THE ECOLOGY OF BRITISH UPLAND LANDSCAPES. I. COMPOSITION OF LANDSCAPES, HABITATS, VEGETATION AND SPECIES

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ABSTRACT

A primary requirement for policy objectives is reliable figures on the composition of any region. Currently there is no comprehensive, definitive set of statistics for the British Uplands, hence the present paper. An overview of the background to the region is first provided, together with some examples of the available figures and a discussion of their limitations. The paper uses a formal structure, with landscapes at the highest level followed by habitats, then vegetation, and finally species, with exact definitions of the categories applied at all levels. The figures are produced from a survey of stratified, random one kilometre squares. The tables give comprehensive figures for Great Britain (GB) as a whole, and also England, Wales and Scotland.

The Uplands are shown to cover 38 % of the country. In terms of UK Broad Habitats, Bog is the most common overall (2062 k ha). It is estimated that 41 % of upland vegetation in Britain is grazed by sheep, and *Cervus elephus* (red deer) are particularly evident in Scotland. Walls (mainly drystone) are the most important linear feature (84 k km) but hedgerows (30 k km) are also widespread. The major vegetation classes are those linked to moorlands and bogs (about 25 %) but those associated with fertile soils are also common (10 %). In terms of species, *Potentilla erecta* (tormentil) is the most frequent species with four other acid grassland species in the top ten. *Calluna vulgaris* (ling heather) has the highest cover in Great Britain (14.8 %).

Keywords*:* stratified random sampling, standard habitat categories, comprehensive national estimates, vascular plant species, linear features, Brexit.

BACKGROUND

The initial comparable analysis of the British Uplands was that of Bunce (1987) using the first set of Countryside Survey (Carey *et al*., 2008) data collected in 1978 (Bunce, 1979). However, data sets collected in subsequent surveys are more comprehensive, enabling analyses (for example of vegetation data) that had not been carried out in 1987. It is therefore timely to repeat the basic analyses, but also to add the greater detail that is now available. Furthermore, as discussed below, official figures for upland habitats are not comprehensive, and moreover are not the product of robust statistical sampling and analysis. Also, as discussed by Monbiot in the British national press (Monbiot, 2017b), there is considerable public interest in the extent and composition of the Uplands because of their importance for leisure activities and biodiversity, as well as for their valued landscapes, as reflected by the extent of protected areas. Finally, the consequences of Brexit are particularly likely to have an impact in the Uplands, so it is therefore valuable to have a statement of their current composition at this time.

The first section of the paper therefore provides a definition of the region before discussing the extent of available figures. The methods of data collection are then described before the results are presented.

INTRODUCTION

After the Ice Age, forest colonised the whole of Britain, with the exception of the high mountains and exposed northern coasts, as summarised by Bunce *et al.* (2014b). Progressive deforestation then took place so that by the 19th Century, under 10 % of the original forest remained. The Victorian sports of deer stalking and grouse shooting further accentuated the process.

After the Second World War, the introduction of agricultural subsidies, followed by accession to the European Union (EU), led to a further increase in sheep numbers as well as a decline in cattle numbers. This historical process is documented by Ratcliffe and Thompson (1988) who updated the classic text of Pearsall (1950), who described the ecological characteristics of the region. Recently Reed *et al*. (2009) have provided detailed discussions of the drivers of change and a review of the dynamics of the Uplands. The particularly important drivers of fire and climate change are covered by Davies *et al.* (2016) and House *et al*. (2010) respectively. The former present a discussion of the significance of the use of fire as a management tool in the Uplands, emphasizing that fire has significant effects on biodiversity and ecosystem function. The latter paper emphasises that there is evidence that climate change is already taking place in the Uplands. Research using a climate envelope model suggests that as much as 50 % of the Uplands will be exposed to climate stress by the end of the 21st Century (Berry *et al*., 2002). However detailed interpretations of the implications of this result are more difficult. A useful description of farming in the Uplands is given by Clother and Finch (2010) with enterprises varying from traditional sheep raising to more intensive use of fertile valleys .

On account of the intense interest in the topic and the need for an update of the increasing pressures, the British Ecological Society convened a meeting to discuss the issues as reported by Evans *et al*. (2017). Many disparate topics were covered, leading to the conclusion that a transformational moment is now evident. The strength of views discussed at the meeting (Evans *et al*., 2017) was focussed on vertebrate predators, climate change and nitrogen deposition.

Paper II (Bunce *et al.*, 2018) provides an extensive discussion of the impacts of policy on the ecology of the Uplands, needing a separate text to cover the complex issues involved.

