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A proposed vegetation classification for the oceanic wet grasslands of Scotland

H.L. Wallace[1]; C.S. Lawson[2]; D.J.G. Gowing[2,3*]

[1]Ecological Surveys (Bangor); [2]Hereford, UK; [3]School of Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes, UK.

*__Corresponding author__: d.j.gowing@open.ac.uk

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Abstract
The lack of clear community definitions for the oceanic wet grasslands of Scotland has resulted in them being overlooked in some conservation schemes, which have tended to focus primarily on the vegetation of the cultivated machair and associated sand dunes. This study recognises five distinct vegetation communities that could be further segregated into ten units equivalent to subcommunities of the British National Vegetation Classification (NVC). These communities show differing ranges in respect of three soil parameters: available phosphorus, pH and organic content. The subcommunities themselves differ in their tolerances to soil moisture, soil fertility and soil reaction, as assessed by their Ellenberg indicator values. The Scottish communities were distinct when compared to communities of the Calthion alliance found in England and Wales with limited overlap. When compared to the Irish Community Classification (IVS) there was more overlap of the data, but alignment to recognised communities was poor. In a broader European context, when compared with data drawn from across twelve alliances, the Scottish communities are mainly associated with the Calthion, yet are discrete from the English and Irish communities of that alliance. They occupy a narrow, central position on the fertility gradient with a broader spread along the hydrological gradient. They are generally less fertile than their English counterparts, which are in turn more fertile than many of the continental communities in the Calthion. The greatest threat to the biodiversity of these grasslands is changing management through both abandonment and intensification, and climate change through increasing rainfall and rising sea levels.

Keywords: Calthion; mesotrophic grassland; species-rich meadow; biodiversity; National Vegetation Classification; machair

Introduction
The review of coverage of the NVC (Rodwell *et al*., 2000) discusses the ongoing problem of classification of vegetation that falls floristically between dune slack communities, especially SD17 (the *Potentilla anserina-Carex nigra* community of the *Potentilla anserina-Agrostis stolonifera* alliance), and the mesotrophic grassland community, MG8, (*Cynosurus cristatus-Carex panicea-Caltha palustris* of the Calthion alliance within the Molinietelia caeruleae). The extensive work of Dargie on the sand dune survey of Scotland (Dargie, 1998), Coll (Dargie & Dargie, 1993) and Tiree (Dargie, 1983), and other studies, including Crawford (1988 in Dargie, 1998) on the Inner and Outer Hebrides, proposed a new rich fen association, with four subtypes; characterised by the presence of *Carex nigra* but with

only sporadic occurrence of *Potentilla anserina*. This vegetation was first noted by Pitkin *et al.,* (1983) on the west coast of North and South Uist. The vegetation has links to the SD17 community, but Dargie (1998) proposed a new community with a series of subcommunities. These communities occur on the inner edge of dune systems that support machair vegetation, and generally occupy the wetter plateaux of windblown sand.

Rodwell *et al.* (2000) recognise a potentially new subcommunity within SD17 (*Potentilla anserina-Carex nigra* dune slack community) which was labelled *Carex nigra-Agrostis stolonifera*. Described as a wet grassland or small sedge fen with abundant *Carex nigra* and frequent *Agrostis stolonifera, Holcus lanatus, Ranunculus repens, Ranunculus acris, Caltha palustris, Silene flos-cuculi, Cardamine pratensis* and *Calliergonella cuspidata* variously enriched by *Carex panicea* and poor fen species, or by *Juncus articulatus* and species of the Potentillion, though not necessarily *P. anserina*. The review reports this new subcommunity to be widely recorded at low altitudes, in wet hollows in pastures and especially common on the west coast of Britain (Cooper & MacIntosh, 1996; Dargie, 1993; 1998).

The question posed by Rodwell (Rodwell *et al.,* 2000) was whether this new vegetation type is best placed within the Calthion (Senecio-Brometum) in the Molinietalia caeruleae (meadows and pastures of moist, often peaty soils) or within the Caricion fuscae (*Carex-Ranunculus flammula*) within the Caricetalia fuscae (small-sedge poor-fens of base-poor waters).

Following discussions with Scottish Natural Heritage (now NatureScot) and a subsequent visit to the Outer Hebrides by the Floodplain Meadows Partnership Steering Group in 2018, it became apparent that the chain of islands may contain as much species-rich wet grassland in terms of area as the whole of mainland Great Britain. The extent and distribution of these grasslands is unmapped, and many of the sites have little or no legal protection against future management change, development, or abandonment. These meadows and pastures, typically in wet machair systems, have evolved through centuries of crofting (a sustainable farming system), but are now threatened by abandonment of farming and changing government policies (Pakeman, 2011; 2017).

Many of the sites in Scotland, especially in the Outer Hebrides, are on damp, soligenous soils, outwith the dune-slack environment. Being affected by windblown sand, including shell fragments, they tend to have a relatively calcareous substrate. Hence the dilemma of whether these communities are best placed within the Caricion davallianae or the Calthion.

The recent Irish Vegetation Classification (IVC; Perrin, 2019) also recognises a series of grassland and rich fen associations in which *Agrostis stolonifera, Carex nigra, Calliergonella cuspidata* and *Caltha palustris* are frequent. These are placed variously in the Cynosurion, Calthion, Junco-Molinion and Caricion davallianae, and provide another link between the Scottish vegetation and these rich communities on the western Atlantic fringes of Europe.

Historic data provided by NatureScot were supplemented by field survey in 2018, 2019 and 2021 to explore the extent and distribution of these species-rich wet grasslands associated with machair systems in Scotland.

The survey objectives were to:

- offer an updated plant community definition for species-rich wet grasslands in machair and other coastal systems of Scotland,
- produce maps detailing the extent of remaining species-rich wet meadows in Scotland that could allow NatureScot to confer protection and support for management,
- provide recommendations about future management of these species-rich wet meadows,

- instigate more detailed research to describe the ecohydrology of the plant communities.

Methods

Data Sources

Relevés were gathered from several sources.

1. The main source was the sand dune survey of Great Britain (Dargie, 1988) and updated data from the 2010 sand dune survey (Pakeman, *pers com*); relevés were selected where vegetation had been identified, by the original surveyor, as representing damp neutral grassland, grassland that was transitional to the *Potentilla anserina-Carex nigra* dune slack community (SD17), and other vegetation types with affinities to the *Cynosurus cristatus-Carex panicea-Caltha palustris* grassland (MG8), being described as 'new types' of MG8 or new fen communities, often designated Mx in sand dune reports.
2. NVC reports where constancy tables were available, quadrats were selected on the basis of the joint occurrence of *Caltha palustris, Carex nigra, Cynosurus cristatus* and *Agrostis stolonifera*, with *Potentilla anserina* only occasional. Sources include NVC surveys of Tiree (Dargie, 1993), Coll (Dargie & Dargie, 1993; Hutcheon & Hutcheon, 2003), Shetland (Crossley, 2016; Acton 2004) and the Uists (Dargie, 1998).
3. In 2018 and 2019, the Floodplain Meadows Partnership (FMP) surveyed sites identified from these reports as supporting new types of MG8 or Mx vegetation, but for which there were no quadrat data available in the earlier reports. Site selection was based on descriptions in previous reports and maps from the sand dune survey, priority was given to larger sites or concentrations of small sites; but sometimes constrained by landowner permissions. In 2019, quadrat data were collected from areas of homogeneous damp grassland at each site selected following the standard NVC protocol (Rodwell, 1991). Samples were recorded on the Uists, Tiree, Coll, Shetland, Orkney and around the north coast of Scotland.
4. Further sets of samples were recorded on the Uists: 123 in 2021 and 50 in 2023. These were from sites identified in (3) above that were not visited in 2019 and also locations on three fields selected for long-term monitoring.

Figure 1 illustrates the geographic range of the samples collected by the surveys mentioned in items (3) and (4) above.

