina crocea	Х		
Sphaerophorus globosus	Х		
Sphagnum angustifolium/ S.	Х		
flexuosum			
Sphagnum capillifolium			Х
Sphagnum contortum			X
Sphagnum cuspidatum			Х
Sphagnum girgensohnii			Х
Sphagnum inundatum			Х
Sphagnum papillosum			Х
Sphagnum quinquefarium			Х
Sphagnum russowii	Х		
Sphagnum subsecundum			Х
Sphagnum teres	Х		
Sphagnum warnstorfii			Х
Stellaria alsine			Х
Straminergon stramineum	Х		
Taraxacum species			Х
Thalictrum alpinum			Х
Thamnolia vermicularis var.	Х		
subuliformis			
Thuidium delicatulum		X	
Thuidium tamariscinum			Х
Thymus polytrichus			X
Trichophorum germanicum		Х	
Trifolium repens.			Х
Triglochin palustris			Х
Utricularia minor			Х

Species name	Present in the original survey only	Present in the re-survey only	Present in both surveys
Vaccinium myrtillus			Х
Vaccinium vitis-idaea			Х
Veronica serpyllifolia	Х		
Viola palustris			Х
Viola riviniana			Х
Warnstorfia exannulata			Х
Warnstorfia fluitans			Х
Warnstorfia sarmentosa			Х

ANNEX 3: SPECIES SYNONYMS

Original species name (1962)	New species name (2013)
Acrocladium cuspidatum	Calliergonella cuspidata (Hedw.) Loeske
Acrocladium giganteum	Calliergon giganteum
Acrocladium sarmentosum	Warnstorfia sarmentosa
Acrocladium stramineum	Straminergon stramineum
Acrocladium trifarium	Pseudocalliergon trifarium
Alicularia scalaris	Nardia scalaris
Aneura cf. sinuata	Riccardia chamedryfolia
Aneura multifida	Riccardia multifida
Callliergon sarmentosum	Warnstorfia sarmentosa
Calliergon trifarium	Pseudocalliergon trifarium
Cerania vermicularis	Thamnolia vermicularis var. subuliformis
Cladonia alpicola	Cladonia macrophylla
Cladonia destricta	Cladonia zopfii
Cladonia impexa	Cladonia portentosa
Cladonia uncialis	Cladonia uncialis subsp. biuncialis
Cratoneuron commutatum	Palustriella commutata
Dicranella squarrosa	Dichodontium palustre
Dicranum starkei	Kiaeria starkei
Ditrichum homomalium	Ditrichum heteromallum
Draba rupestris	Draba norvegica
Drepanocladus exannulatus	Warnstorfia exannulata
Drepanocladus fluitans	Warnstorfia fluitans
Drepanocladus revolvens	Scorpidium revolvens
Leontodon autumnalis	Scorzoneroides autumnalis
Lophozia alpestris	Leiocolea alpestris
Lophozia cf. attenuata	Barbilophozia attenuata
Lophozia floerkii	Barbilophozia floerkei
Lophozia lycopodioides	Barbilophozia lycopodioides
Mnium pseudopunctatum	Rhizomnium pseudopunctatum
Mnium undulatum	Plagiomnium undulatum
Pellia fabbroniana	Pellia endiviifolia
Peltidea aphthosa	Peltigera aphthosa
Peltidea leucophlebia	Peltigera aphthosa var. leucophlebia
Polygonum viviparum	Persicaria vivipara
Platysma glaucum	Platismatia glauca
Polytrichum alpestre	Polytrichum strictum
Polytrichum alpinum	Polytrichastrum alpinum
Polytrichum norvegicum	Polytrichastrum sexangulare
Polytrichum urnigerum	Pogonatum urnigerum
Pseudoscleropodium purum	Scleropodium purum
Sphagnum auriculatum	Sphagnum denticulatum/ S. inundatum
Sphagnum plumulosum	Sphagnum quinquefarium

Original species name (1962)	New species name (2013)
Sphagnum recurvum	Sphagnum angustifolium/ S. flexuosum
Sphagnum warnstorfianum	Sphagnum warnstorfii
Stellaria alsine	Stellaria uliginosa
Stereocaulon evolutoides	Stereocaulon saxatile
Stereocaulon vesuvianum	Stereocaulon vesuvianum var. vesuvianum
Trichophorum cespitosum	Trichophorum germanicum
Triglochin palustre	Triglochin palustris

ANNEX 4: DIVERSITY METRICS

Key metrics of plant diversity in the two surveys: mean species richness, mean Shannon-Weaver diversity index and mean heterogeneity index for both the original survey and the resurvey, and for each broad habitat type and all plots together. Figures are means for each plot. P values are derived from paired t-tests for species richness, pair-wise comparisons using Wilcoxon rank sum tests for the diversity index, and analysis of variance tests for the heterogeneity index. P values in bold are significant below the 5% level.

Metric	Broad habitat type	Original survey (1952)	Re-survey (2013)	Change	Р
Species	Acid grassland	20.3	17.1	-3.2	0.068
richness	Upland fen, marsh & swamp	19.4	20.1	0.7	0.768
	Montane habitats	22.2	21.5	-0.7	0.631
	All plots	21.4	20.2	-1.2	0.135
Shannon-	Acid grassland	2.033	2.164	0.131	0.279
Weaver diversity	Upland fen, marsh & swamp	1.854	2.192	0.338	0.551
index	Montane habitats	2.063	2.456	0.392	<0.001
	All plots	2.032	2.325	0.293	0.007
Heteroge-	Acid grassland	0.456	0.354	-0.102	0.019
neity index	Upland fen, marsh &	0.576	0.555	-0.021	0.446
(distance	swamp				
to	Montane habitats	0.576	0.519	-0.057	0.022
centroid)	All plots	0.589	0.538	-0.051	0.005

ANNEX 5: ADONIS TESTS

Comprehensive results for the adonis (multivariate analysis of variance) tests to check for significant differences in species composition between the original survey and the re-survey.

		Degrees of freedom	Sum of squares	Mean squares	F. Model	R ²	Pr(>F)
	Survey	1	1.479	1.479	5.912	0.129	<0.001
Acid grasslands	Residuals	34	10.009	0.25	0.871		
-	Total	35	11.489				
Upland fens,	Survey	1	0.229	0.229	0.563	0.025	0.915
marshes &	Residuals	22	8.965	0.407	0.975		
swamps	Total	23	9.194				
Montane habitats	Survey	1	0.767	0.767	2.076	0.045	0.002
	Residuals	40	16.258	0.369	0.955		
	Total	41	17.025				
All plots	Survey	1	1.595	1.595	4.218	0.036	0.005
	Residuals	114	43.105	0.378	0.964		
	Total	115	44.7				

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