The structure of the analyses follows the principles described by Bunce (1999). The approach is and overall results of the Countryside Survey project are described by Norton *et al*. (2012) and Carey *et al*. (2008), and further details are provided at: www.countrysidesurvey.org.uk. Each level is explicit and is formed of complexes of classes of the previous stage. The levels are as follows:

1. **Landscape**: The general concept of the Uplands is usually applied at the landscape level involving complexes of habitats (see below) and vegetation. There are therefore habitats usually associated with the lowlands in upland valleys, such as fertile grassland. Such habitats are not only important visually, but are often important for biodiversity, for example as feeding grounds for geese (particularly greylag, *Anser anser*). Historically there was more variation in land covers such as crops. In the present paper, Upland landscapes are determined by the appropriate classes of an environmental classification derived from statistical analysis of environmental data from all 1 km squares in Great Britain (Bunce *et al*., 1996).
2. **Habitats**: in the present paper, the Broad Habitats of the UK Biodiversity Action Plan (Jackson, 2000) are used. (This is also the level used in the EU, in the Habitats Directive (Council Directive 92) for Natura 2000 (European Commission, 1992), and the two classifications have been linked by Bunce *et al*. (2012) to enable comparisons). The scale of habitats varies according to the species involved. Thus, a butterfly such as the Adonis blue (*Lysandra bellargus*) may occupy only a patch of calcareous grassland, but a large bird may use several habitats (for example, a golden eagle (*Aquila chrysaetos*) may inhabit cliffs, trees, and a range of moorland and heathland habitats). In the present paper the habitats are recorded in the field as standardized spatially explicit units within dispersed random 1 km squares stratified according to the environmental classification (see below).
3. **Vegetation classes**: in the present paper, the vegetation classes ('Countryside Vegetation Classes') used are determined by statistical analysis of plant species recorded from dispersed random 200m square plots within the same 1 km squares (5 per square), as defined in Bunce *et al*. (1999b).
4. **Vegetation species**: these are important in their own right because they have links to other taxa, for example *Calluna* has links to grouse (*Lagopus lagopus scotica*). They are also key determinants of many habitats and form the basic structure of vegetation classes.

Definition of Uplands and extant figures

A paper on afforestation in the Uplands (Bunce *et al*., 2014b) used a comparable procedure to that given in the present paper to define the region, in that statistically derived relevant environmental classes were used to produce the map, as shown in Figure 1 below.

There is often a degree of circularity in the definitions used in the literature. Two of the best definitions are:

1. Averis et al. (2004), where upland is defined as the areas of the country which have an upland environment regardless of altitude. They are usually wetter and cooler than the lowlands and are windier and usually with poor soils.
2. Definition 1 (above) is consistent with that used to describe Less Favoured Areas (LFAs) in the EU agricultural grant system which is as follows: an area with natural handicaps (lack of water, poor climate and associated short crop season and infertile soils) (European Commission, 2018). The social criterion of declining populations as used in the EU definition of LFAs certainly applies, although it is not ecological.

The most complete figures are provided within the Biodiversity Action Plan Reporting System (BARS) (JNCC, 2012). However, not only do the figures not cover the entire landscape, as described below, but the methods of derivation are not discussed, presumably because they are extracted from a variety of sources. Areas of the following habitats were not available from this source:

1. Habitats usually associated with lowlands and not characteristic of the uplands, but are commonly present in upland landscapes, especially valleys (for example, fertile grasslands).
2. Inland rock and scree.
3. Mountain heath and willow scrub.
4. Upland flushes and swamps.

MATERIALS AND METHODS

Landscapes

In the present paper, upland landscapes are defined according to an integrated multivariate analysis (Hill & Šmilauer, 2005) of environmental data (for example climatic data, topographic data, human geographical features and geology data) originally providing 32 classes (or 'Land Classes') within Great Britain (GB). This classification was first developed in the late 1970s, and is termed the 'ITE Land Classification' (Bunce *et al*., 1996). The same classification was later modified to accommodate devolution in Scotland and Wales, leading to 45 rather than the original 32 classes by 2007 (Bunce *et al*., 2007). The interpretation of the environmental characteristics of the classes enables those that fit the definition of the Uplands to be identified, as shown in Fig. 1. All the data described below have been collected as part of GB Countryside Survey, as described by Norton *et al*. (2012), using the environmental Land Classification framework, developed over 40 years, as described by Sheail & Bunce (2003). The analytical procedure used to produce national estimates from the data collected within this framework calculates the mean values for the various parameters collected in the 1km survey squares, for each of the Land Classes. Estimates for each Land Class are then combined for either the whole of Great Britain, or for each of England, Scotland and Wales. The national estimates of Broad Habitats for 2007 (Brown *et al*., 2014a) with standard errors are publicly available via the NERC Environmental Information Data Centre along with the linear feature data (Brown *et al*., 2014b) and vegetation data (Bunce *et al*., 2014a).