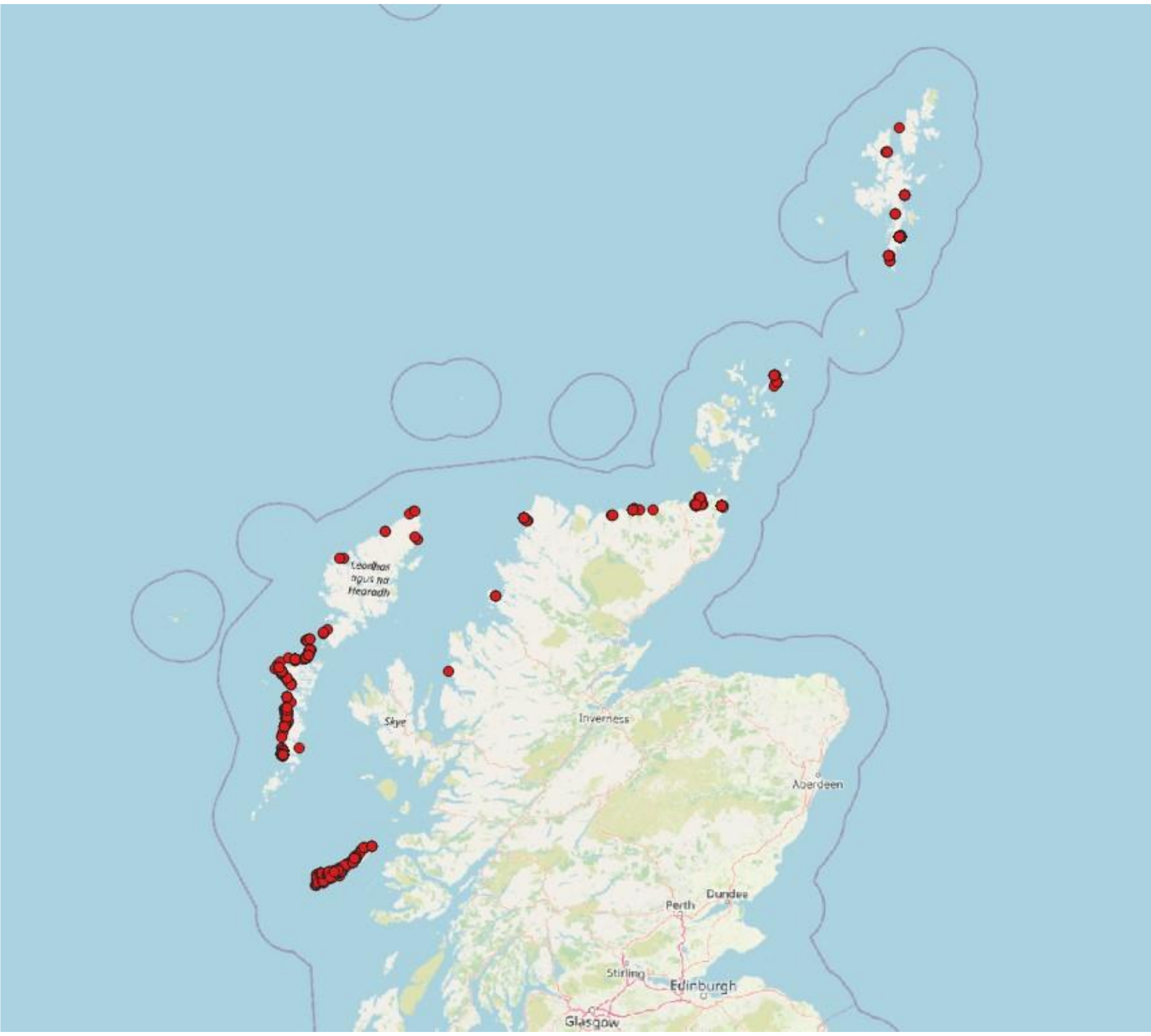

Figure 1. The location of grassland relevés collected by FMP surveys in the period 2018-2023.

Data analysis
Where the original data had been collected using the DOMIN scale of relative abundance, values were converted to percentage cover classes using the conversion of Currall (1987). The 835 quadrats from the pre-2021 surveys (1, 2, 3 above) were analysed using the TWINSPAN program in the Juice Suite of programs (Tichŷ & Holt, 2006).

The analysis was run with five cut levels (0, 1, 2, 5 and 33%), minimum group size of 5 and 30 clusters.

Optimclass (Tichŷ *et al.,* 2010), also available in the Juice software package, was used to produce a hierarchical tree of the divisions with a Fisher threshold of 0.0001, and flexible beta set at -0.25.

The endgroup clusters[1] were then assessed for internal homogeneity using Sorensen-Bray-Curtis analysis within Juice, and between group dissimilarity using Bray Curtis in

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[1]

Endgroup: the lowest level of division in a hierarchical twinspan analysis
Cluster: computer generated grouping of end-groups based on predetermined mathematical criteria.
Noda: groups of endgroups or clusters representing abstract vegetation units before they are linked to pre-existing vegetation communities.

Systat, and tested individually against units of the NVC using the Czekanowski coefficient of similarity (Malloch, 1998). A modified version of MATCH, produced during a previous analysis of MG4 and MG8 data was used, which includes the revised communities of the Calthion alliance (Wallace & Prosser, 2017).

A synoptic table (based on the percentage frequency of species in each cluster) was produced for the 29 clusters and these were manually ordered based on a combination of statistical similarity coefficients and visual observation of the tables leading to recognition of clearly defined groups of preferential and differential species following the guidelines of Mueller-Dombois & Ellenberg (1974).

The final aggregation into fifteen noda was based on visual ordering of synoptic tables within each section of the TWINSPAN two-way table.

Seven of the noda were assigned to NVC community types that we deemed to be out of the scope of our focus on the Calthion; namely MG5, MG6, SD8, SD17 and swamp communities. The 233 quadrats in these types were omitted from further analyses. The remaining eight noda, comprising 602 quadrats, were all considered to represent forms of oceanic wet grassland. Five communities, some with subcommunities, were proposed (Wallace *et al.,* 2020).

The 602 quadrats were combined with the 173 quadrats recorded from later surveys on the Uists, the resulting 775 quadrats were subject to TWINSPAN analysis. The allocation of the original 602 quadrats in this analysis was compared to their end group allocation in the preliminary analysis. Most quadrats from the preliminary analysis remained end-group faithful and the new quadrats were allocated to one of the five recognised communities. The larger data set allowed for the subdivision of some of the communities into subcommunities, resulting in 10 noda considered to be floristically distinct. These 10 noda form the basis of the final community descriptions (Table 1).

Community – Environment relationships

Vegetation and soil samples were collected from 50 quadrats in 20 fields across North and South Uist during 2021 and 2023. At each site, the vegetation was sampled in 1 m × 1 m quadrats and all vascular plants and bryophytes recorded. Five soil cores, 2 cm diameter and 10 cm deep, were taken and pooled to give one sample for each quadrat to determine soil phosphorus availability, soil pH and organic matter content. Ten undisturbed cores were also collected to determine the bulk density of the soils. The sampling locations were stratified to cover the range of plant communities recorded.

All the soils were sieved (2 mm) and air dried at 40^{o}C. The air-dried soil was analysed for Olsen extractable phosphorus (Gilbert *et al.,* 2009), and pH. The soil organic matter (SOM) concentration (%) was determined for each soil sample using loss on ignition (LOI) methods, 5 g of oven-dried soil at 375^{o}C for 16 hours.

Mean Ellenberg scores were calculated for the species list in each quadrat, using the original scores of Ellenberg (1988) as a surrogate for soil hydrology and soil chemistry.

The relationship between plant community and soil environmental variables was analysed using ANOVA in R, with the plant community as a fixed effect and field (location) included as a random effect.

Comparison with Calthion communities of England and Wales

The Scottish noda were tested for their similarity to communities of the Calthion group of communities described for England and Wales (Wallace & Prosser, 2017). This analysis combined the 602 wet grassland quadrats from the original Scottish analysis (Wallace *et al.,* 2020) with 2051 quadrats from Prosser & Wallace (2017) that were allocated either to the two subcommunities of *Carex nigra-Potentilla anserina-Senecio aquaticus* grassland

(MG14) or the four subcommunities of *Cynosurus cristatus-Carex panicea-Caltha palustris grassland* (MG8), giving a total data set of 2653 quadrats.

This full data set was subject to TWINSPAN analysis using the Juice software and DCA analysis (PC-ORD). The allocation of quadrats to end-groups was used to assess the discreteness of each nodum across the data set, end-group similarity coefficients were also calculated for each end-group using the revised Calthion communities of Wallace & Prosser (2017).

Comparison with the wet neutral grasslands of Ireland

Comparison of the 775 Scottish quadrats with the Irish Vegetation Classification (IVC, Perrin, 2021) was carried out at the community and subcommunity level using the automated classification tool ERICA v6.1 (Perrin, 2019). Non-metric multidimensional scaling (NMDS) was carried out using the vegan package in R. Data for the NMDS comprised all the Scottish data plus the Irish data from the 17 communities from the Irish Vegetation Classification (IVC; Perrin, 2019) highlighted in the ERICA analysis as having affinities with the Scottish categories (5369 quadrats)

ERICA (Engine for Relevés to Irish Communities Assignment) uses a fuzzy cluster analysis called noise clustering. It calculates, for each plot, a degree of membership to each of the communities defined by the IVC. Membership can also result in assignment to a 'noise' class which represents outliers which are not adequately described in the current IVC classification. All membership values total to 1. A plot can thus be assigned to a vegetation community if membership to that community => 0.5, conversely a plot will be unassigned and placed in the noise class if membership is <= 0.5. Finally, a plot may be considered transitional if membership is < 0.5 for all vegetation communities and for the noise category. For ease of interpretation the maximum values for fuzzy membership of a group are presented as a percentage.

Wider European perspective

The Scottish units were compared against 102 noda from across Europe spanning twelve alliances following the approach taken for the Calthion analysis of England and Wales (Wallace & Prosser, 2017) and floodplain meadows analyses of Prosser *et al.* (2023). DCA analysis was carried out on the floristic data with a secondary matrix comprising four proxy environmental variables including Ellenberg scores for soil reaction (R), soil fertility (N), soil moisture (F) and a categorical variable for the published alliance for each noda.

Results

Community descriptions

The new syntaxa proposed following the analysis are set out in Tables 1 and 2.

Agrostis stolonifera-Bellis perennis grassland *(AgBp)*

The two units of the *Agrostis stolonifera-Bellis perennis* grassland have constant *Agrostis stolonifera* and *Ranunculus acris,* but *Carex nigra* and *Caltha palustris* are no more than occasional; they lack poor fen species but have higher frequencies of neutral grassland species including *Bellis perennis, Cerastium fontanum, Rumex acetosa and Lolium perenne*. Preferential species in Table 2 (*Bellis perennis* to *Cirsium arvense*).

Table 1. Summary of names for the proposed Scottish Oceanic wet grassland communities and subcommunities with proposed NVC codes

Abbreviation	Vegetation community	Sub-community	Proposed NVC code
AgBpa	*Agrostis stolonifera-Bellis perennis* grassland	*Ranunculus repens* subcommunity	MG17a
AgBpb	*Agrostis stolonifera-Bellis perennis* grassland	*Lolium perenne* subcommunity	MG17b
AgCfa	*Agrostis stolonifera-Carex flacca* grassland	*Potentilla anserina-Bellis perennis* subcommunity	MG18a
AgCfb	*Agrostis stolonifera-Carex flacca* grassland	Typical subcommunity	MG18b
AgCfc	*Agrostis stolonifera-Carex flacca* grassland	*Plantago maritima* subcommunity	MG18c
AgCfd	*Agrostis stolonifera-Carex flacca* grassland	*Succisa pratensis* subcommunity	MG18d
CaCna	*Caltha palustris-Carex nigra* grassland	*Potentilla anserina* subcommunity	MG19a
CaCnb	*Caltha palustris-Carex nigra* grassland	*Hydrocotyle vulgaris-Ranunculus flammula* subcommunity	MG19b
CnPe	*Carex nigra-Potentilla erecta-Rhytidiadelphus squarrosus* grassland		MG20
MG14c	*Carex nigra-Agrostis stolonifera-Senecio aquaticus* community	Proposed *Potentilla anserina* subcommunity	MG14c

Table 2. Synoptic table for the ten oceanic wet grassland vegetation units. Values are percentage frequency of occurrence of species in each unit. Any species present at >5% frequency in any one unit are included. Community names are abbreviated here as column headings; the full names are given in Table 1.

	AgBp	AgBp	AgCf	AgCf	AgCf	AgCf	CaCn	CaCn	CnPe	MG14
	a	b	a	b	c	d	a	b		c
Number of samples	66	102	33	50	62	110	140	124	56	32
Mean species/quadrat	24	19	23	26	30	24	20	23	19	14
Min-Max species /quadrat	13-26	8-35	14-35	13-49	16-46	15-40	10-48	6-43	11-34	4-23
Holcus lanatus	94	86	100	90	85	95	85	82	91	22
Agrostis stolonifera	80	72	88	78	79	71	71	69	43	84
Trifolium repens	91	92	94	82	87	77	49	64	41	9
Ranunculus acris	77	71	91	90	89	82	59	59	45	6
Anthoxanthum odoratum	62	20	12	62	66	66	63	52	91	6
Carex nigra	62	14	45	88	87	95	91	95	89	53
Cynosurus cristatus	77	61	82	88	69	62	29	40	14	6
Potentilla anserina	58	42	94	56	61	50	66	19	2	84
Juncus articulatus	64	22	27	50	47	35	33	65	18	31
<u>*Species preferential to AgBp*</u>										
Bellis perennis	91	83	70	60	65	11	6	23	2	9
Rumex acetosa	76	60	33	36	8	28	61	19	36	28
Ranunculus repens	88	59	24	46	39	15	35	32	2	53
Rhinanthus minor	80	46	45	36	44	15	12	19	2	28
Euphrasia officinalis	74	39	55	48	63	26	6	17	2	3
Juncus bufonius	29	11	3	6	8	2	4	2	.	.
Sagina procumbens	39	16	6	22	18	12	11	23	.	13
Trifolium dubium	30	1	.	2	3	.	1	2	.	.
Kindbergia praelonga	29	4	3	4	3	5	12	3	11	6
Brachythecium rutabulum	35	6	12	2	3	5	24	10	2	9
Myosotis discolor	17	7	.	.	.	.	.	.	.	.
Lolium perenne	44	75	6	28	10	5	1	1	.	9
Cerastium fontanum	62	74	58	56	48	33	25	37	34	6
Poa pratensis	17	46	27	48	29	25	11	10	9	3
Odontites vernus	15	26	18	6	.	2	2	.	.	28
Heracleum sphondylium	2	22	3	4	.	.	1	.	.	.
Cirsium arvense	.	13	3	2	.	.	1	.	.	.
<u>*Species preferential to AgCf*</u>										
Carex flacca	6	7	94	82	71	50	11	30	4	.
Festuca rubra	35	69	94	86	89	62	37	48	50	6
Plantago lanceolata	47	63	85	76	82	68	16	17	4	.
Prunella vulgaris	18	27	61	72	76	30	8	37	.	.
Luzula campestris	5	8	39	30	42	20	3	11	11	.
Trifolium pratense	32	30	45	58	69	34	5	6	2	.
Vicia cracca	42	33	39	48	56	38	26	13	.	3
Dactylorhiza fuchsii	23	7	55	8	18	28	21	8	5	.