Site Selection

The procedure for site selection for survey applies to both habitats and vegetation and is described below. Sites are based on a series of 1km survey units, selected on a random basis from within the Land Classification framework, described above. Initially, in the late 1970s, it was decided that eight 1km square survey sites from each of the 32 classes were the minimum to get a representative sample for the whole of Britain. Accordingly, eight dispersed random squares were drawn from each of the classes giving a total of 256 squares, of which the majority were surveyed in the summer 1978. In subsequent surveys, the sample number was increased in proportion to the size and number of the Land Classes as follows: 1984 - 382 squares, 1990 - 506 squares, 1998 – 569 squares, 2007 – 591 squares. In 2007, 238 of these squares were located in upland Land Classes.

Habitats

Information is recorded for landscape features, habitats and land cover and for each of the 1 km survey squares ensuring complete coverage (Wood *et al*., 2018). Initially the data were recorded on standard forms as described in the field handbook (Bunce, 1978). In the most recent survey in 2007, records were made digitally, using rugged field computers. Each parcel is ascribed a primary land cover code, as given in the field handbook (Maskell *et al*., 2008), followed by details of the species composition of vascular plants with over 10 % cover and information on land use or management (such as the type of grazing animals). These data enable each parcel to be allocated to the Broad and Priority Habitats of the UK Action Plan (Jackson, 2000; Maddock, 2008). Definitions and methodologies of individual vegetation and landscape mapping survey components are documented in Wood *et al*. (2017) and Wood *et al*. (2018). Full details of the Countryside Survey are given by Norton et al. (2012) and Carey *et al*. (2008). Other European habitat classifications can also be derived from these classes as shown by Bunce *et al*. (2012). Linear features such as hedgerows, and point features such as trees, are also recorded using standard codes.

Vegetation

Vegetation data were recorded from five dispersed random main plots in each 1 km square and, initially in 1978, from six plots placed along hedgerows, water courses and roadsides (later increased according to landscape variations in survey squares) (Wood *et al*., 2017). The presence and cover of all vascular plants, and a selected range of readily identifiable bryophytes and macro-lichens, were recorded on standard waterproof paper sheets, and later on hand held field computers. The main plots are 200m square and the linear plots 10 m by 1m, as described by Wood *et al*. (2017) including information about the re-location procedure. Management information was also recorded. A total of 5953 plots of all types were recorded in upland Britain in 2007, including 1136 main (X) plots (E: 252, S: 649, W: 235).

Species

The most frequent and highest cover species were derived from the main plots, and are provided for GB and England, Scotland and Wales separately.

RESULTS

Landscapes

The distribution of the upland Land Classes, derived from the ITE Land Classification (Bunce *et al*., 1996), is shown in Figure 1, and the related area figures in Table 1. The distribution patterns clearly show the moorlands of Exmoor and Dartmoor and the Malvern Hills in South West England, and the dominance of uplands in Wales. In the North of England, there are the Pennines, the Lake District and the North York Moors. In Scotland, the Southern Uplands and the Highlands are clearly uplands, but also the lower land of the North West and all the Western Isles are marginal uplands, because of the more northern climate, similar to that in South West Norway. The map corresponds closely to the appropriate classes of the climate map of Europe of Metzger *et al.* (2005).

Table 1 shows the contrast between the three countries, with England having the lowest proportion of Uplands (12 %), then Wales (48 %), and Scotland having the largest overall area of both true and intermediate Uplands (73 %).

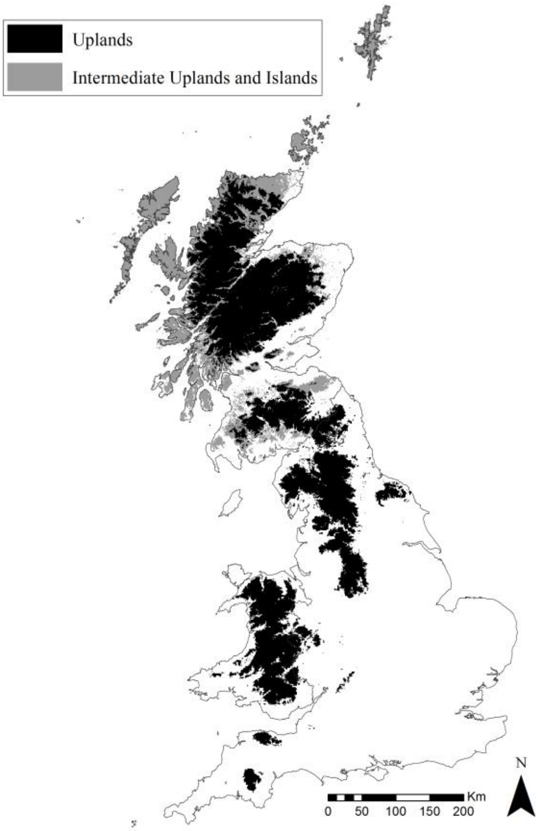
The total area of Uplands given by Bunce (1987) was 7.7 m ha (39 %), of which only 4.6 m ha (23 %) are upland vegetation. The total figure is consistent with the figure of 40 % given by Royal Society for the Protection of Birds (RSPB, 2007) and that of over 30 % quoted by Monbiot (2017a). There is, therefore, a broad consensus of the general area, but it is the detail and comprehensive coverage which is lacking - hence the present article.