Poa humilis	21	10	52	2	3	11	15	2	16	.
Neottia ovata	2	2	30	8	10	5	1	.	.	.
Jacobaea vulgaris	3	17	27	14	15	3	4	2	.	3
Silene flos-cuculi	38	11	21	60	53	76	56	67	66	3
Scorzoneroides autumnalis	38	38	15	60	69	30	8	33	4	3
Lathyrus pratensis	5	6	3	26	26	34	16	5	4	.
Plantago maritima	.	1	.	12	82	4	.	6	.	.
Succisa pratensis	.	.	3	18	69	52	9	24	61	.
Molinia caerulea	.	1	.	.	42	29	4	14	14	.
Lysimachia tenella	.	2	3	8	35	10	.	23	.	.
Lotus corniculatus	.	8	18	52	84	24	2	6	4	.
Juncus balticus	.	1	.	2	37	5	.	3	.	.
Ophioglossum vulgare	.	3	9	10	26	3	2	.	2	.
Dactylorhiza incarnata	5	4	24	10	21	5	3	2	.	.
Equisetum arvense	12	17	24	26	31	6	6	4	4	6
Carex arenaria	.	3	24	24	13	4	1	.	.	3
Linum catharticum	.	3	24	14	18	2	.	.	.	.
Pinguicula vulgaris	.	.	.	.	21	1	.	13	.	.
Plagiomnium undulatum	11	1	21	10	6	21	14	12	2	.
<u>*Species preferential to CaCn*</u>										
Caltha palustris	70	9	9	40	29	47	72	69	45	44
Calliergonella cuspidata	41	7	27	36	26	58	56	65	18	25
Cardamine pratensis	50	18	24	34	37	37	51	51	43	50
Epilobium palustre	20	2	24	18	8	33	63	57	54	41
Angelica sylvestris	6	2	9	14	6	27	47	4	36	6
Filipendula ulmaria	2	1	3	14	15	10	31	10	.	3
Phragmites australis	5	1	.	4	.	5	21	4	2	13
Juncus effusus	17	8	.	12	.	12	29	19	20	13
Ranunculus flammula	2	.	.	18	39	15	23	62	27	31
Hydrocotyle vulgaris	.	2	9	14	52	44	19	58	2	.
Carex panicea	6	8	3	14	39	25	9	41	18	6
Pedicularis palustre	.	.	.	2	6	12	2	36	.	.
Mentha aquatica	.	.	.	.	.	16	15	23	.	6
Sagina nodosa	.	2	.	2	3	5	1	17	.	.
Oenanthe lachenalii	.	.	.	2	11	14	3	17	.	.
Triglochin palustre	9	1	.	8	6	4	6	19	2	3
<u>*Species preferential to CnPe*</u>										
Rhytidiadelphus squarrosus	17	10	45	2	6	25	26	13	75	.
Potentilla erecta	.	2	.	4	15	24	2	3	63	.
Equisetum palustre	18	3	36	6	11	41	29	40	55	.
Comarum palustre	.	.	.	2	.	9	14	26	36	3
Eriophorum angustifolium	.	.	6	8	10	26	8	51	55	.
Equisetum fluviatile	67	2	24	14	3	43	44	21	57	56
Carex echinata	.	.	.	6	6	16	4	21	43	.
Viola palustris	.	1	.	2	2	1	1	.	32	.
Luzula multiflora	3	1	3	14	16	13	9	7	27	.
Agrostis canina	.	7	.	6	.	7	4	2	32	.

Species preferential to MG14c										
Persicaria amphibia	56	13	12	6	.	7	23	6	.	75
Galium palustre	5	.	.	4	6	12	40	40	20	66
Poa trivialis	35	32	30	30	6	31	34	24	2	41
Jacobaea aquatica	8	.	18	14	15	33	48	35	11	53
Myosotis laxa	38	3	.	6	2	2	14	15	.	47
Glyceria fluitans	2	1	.	.	.	.	.	.	.	13
Alopecurus geniculatus	14	3	.	2	.	.	3	2	.	47
Calliergon cordifolia	5	.	.	.	.	1	9	6	5	44
Eleocharis palustris	3	1	9	14	11	13	19	19	11	28
Stellaria alsine	2	.	.	2	.	2	5	2	2	16

Compared to the two *Caltha-Carex nigra* subcommunities, the two units of the *Agrostis-Bellis* grassland have lower frequencies of *Carex nigra* and *Caltha palustris,* but retain occasional *Juncus articulatus* and are distinct in their higher frequencies of species characteristic of generally drier soil profiles, notably *Cynosurus cristatus, Bellis perennis, Cerastium fontanum, Festuca rubra, Euphrasia* spp, *Trifolium pratense, Rumex acetosa, Lolium perenne*.

Compared to the *Agrostis stolonifera-Carex flacca* community, they share the constant species *Holcus lanatus, Agrostis stolonifera, Trifolium repens, Ranunculus acris, Anthoxanthum odoratum* and *Cynosurus cristatus* with frequent *Potentilla anserina*. They are however distinguished from that unit by lower frequencies of *Carex flacca, Festuca rubra, Plantago lanceolata, Luzula campestris, Silene flos-cuculi* and higher frequencies of *Rumex acetosa, Ranunculus repens, Rhinanthus minor, Lolium perenne and Cerastium fontanum*. The high frequency of *Bellis perennis* is a feature of both the *Agrostis-Bellis* grassland and some of the subunits of *Agrostis-Carex flacca*.

Although it has a high frequency of *Cynosurus cristatus*, the *Agrostis stolonifera-Bellis perennis* grassland is distinct from the *Cynosurus cristatus-Centaurea nigra* grassland community (MG5) of the NVC due to the very low frequency of *Centaurea nigra* and *Dactylis glomerata*. A comparison of the new community with the MG5 community of the NVC is displayed in Table A1 of the appendix.

Species preferential to the *Ranunculus repens* subcommunity (AgBpa) include *Ranunculus repens, Rhinanthus minor, Caltha palustris, Euphrasia* spp., *Juncus articulatus, Carex nigra, Anthoxanthum odoratum, Cardamine pratensis, Polygonum amphibium, Calliergonella cuspidata, Myosotis laxa, Juncus bulbosus, Sagina procumbens, Trifolium dubium, Kindbergia praelonga, Brachythecium rutabulum* indicating a flora tolerant of damper soil conditions.

Species preferential to the *Lolium perenne* subcommunity (AgBpb) include, in addition to *Lolium perenne, Cerastium fontanum, Poa pratensis, Odontites vernus* and *Heracleum sphondylium*. Species generally associated with more fertile soils.

Both subunits of *Agrostis stolonifera-Bellis perennis* grassland have high fertility compared to all but the MG14c unit, as indicated by Ellenberg N scores, whilst they differ from each other primarily in their moisture tolerance; the *Ranunculus repens* unit supporting vegetation tolerant of damper soil conditions, as indicated by mean Ellenberg F scores whilst the *Lolium perenne* subcommunity (AgBpb) supports the driest vegetation of the Oceanic wet grassland associations described here. The two units however differ in both their soil moisture tolerance and soil fertility and although sharing many species in common show a shift towards the SD8 *Festuca rubra-Galium verum* dune grassland community that many of the stands grade into on the dry machair.

Both subcommunities of the *Agrostis-Bellis* grassland appear to be widely distributed across Scotland. At a local level on the Uists, where more detailed distribution patterns are available, the *Agrostis-Bellis* vegetation appears in close proximity to the cultivated machair - and may, in places, have been subject to past cultivation. At North Boisdale it grades into sand dune vegetation of the SD8 community.

Agrostis stolonifera-Carex flacca grassland *(AgCf)*
Occupying the central area of the TWINSPAN this community retains constant *Agrostis stolonifera, Carex nigra, Holcus lanatus, Trifolium repens, Ranunculus acris, Cynosurus cristatus* and frequent *Anthoxanthum odoratum, Potentilla anserina* and *Juncus articulatus.* The community preferential species are *Carex flacca* to *Plagiomnium undulatum* in Table 2. In the TWINSPAN analysis four discrete groupings were apparent in which *Carex flacca, Festuca rubra, Plantago lanceolata* and *Prunella vulgaris* were all constant with frequent *Trifolium pratense, Luzula campestris* and *Vicia cracca* distinguishing this from both the AgBp and CaCn grasslands.

In addition, the units shared, with the *Agrostis-Bellis* grassland, constant *Holcus lanatus, Agrostis stolonifera, Trifolium repens, Ranunculus acris, Anthoxanthum odoratum, Carex nigra* and *Cynosurus cristatus*.

The groups are not adjacent to each other in the two-way table and thus suggest different origins and site conditions. Three of the subcommunities appear close to the *Agrostis-Bellis* grassland whilst the fourth may have closer links to the *Caltha-Carex nigra* grassland.

The four units are significantly different in terms of soil moisture tolerance and soil fertility.
(a) *Potentilla anserina-Bellis* subcommunity
Higher fertility and base status than (c) and (d). Distinguished from the other subunits by constant *P. anserina* and *B. perennis* and frequent *Dactylorhiza fuchsii, Poa humilis, Rhytidiadelphus squarrosus* but low frequencies of *Carex nigra, Silene flos-cuculi, Anthoxanthum odoratum, Lotus corniculatus, Caltha palustris* and *Lathyrus pratensis*.
(b) Typical subcommunity
Shares, with the *Plantago maritima* and *Succisa* subunits, constant *Carex nigra, Silene flos-cuculi, Anthoxanthum odoratum* and frequent *Lotus corniculatus, Caltha palustris* but is distinguished from them by higher frequency of *Prunella vulgaris, Juncus articulatus, Lolium perenne, Scorzoneroides autumnalis, Poa pratensis, Ranunculus repens*.
(c) *Plantago maritima* subcommunity
In the *Plantago maritima* subcommunity a number of species more characteristic of damp dune slack vegetation are frequent including *Molinia caerulea, Plantago maritima, Hydrocotyle vulgaris, Ranunculus flammula, Lysimachia tenella, Pinguicula vulgaris*. This subcommunity is the stronghold of *Juncus balticus* in these grasslands.
(d) *Succisa pratensis* subcommunity
Distinguished from the *Plantago maritima* subcommunity by higher frequencies of *Calliergonella cuspidata, Equisetum fluviatile, Jacobaea aquatica, Angelica sylvestris, Eriophorum angustifolium* and *Potentilla erecta*.

Caltha palustris-Carex nigra grassland *(CaCn)*
The preferential species for this community are the block from *Caltha palustris* to *Triglochin palustris* (Table 2). This grassland is characterised by constant *Carex nigra* and *Caltha palustris* with frequent *Epilobium palustre*. The two subunits are distinguished from each other by the higher frequency of tall fen meadow herbs in the *Potentilla anserina*

unit, including *Equisetum fluviatile, Angelica sylvestris, Filipendula ulmaria* and *Juncus effusus* whilst the *Hydrocotyle vulgaris-Ranunculus flammula* subunit is characterised by low growing, poor fen species, with constant *Calliergonella cuspidata, Silene flos-cuculi, Hydrocotyle vulgaris, Juncus articulatus* and *Ranunculus flammula*. These two units retain some affinities with the dune slack SD17c sub community with occasional records for *Triglochin maritima, Sagina nodosa* and *Oenanthe lachenalii*. In earlier surveys of Dargie many of these quadrats were classified as MG8 or various forms of Mx and Mxt.

This grassland has higher soil moisture tolerance than the *Agrostis-Bellis* or *Agrostis-Carex flacca* communities, and lower soil fertility than the *Agrostis-Bellis* community. *Cynosurus cristatus* is notable for its low frequency compared to the *Agrostis-Bellis* or *Agrostis-Carex flacca* grasslands, whist *Caltha* and *Calliergon* are characteristic species together with *Epilobium palustre*. The two subcommunities seem to represent different soil fertility status, the *Hydrocotyle vulgaris-Ranunculus flammula* having significantly lower Ellenberg N scores than the *Potentilla anserina* subcommunity.

(a) *Potentilla anserina* subcommunity

This grassland has constant *Potentilla anserina* and *Rumex acetosa*. The higher fertility is indicated by the presence of tall herbs species including *Angelica sylvestris* and *Filipendula ulmaria* and also *Juncus effusus* and *Phragmites australis* (species generally scarce in the other grasslands and no more than occasional in the CnPe and MG14 communities) tending to give a rather rank appearance.

(b) *Hydrocotyle vulgaris-Ranunculus flammula* subcommunity.

In contrast to the *Potentilla anserina* subcommunity the *Hydrocotyle vulgaris-Ranunculus flammula* subcommunity tends to be low growing and dominated by *Hydrocotyle* and *Juncus articulatus* with frequent small sedges, notably *Carex nigra, Carex panicea* and *Carex flacca* with occasional *Carex echinata*. Links to dune slack, and base-rich mire associations are evident in the presence of *Pedicularis palustris, Lysimachia tenella, Triglochin maritima,* whilst the wetness of some stands is evidenced by the occasional records of *Comarum palustre* and *Eriophorum angustifolium*.

Carex nigra-Potentilla erecta-Rhytidiadelphus squarrosus grassland *(CnPe)*

This community is largely restricted to the Aith meadows on the Shetlands, but with some records from the Uists, notably at Kilpheder.

Stands have the lowest fertility and lowest base status of all the grasslands described. Their moisture status is high and similar to the *Caltha-Carex* nigra grasslands.

Distinct from the other grasslands in having low frequency of *Potentilla anserina* and from all but the MG14 grassland in the low frequency of *Cynosurus cristatus, Trifolium repens* and *Ranunculus acris*. No subunits are recognised.

The characteristic species (Table 2 *Rhytidiadelphus squarrosus* to *Agrostis canina*); in addition to *Holcus lanatus, Anthoxanthum odoratum* and *Carex nigra* include *Rhytidiadelphus squarrosus, Potentilla erecta, Equisetum palustre, Eriophorum angustifolium, Equisetum fluviatile*.

Potentilla anserina subcommunity of the *Carex nigra-Agrostis stolonifera- Senecio aquaticus* grassland *(MG14c)*

This is species-poor vegetation, averaging only 14 species m^{-2}. Although *Agrostis stolonifera* and *Potentilla anserina* remain constant, most of the species characteristic of the *Caltha-Carex nigra, Agrostis-Carex flacca* and *Agrostis-Bellis* grasslands are scarce; most notably *Holcus lanatus, Trifolium repens, Ranunculus acris, Anthoxanthum odoratum, Cynosurus cristatus,* whilst *Juncus articulatus* is only occasional.

The vegetation is characterised by constant *Agrostis stolonifera, Potentilla anserina, Persicaria amphibia* and *Galium palustre* with frequent *Equisetum fluviatile, Jacobaea* *aquatica, Carex nigra, Cardamine pratensis, Myosotis laxa, Alopecurus geniculatus, Calliergon cordifolia, Caltha palustris, Poa trivialis* and *Epilobium palustre*.

The Ellenberg score for soil moisture is the highest of all the ten grassland units described, whilst the fertility score is also high and similar to those for the *Agrostis-Bellis* community.

Tending to occupy hollows and less freely drained area, the majority of records are from the Uists.

Community – Environmental relationships

Measured soil parameters

There was a significant relationship between plant community and all three of the soil environmental variables measured (soil pH, available phosphorus, and soil organic matter) (Table 3). There was no significant site effect on the soil pH or soil organic matter. However, there was a significant site effect on the availability of phosphorus (Table 3).