Table 1: Percentage and area of upland landscapes in Great Britain, England, Scotland and Wales derived from the Environmental Land Classes of Bunce *et al.* (2007) with upland characteristics.

England: classes 16 and 20-23, Scotland true Uplands 29-32, Intermediate Uplands and Islands 27-28, 36-40 and Wales: classes 17-19 and 45.

	%		Area ('000a ha)	
Great Britain	**38 %**		8791	
England	12 %		1574	
Scotland (true uplands)	38 %	73 %	3203	6190
Scotland (intermediate uplands and islands)	35 %		2987	
Wales	48 %		1027	

Fig. 1: Distribution of upland Land Classes in Britain, derived from the ITE Land Classification (Bunce *et al.*, 2007)



Habitats

The figures given in Table 2 are comparable with those given by JNCC (2012), for Upland Heath: England 243 k ha (present paper 270 k ha), Scotland 778 k ha (826 k ha), Wales: 80 k ha (112 k ha). The differences are wide for bog because of different definitions, especially in regard to blanket bog, to the extent that comparisons are not useful.

Table 2 shows that the bog habitat is the most widespread in GB covering 2062 k ha although it is not so extensive in England and Wales because, as Table 1 shows, Scotland has the major proportion of upland landscapes and is dominated by bog. Acid grassland covers 1442 k ha and dwarf shrub heath 1208 k ha, which is the *Calluna vulgaris* (ling heather) dominated habitat often used by grouse (see Table 3). Although heather moorland is often associated in public perception with the Uplands, there is actually more acid grassland overall than dwarf shrub heath, reflecting the impact of grazing.

The importance of the influence of man is further highlighted by the proportion of highly managed habitats (grasslands and coniferous forest) which is almost 50 %, indicating that the Uplands are not the wilderness that they are often perceived to be (Smith *et al*., 2012) and also showing the importance of objective figures. The most comparable complex of habitats elsewhere in Europe is in Western Norway, as reflected in the Environmental classes of Metzger *et al.* (2005), although there is more semi-natural birch and pine woodland, and less grassland, than in Scotland.

Table 2 shows that, surprisingly, in England the typical upland habitats bog and dwarf shrub heath together occupy a smaller area than the two generally lowland habitats improved and neutral grassland. This pattern is even more pronounced in Wales where improved grassland is the most abundant Broad Habitat reflecting the less rugged terrain allowing vehicular access for fertilizer application. Both Scotland and Wales have over 10 % coniferous forest indicating the impact of plantations of exotic conifers as described by Bunce *et al*. (2014b). Another surprising figure is the relatively low cover of bracken in all three countries, which is often considered to be a major problem. This could be because it is often present as part of the acid grassland habitat, not in sufficient density (>95 %) to be recorded as a Broad Habitat in its own right. Arable land only features in England, whereas the relatively high figure for standing water in Wales and Scotland reflects the presence of reservoirs in the former and natural lochs in the latter.

Table 2: The top ten Broad Habitats of the UK Biodiversity Action Plan (Jackson, 2000) in upland landscapes in England, Scotland and Wales. Ranked in terms of extent in each country. Percentage in column 1, area in column 2.

Great Britain	%	Area ('000s ha)	England	%	Area ('000s ha)	Scotland	%	Area ('000s ha)	Wales	%	Area ('000s ha)
Bog	25 %	2061.6	Acid grassland	23 %	349.4	Bog	33 %	1888.1	Improved grassland	26 %	262.7
Acid grassland	17 %	1442.0	Dwarf shrub heath	18 %	269.7	Acid grassland	16 %	900.9	Acid grassland	19 %	191.7
Dwarf shrub heath	15 %	1207.7	Neutral grassland	16 %	237.1	Dwarf shrub heath	14 %	825.8	Dwarf shrub heath	11 %	112.3
Coniferous woodland	11 %	949.1	Improved grassland	15 %	224.9	Coniferous woodland	14 %	774.6	Neutral grassland	10 %	104.2
Improved grassland	10 %	814.7	Bog	9 %	133.9	Improved grassland	6 %	327.1	Coniferous woodland	10 %	102.4
Neutral grassland	6 %	525.0	Coniferous woodland	5 %	72.1	Neutral grassland	3%	183.8	Broadleaved, mixed and yew woodland	9 %	89.6
Broadleaved, mixed and yew woodland	3 %	250.1	Bracken	4 %	56.7	Fen, marsh and swamp	3 %	167.0	Bog	4 %	39.6
Fen, marsh and swamp	3 %	239.1	Fen, marsh and swamp	3 %	50.4	Broadleaved, mixed and yew woodland	2 %	120.2	Bracken	3 %	33.1
Bracken	2 %	198.4	Broadleaved, mixed and yew woodland	3 %	40.4	Bracken	2 %	108.6	Fen, marsh and swamp	2 %	21.7
Arable and horticultural	1 %	116.3	Arable and horticultural	2 %	34.1	Standing water and canals	1 %	81.9	Standing water and canals	1 %	14.8