Table 3. The relationship between plant communities and measured soil parameters: *p* indicates the significance of differences between plant communities, values in bold are statistically significant ($p < 0.05$)

	Plant community				site		
Environmental variable	df	F	*p*-value		df	F	*p*-value
Soil pH	2	62.807	**< 0.001**		19	1.184	0.34
Available phosphorus (mg l^{-1})	2	7.121	**0.0033**		19	4.196	**< 0.001**
Soil organic matter LOI (%)	2	16.045	**< 0.001**		19	1.643	0.12

The data are presented as Box and whisker plots (Fig. 2) at a community level for the three principal oceanic wet grassland communities; AgBp, AgCf and CaCn. Soil pH (Fig. 2a), 2Available phosphorus (mg l^{-1}) (Fig. 2b) and 2Soil organic matter (Loss-on-ignition -%) (Fig. 2c).

The highest soil pH (mean > 7.7) and lowest soil organic matter (mean < 12.5%) was found in the *Agrostis stolonifera-Bellis perennis* (AgBp) and *Agrostis stolonifera-Carex flacca* (AgCf) grasslands.

There was no significant difference in pH and soil organic matter between the AgBp and AgCf plant communities. The *Caltha palustris-Carex nigra* grassland (CaCn), however, was significantly different to both the AgBp and AgCf grasslands in respect of both soil pH and soil organic matter. The soil pH of the *Caltha palustris-Carex nigra* grassland (CaCn) (mean = 5.9) was significantly lower than the other two grassland types, while the soil organic matter was significantly higher (mean = 39.0%).

Available soil phosphorus across the 50 quadrats was low and ranged from 2.1-16.5 mg l^{-1}. The *Agrostis stolonifera-Carex flacca* (AgCf) and *Caltha palustris-Carex nigra* grasslands (CaCn) had the lowest available phosphorus (mean < 8.6 mg l^{-1}). Tukey's HSD showed there was no significant difference between these two communities in available phosphorus. The *Agrostis stolonifera-Bellis perennis* (AgBp) had significantly higher levels of phosphorus (Fig. 2b).

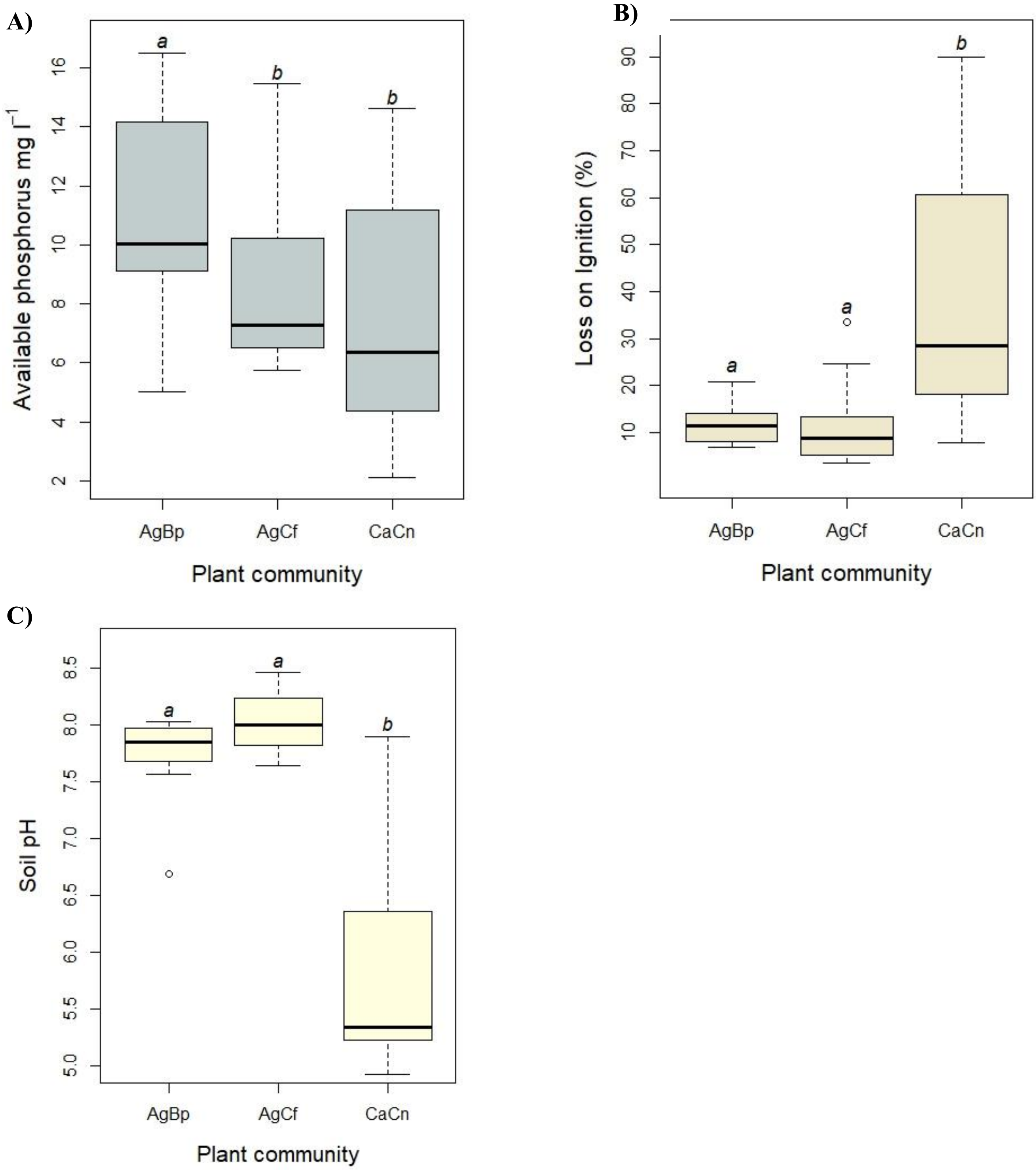


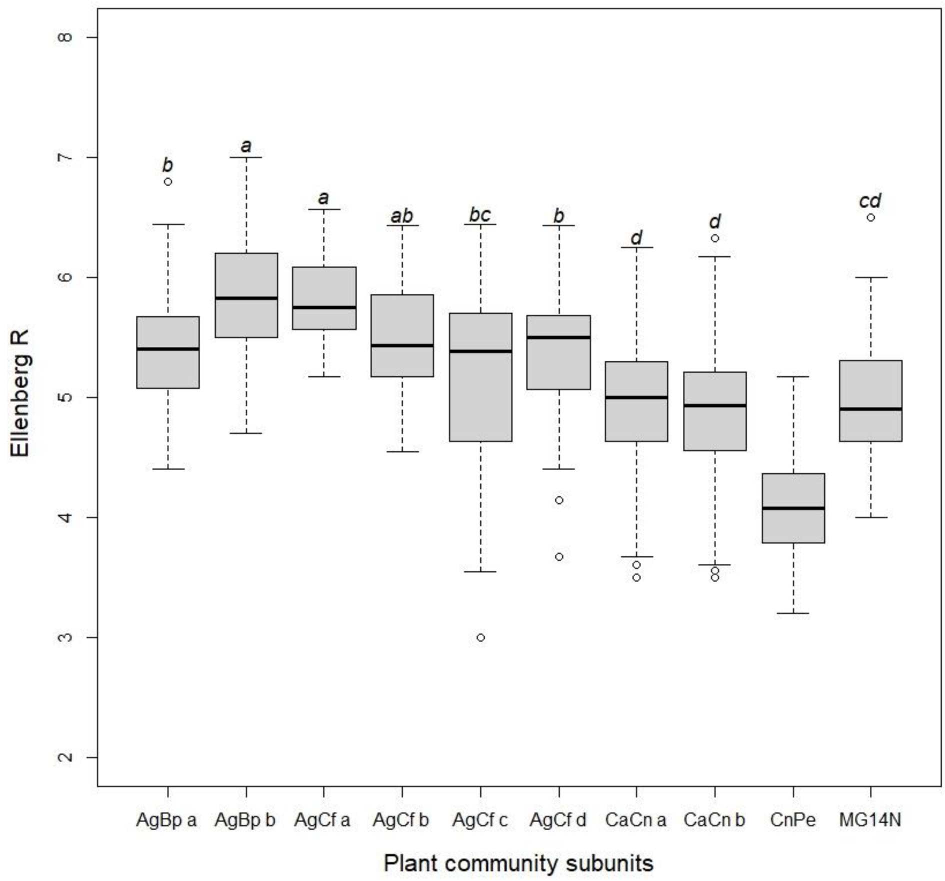
Figure 2. Box and whisker plots for measured soil parameters for the three principal communities; *Agrostis stolonifera-Bellis perennis* (AgBp) (n = 12), *Agrostis stolonifera-Carex flacca* (AgCf) (n = 18) and *Caltha palustris-Carex nigra* grassland (CaCn) (n = 20). a) available phosphorus, b) soil organic matter and c) soil pH. Significance was assessed using Tukey Honestly Significant Difference and pairwise comparisons. Means denoted by the same superscript letter are not significantly different

Ellenberg scores
Ellenberg scores for each of the ten units are plotted as box and whisker diagrams (Fig. 3). Differences between units were tested using Kruskal Wallis analysis (Table 4). Post-hoc tests were carried out using the Dunn test and the *p*-values were adjusted for multiple comparisons using the Holm adjustment (Dunn, 1964).

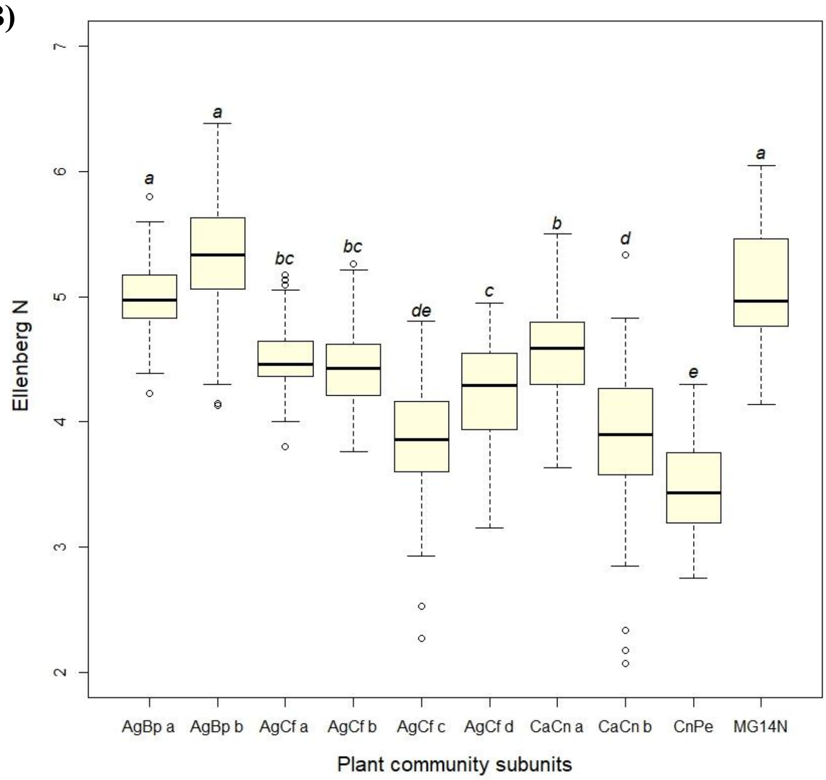
Table 4. Results of Kruskal Wallis analysis for differences in Ellenberg scores (for R, N and F) between vegetation units

Ellenberg value	**Chi-squared**	**df**	**Probability**
Reaction (R)	310.86	9	< 0.001
Fertility (N)	554.23	9	< 0.001
Soil moisture (F)	509.95	9	< 0.001

A)



B)



C)

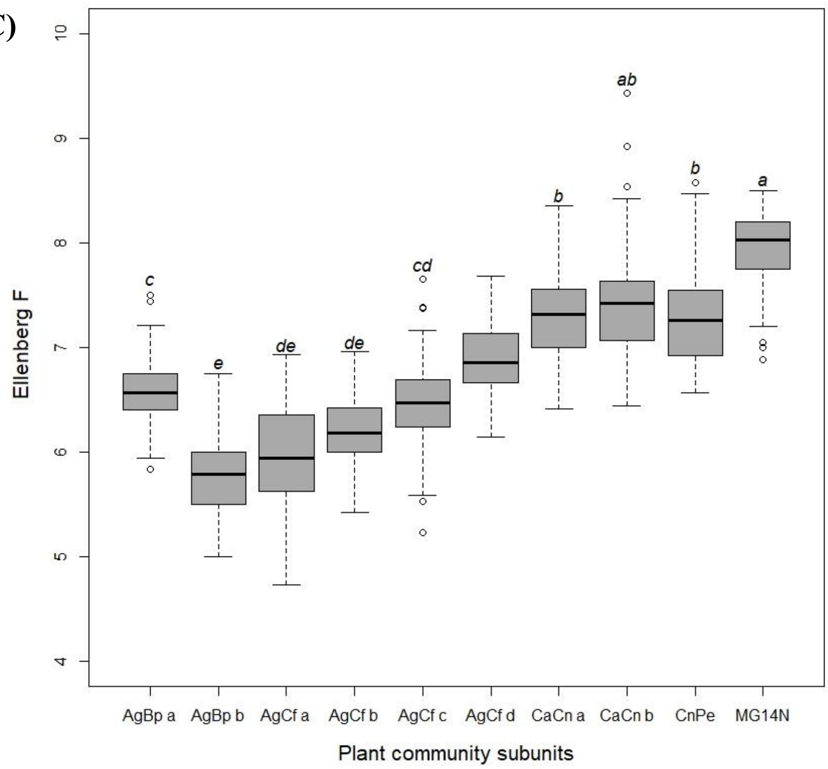


Figure 3. Box and whisker plots show variation in Ellenberg scores from 775 samples taken across ten vegetation units. a) soil reaction, b) soil fertility and c) soil moisture. The box represents the central 50% of samples (the ends the 1st and 3rd quartiles and the horizontal line the median value), the * outwith the boxes indicate outliers. Lower case letters indicate the significance of differences in the median between units using Dunn's multiple comparison test; bars with the same letter are not significantly different from each other.

Ellenberg F
Ellenberg F, an indicator of the vegetation's tolerance to soil moisture – the higher the value the more tolerant the vegetation is to high soil moisture, the lower the value the more tolerant the vegetation is to soil droughting. The vegetation most tolerant of high soil moisture is the new subcommunity of MG14, which has a significantly higher F value than all but the CaCn b unit; the CnPe and CaCn a are also tolerant to moderately high soil moisture whilst the AgBpb grassland is the least tolerant of moist soils.

The four units of AgCf are significantly different to each other in terms of soil moisture tolerance and soil fertility. The *Succisa pratensis* subcommunity (d) has the highest soil moisture tolerance, followed by the *Plantago maritima* subcommunity (c) whilst the Typical (b) and *Potentilla anserina-Bellis* (a) subcommunities are significantly drier. In contrast the *Plantago maritima* subcommunity has significantly lower Ellenberg N scores than the other units of *Agrostis-Carex flacca*.

Ellenberg N
Ellenberg N provides a surrogate for the soil's fertility, high values indicate a vegetation tolerant of moderately fertile soils, whilst a low value indicates vegetation of soils of generally low fertility.

Again, the new MG14 unit has the highest value, together with both AgBp subcommunities, possibly indicating their past cultivation history. The lowest fertility soils seem to be associated with the CnPe, CaCn b and AgCf c communities.

Ellenberg R
A surrogate for soil base status, but not directly related to soil pH. The lowest values are for the CnPe community and the highest for the AgBpb unit, and subcommunities a and b of the AgCf grassland, vegetation associated with a closer proximity to the adjacent sand dune communities.

An NDMS analysis of the 775 quadrats shows the segregation of quadrats allocated to different communities and the relative strength of the environmental variables (Fig. 4).