Table 3: Percentage and area of grazing animals recorded in land parcels within the sample 1 km squares (Brown *et al.*, 2016).

Upland Zone	Animal	% upland area grazed	Area ('000ha)
Uplands (England)	Cattle	4.2	65.6
	Deer	0.1	1.1
	Grouse	7.1	112.1
	Sheep	39.9	628.4
	Any grazing animal	*45.3*	*713.1*
Intermediate uplands and Islands (Scotland)	Cattle	3.3	97.7
	Deer	11.8	352.5
	Grouse	2.3	69.5
	Sheep	42.5	1270.5
	Any grazing animal	*50.8*	*1516.7*
True uplands (Scotland)	Cattle	0.7	21.4
	Deer	37.4	1197.0
	Grouse	17.5	559.1
	Sheep	37.8	1209.9
	Any grazing animal	*56.5*	*1808.5*
Uplands (Wales)	Cattle	4.1	42.4
	Sheep	47.4	487.4
	Any grazing animal	*48.7*	*500.0*

The figures in Table 3 demonstrate the dominance of sheep grazing throughout the British Uplands and explain the dominance of acid grassland over dwarf shrub heath. The removal of sheep grazing and the subsequent shift from acid grassland to dwarf shrub heath species is discussed by Hill *et al*. (1992). The figures for cattle are low – being present in about 4 % of Uplands in England, Wales and the Scottish Intermediate Uplands, and under 1 % in the true Scottish Uplands. These figures emphasize the decline of hill cattle - even more so considering that valleys were included. Sheep were present in almost 50 % of the Uplands in all countries with Wales having the highest figure. Grouse are absent from Wales, very low in the intermediate Uplands in Scotland (2.3 %) but common in England (7.1 %) and highest in the Scottish Highlands (17.5 %), indicating the importance of shooting in this region. Red deer are absent from Wales, very low in England (0.1 %) but high in the intermediate Scottish Highlands (11.8 %) but highest in the true Highlands (37.4 %) which are the focus of deer stalking.

Table 4: Estimates of the length of linear features and percentages in the uplands of Great Britain, England, Scotland and Wales.

Feature	Great Britain		England		Scotland		Wales	
	Mean length (000s km)	*% of total linears in GB*	*Mean length (000s km)*	*% of total linears in England*	*Mean length (000s km)*	*% of total linears in Scotland*	*Mean length (000s km)*	*% of total linears in Wales*
Managed hedgerows	29.66	6.2 %	9.4	2.4 %	2.6	12.4 %	17.6	32.7 %
Walls	84.19	48.4 %	43.9	53.9 %	34.0	43.3 %	6.3	46.7 %
Lines of trees/relict hedges & fence	18.72	16.4 %	5.6	7.7 %	2.8	23.1 %	10.4	34.7 %
Lines of trees/relict hedges	14.9	13.1 %	5.6	6.8 %	4.0	30.2 %	5.4	28.5 %
Bank/grass strip	12.29	19.2 %	2.4	5.6 %	4.0	64.9 %	5.9	36.7 %
Fence	181.4	27.3 %	33.1	9.1 %	114.4	50.5 %	33.9	45.7 %

There is a surprising number of hedges as well as lines of trees/relict hedges in all three countries; these are important as landscape features as well as for biodiversity. Although these are not usually associated with the Uplands, they are present in the valleys linked to the two generally lowland habitats. Again, the comprehensive coverage of the present paper has identified the importance of these habitats in the Uplands. The lengths of wall (mainly drystone) are especially high in England (43.9 k km) and Scotland (34 k km) but there are also significant lengths in Wales (6.3 k km). Their extent is a unique feature of the British Uplands not found to the same extent elsewhere in Europe and represents an important resource for landscape character and biodiversity. Fences predominate in Wales (33.9 k km) and Scotland (114.4 k km) but are not so important for biodiversity.

Table 5: Frequency of the top ten classes of the Countryside Vegetation System (Bunce *et al.*, 1999a) in upland Great Britain. Numbers of plots that fell in that class and the overall percentage in upland Great Britain. (Note: this is all plot types)

Great Britain	No. plots *(total 5953)*	%
Rushy moorland grass/streamsides on peat soils	493	8 %
Moorland grass/heath on podzolic soils	306	5 %
Moorland grass	281	5 %
Cotton grass bog	245	4 %
Saturated bog	226	4 %
Moorland grass/bog on peaty gley/peat soils	223	4 %
Moorland grass/heath/bog	217	4 %
Rye-grass/bent grass grassland	212	4 %
Bracken/acid grassland	212	4 %
Fertile mixed grassland	186	3 %

Table 5 shows a rather different balance of vegetation in the landscape than the Broad Habitat extents, which are mapped as complete cover in each survey square (therefore including habitats such as open water and urban which do not have vegetation plots placed within them). It is important to note that the names of the Countryside Vegetation System (CVS) classes are only convenient labels to help interpretation of the 100 classes, which are determined on the basis of multivariate analysis (TWINSPAN, Hill & Šmilauer (2005)) of the complete species composition in each plot. They are, therefore, independent of the habitat classes. A full discussion of the results is given in Bunce *et al*. (1999a).

The most abundant class (rushy moorland grass/streamsides on peat soils) reflects the dominance of wetness in determining the composition of the vegetation and occurs by springs and seepages as well as beside streams. The next three classes (moorland grass/heath on podzolic soils, moorland grass, cotton grass bog) show the strong relationship of much of the vegetation in the Uplands with bogs in a broad context, reflecting the difficulty of defining bogs when mapping discrete polygons. The next two classes (saturated bog, moorland grass/bog on peaty gley/peat soils) show the complex intergrades of moorlands, heaths and bogs that are abundant in the Uplands, which are widespread. Two of the last three classes confirm the extent of vegetation with lowland affinities shown in the habitat results (rye-grass/bent grass grassland, fertile mixed grassland). The other class (bracken/acid grassland) indicates that there is an intergrade between acid grassland and bracken, with the abundance of bracken changing, depending on management.

Table 6: The top ten most frequent species in the dispersed random 200 m square (main) plots within the sample squares in England, Scotland and Wales (excluding bryophytes and lichens).

	Great Britain	No. of plots	Freq.	England	No. of plots	Freq.	Scotland	No. of plots	Freq.	Wales	No. of plots	Freq.
1	*Potentilla erecta*	666	59 %	*Galium saxatile*	152	60 %	*Potentilla erecta*	499	77 %	*Agrostis capillaris*	176	75 %
2	*Calluna vulgaris*	658	58 %	*Deschampsia flexuosa*	142	56 %	*Calluna vulgaris*	472	73 %	*Holcus lanatus*	128	54 %
3	*Molinia caerulea*	512	45 %	*Calluna vulgaris*	135	53 %	*Molinia caerulea*	387	60 %	*Cerastium fontanum*	117	50 %
4	*Anthoxanthum odoratum*	506	45 %	*Anthoxanthum odoratum*	135	53 %	*Trichophorum cespitosum*	333	51 %	*Trifolium repens*	116	49 %
5	*Agrostis capillaris*	502	44 %	*Agrostis capillaris*	133	53 %	*Erica tetralix*	328	51 %	*Anthoxanthum odoratum*	108	46 %
6	*Galium saxatile*	492	43 %	*Vaccinium myrtillus*	129	51 %	*Eriophorum angustifolium*	297	46 %	*Lolium perenne*	106	45 %
7	*Deschampsia flexuosa*	490	43 %	*Nardus stricta*	124	49 %	*Juncus squarrosus*	292	45 %	*Galium saxatile*	104	44 %
8	*Vaccinium myrtillus*	488	43 %	*Festuca ovina agg.*	123	49 %	*Narthecium ossifragum*	284	44 %	*Vaccinium myrtillus*	96	41 %
9	*Juncus squarrosus*	454	40 %	*Holcus lanatus*	112	44 %	*Anthoxanthum odoratum*	263	41 %	*Ranunculus repens*	90	38 %
10	*Nardus stricta*	445	39 %	*Juncus effusus*	104	41 %	*Vaccinium myrtillus*	263	41 %	*Deschampsia flexuosa*	86	37 %

This table (6) shows that *Potentilla erecta* (tormentil), a species of acid soils, is the most frequent species in upland Britain, with four other acid grassland plants in the top ten. Table 6 provides further detail of the composition of the vegetation and habitats and confirms the differences in the three countries as indicated by the composition of habitats. The species that have the highest frequency in Wales are all grassland plants, with the exception of *Vaccinium myrtillus* (bilberry), and also includes three species from fertile soils (*Trifolium repens* (white clover), *Lolium perenne* (perennial rye-grass), *Ranunculus repens* (creeping buttercup)). By contrast, the widespread species in England include none from fertile soils with the exception of *Holcus lanatus* (Yorkshire fog) and are otherwise evenly divided between those of acid grasslands and heathland. In Scotland, all the species are from acid soils and wet peats with three species of dwarf shrubs *(Calluna vulgaris, Erica tetralix, Vaccinium myrtillus)*, emphasizing the extreme oceanic nature of the region and its similarity with Norway.

In terms of species coverage, although not appearing in a high position in the frequency table, *Calluna vulgaris* (Ling heather) has the highest cover overall in plots in the British Uplands (mean per plot, 14.8 %). A series of histograms presented in the Supplementary Material (S1) show the variation in cover within plots of the species in Table 7. Cover of *Calluna* in particular is shown to dominate some plots. *Calluna* dominates in England (14.7 %) and Scotland (18.7 %), demonstrating the importance of this species overall (although it is only in tenth position in Wales). The extent of this species is not reflected in the habitat or vegetation tables but confirms the public perception of the purple colour of the British Uplands during flowering of this species in summer. *Lolium perenne* (perennial rye-grass) appears as the dominant species in Wales, in second position in England and fifth in Scotland, further confirming the importance of fertile fields in the Uplands. Otherwise, Scotland has the most bog species for example *Molinia caerulea* (purple moor grass) and *Tricophorum caespitosum* (deer grass). By contrast, England has the most acid grassland species, for example *Agrostis capillaris* (bent grass) and *Deschampsia flexuosa* (wavy hair grass), whereas Wales has the most bracken (*Pteridium aquilinum*).

Table 7: Average percentage cover of the top ten species (with the greatest overall cover) recorded in the dispersed random 200 m square (main) plots within the sample squares in Great Britain (excluding bryophytes and lichens)

	Great Britain	Mean cover per plot	England	Mean cover per plot	Scotland	Mean cover per plot	Wales	Mean cover per plot
1	*Calluna vulgaris*	14.8	*Calluna vulgaris*	14.7	*Calluna vulgaris*	18.7	*Lolium perenne*	17.7
2	*Molinia caerulea*	10.7	*Lolium perenne*	9.0	*Molinia caerulea*	13.5	*Agrostis capillaris*	12.6
3	*Lolium perenne*	8.1	*Vaccinium myrtillus*	8.3	*Trichophorum cespitosum*	9.5	*Molinia caerulea*	7.2
4	*Trichophorum cespitosum*	5.7	*Agrostis capillaris*	7.5	*Picea sitchensis*	5.9	*Pteridium aquilinum*	5.8
5	*Agrostis capillaris*	5.6	*Deschampsia flexuosa*	7.2	*Lolium perenne*	4.3	*Vaccinium myrtillus*	5.7
6	*Picea sitchensis*	5.0	*Molinia caerulea*	7.0	*Eriophorum vaginatum*	4.0	*Nardus stricta*	5.6
7	*Nardus stricta*	4.5	*Pteridium aquilinum*	5.9	*Nardus stricta*	3.7	*Picea sitchensis*	5.2
8	*Vaccinium myrtillus*	4.0	*Nardus stricta*	5.8	*Eriophorum angustifolium*	3.3	*Trifolium repens*	4.9
9	*Pteridium aquilinum*	3.8	*Holcus lanatus*	5.5	*Holcus lanatus*	2.6	*Holcus lanatus*	4.8
10	*Holcus lanatus*	3.7	*Festuca ovina agg.*	5.2	*Deschampsia flexuosa*	2.6	*Calluna vulgaris*	4.4

The role of grazing animals in the Uplands

Sheep are the most widespread domestic grazing animal throughout the British Uplands as shown in Table 3, and not only have had a major role in the formation of the present composition of the vegetation, but also in maintaining its current condition. The total breeding flock of sheep, as defined by the Annual Statistics for sheep and lambs on December 1 (Department for Environment Food & Rural Affairs, 2018), has declined somewhat since its peak of 31 million in 1998 to 22.0 million in 2008, recovering slightly to 23.3 million in 2017. Whilst these figures are for the whole country, not just the Uplands, they give an indication of the extent of the grazing pressure. (It would be a major exercise to extract separate figures for the Uplands, and Parish figures are often misleading (for example Scottish Government (2016)), as the sheep may all be in the valleys and may not use the hills at all, as in Ennerdale in the English Lake District). Fuller & Gough (1999) discuss the changes in sheep numbers in the Uplands and emphasize that the effect of grazing on the structure of semi-natural vegetation reduces their value for birds.

Table 3 shows that red deer are mainly in Scotland, although there are local herds in the Lake District and Exmoor. Whilst estimates of numbers have to be treated with caution, Clutton-Brock *et al*. (2004) indicate that the population was around 150,000 in 1960 but had risen to 400,000 by 2004. Flyn (2017) quotes a current figure of 1.5 million, which seems high, although it is generally accepted that numbers are still increasing. Flyn (2017) also suggests the reasons behind the increases, which are partly due to the absence of any predator but mainly because shooting female deer is not profitable. The call for a mass cull is very controversial and is unlikely to take place at present for a variety of reasons, varying from the views of landowners and professional hunters to the attitude of the public. What is beyond doubt is that currently the number of deer is having a negative influence on the vegetation and prohibit tree regeneration, as discussed by Bunce *et al*. (2014b). Some estates (for example, the National Trust for Scotland at Mar Lodge), are now reducing numbers and regeneration is resulting (Gill & Morgan, 2010). Other estates, such has Abernethy and Glenfeshie are also reducing numbers, a trend followed by publicly owned land (such as that of Forest Enterprise).

There is much discussion about the possibility that Brexit may result in the loss of sheep farming in the Uplands, leading to the suggestion that the hills will become dense scrub. However, this consequence may be variable. Hill *et al.* (1992), show that although change is rapid at first, eventually competitive species such as *Calluna vulgaris* and *Nardus stricta* take over the sward to the extent that other species are then unable to colonise. Also, there is an absence of tree seed in many upland landscapes (for example the Southern Uplands of Scotland). Table 7 shows that *Calluna*, *Vaccinium*, *Eriophorum*, *Molinia*, *Nardus* and *Tricophorum* are the major cover species in the Uplands, which can all form a dense impenetrable sward, resistant to change, thereby forming plagioclimaxes, as seen in forest rides.

The expansion of tree cover is therefore likely to be variable depending on soil type, altitude and the past history of the vegetation. For example, abundant tree colonisation by Scots pine (*Pinus sylvestris*) is shown in the pictures of Bain (2013) adjacent to native pinewoods, and birch (*Betula* species) in the picture of Ennerdale in Bunce *et al*. (2014b). There is also a history of rapid tree regeneration in Norway and the Pyrenees, although the soils are different from most British Uplands.

Further research is needed to establish whether sheep are still transferred to the higher mountain land, as there is some evidence from the English Lake District and the Cheviots that this practice is in decline.

Genetic diversity in the Uplands.

The Uplands contain important resources of genetic diversity in the wide range of native cattle and sheep breeds present. For example, cattle are represented by Welsh Black, Galloway and Scottish Highland breeds, all of which originated in the Uplands. There are also many sheep breeds often localised in their occurrence (such as Welsh Mountain (Wales), Herdwick (The Lake District), Scottish Blackface (Scottish mountains) and Soay sheep (the Hebrides)). Wild goats are also present, for example in Snowdonia and The Cheviots, and local breeds of ponies in Dartmoor and Snowdonia. Both the latter have been notified as threatened breeds (Murray, 2007).

DISCUSSION

There seems little doubt that major changes in upland habitats will occur in the future, as they have throughout history, but particularly following Brexit. The policy issues driving some of these changes are addressed in the second part of this paper (Bunce *et al.*, 2018). Changes are likely to be very different at regional levels, with isolation from markets and landscape structure being key factors. For example, the rounded hills of central Wales could be suitable for large scale ranching agriculture run by a few farms, whereas the rugged landscapes of North West Scotland could not be managed as large units. Elsewhere in Europe, for example in the Pyrenees (Baudry & Bunce, 1991), similar heterogeneous landscapes have largely been abandoned, a process that to date has not happened in Britain, although the first signs can be seen in the far North West of Scotland.

Throughout the upland region, social structure is likely to have a major influence, as is recognised in the definition of Less Favoured Areas, and in common with mountainous regions elsewhere in Europe. On the one hand, there is an aging population, with young people not being willing to take up the hard lifestyle, but there is also the effect of isolation of communities especially in the Highlands and Islands of Scotland. The changing social structure is well shown in the Shetlands with the widespread abandonment of subsistence crofting, accelerated by the financial influence of the oil industry (Wood & Bunce, 2016).

Affluent sections of society have also had a major influence on rural housing in the case of second home ownership, indirectly linked to recreation. Under current economic conditions, this process is likely to continue and could be beneficial to the environment, as such people often wish to maintain traditional landscapes. The social impact of rising house prices is, however, a different matter and is perceived to be leading to a decline in schools and other local services, and changes in social structure (discussed in Hodge & Monk (2004); Stockdale *et al*. (2000)).

Finally, climate change could have a range of influences from reducing sub-arctic vegetation on the one hand, to increasing the potential for crop growth in fields in the valleys on the other. There are also likely to be major regional differences because of the wide climatic gradient in GB.

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