Soil moisture and soil fertility show the strongest relationship with Axis 1 (Table 5), with opposite relationships; soil moisture is positively correlated (i.e. moisture increases with increasing axis score) whilst soil fertility is negatively correlated (decreasing with increasing axis 1 score).

Soil reaction opposes the moisture gradient, decreasing on Axis 1. Soil fertility and soil moisture are both positively related to Axis 2.

- The MG14c subcommunity (blue dots) occupies the more fertile soils of high moisture, i.e. high axis 2 scores.
- The CnPe grassland (green dots) occupies less fertile but slightly wetter substrates, i.e. lower axis 2 scores and slightly higher axis 1 scores.
- The two subcommunities of *Caltha-Carex nigra* (CaCn) (purple dots) occupy the wettest and least fertile sector of the plot, with high Axis 1 and low axis 2 scores,
- *Agrostis-Carex flacca* community (dark green) appears to be in the middle of the hydrological gradient with lower fertility than the *Caltha-Carex* grassland. There is considerable overlap between AgCf and CnPe.
- The two subcommnities of *Agrostis-Bellis* (AgBp) (yellow dots) are at the driest and most fertile end of the gradients, i.e. low axis 1 scores.

The bivariate ellipses in Figure 4 further support the distinctiveness of some of the units.

The ellipses for AgBp, AgCf and CnPe follow the fertility gradient with AgBp at the more fertile end (high Axis 2 and low Axis 1 scores) whilst CnPe has the lowest Axis 2 and highest Axis 1 scores. Conversely on the hydrological gradient MG14c occupies the highest axis 2 sector of the plot, with CaCn in the centre and AgCf in the lower sector.

Axis 1 appears weakly negatively associated with soil reaction. The more basic groups being the AgCf and *Agrostis-Bellis* grasslands whilst the most acidic units are the CnPe and the *Caltha-Carex nigra* (CaCn) communities.

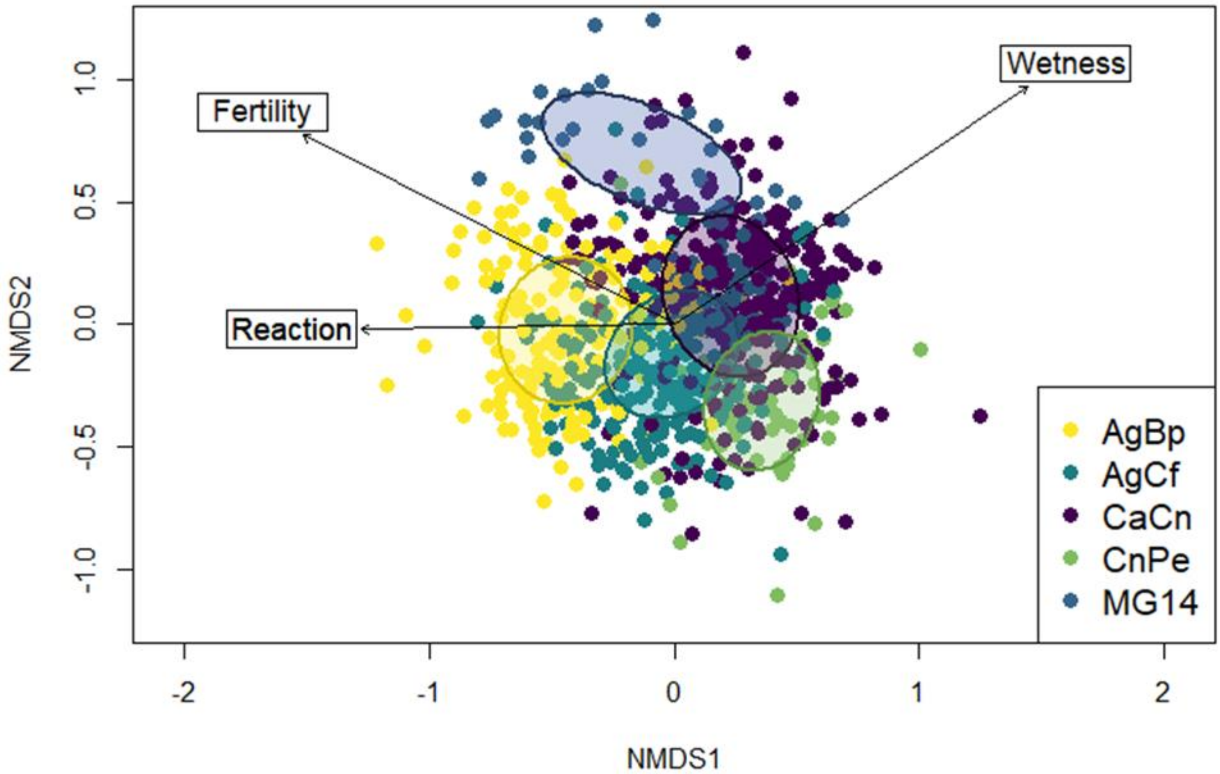


Figure 4. The first two axes of NMDS with 775 quadrats (divided into the five communities) plotted. The ellipses show the standard deviation around the centroid and the Ellenberg variables are plotted as vectors; F – wetness / soil moisture, N – fertility, R - reaction.

Table 5. Correlation between NMDS axes and Ellenberg scores for reaction (R), fertility (N) and soil moisture (F).

Ellenberg	**NMDS axis 1**	**NMDS axis 2**	**r^2**	**Probability**
Reaction (R)	-0.99988	-0.01538	0.2876	0.001 ***
Fertility (N)	-0.89135	0.45331	0.5098	0.001 ***
Soil moisture (F)	0.82969	0.55823	0.5328	0.001 ***

Comparison of the Scottish grasslands with the Calthion of England and Wales

Data were combined for the communities considered to represent the Calthion from England, Wales, and the newly defined oceanic wet grasslands from Scotland.

From England and Wales: a total of 2051 quadrats from the 2017 Calthion Review (Wallace & Prosser, 2017).

- *Carex nigra-Potentilla anserina-Sececio aquaticus* grassland; MG14a, MG14b,
- the four subcommunities of *Cynosurus cristatus-Carex panicea-Caltha palustris* grassland, MG8a, b, c, d.

From Scotland: a total of 602 quadrats from the Review of Oceanic wet grasslands (Wallace *et al.,* 2020) including the new *Potentilla anserina* subcommunity of MG14 *Carex nigra-Potentilla erecta-Rhytidiadelphus squarrosus* grassland and CnPe (retained as it might maintain a link to the less calcareous, inland sites)

- two subcommunities of the *Caltha-Carex nigra* community
- four subcommunities of *Agrostis stolonifera-Carex flacca* community
- two subcommunities of *Agrostis stolonifera-Bellis perennis* community

The full data set of 2653 quadrats were subject to TWINSPAN analysis (using Juice software).

The TWINSPAN was run with 20 endgroups, although this resulted in some large groups, a second run with 25 endgroups only resulted in splitting of those already clearly defined groups and provided no further clarification. All results presented are thus based on the 20-end group analysis.

All quadrats were coded according to their vegetation community allocation from the 2017 and 2020 reports. The Hierarchical tree and distribution of community types across the endgroups gave confidence in the robustness of previous analyses and community allocations. Data were presented at a workshop of phytosociologists, and it was generally agreed that the Scottish types were distinct from their England and Wales counterparts.

The analysis confirmed the integrity of the original classifications with many of the communities occurring almost exclusively within a single, or adjacent, endgroups, with very little mixing of quadrats from different communities.

For example, 89% of samples that were previously assigned to MG8b (Wallace & Prosser, 2017) occurred in a single endgroup whilst 83% of samples previously assigned to MG8d occurred in a different endgroup. Conversely, 78% of the AgCf quadrats from the Scottish analysis occurred in a single endgroup.

There was also very little mixing of the English and Scottish quadrats within endgroups. This separation is displayed as an ordination plot in Figure A1 of the appendix, in which all the new communities appear to be distinct from the existing mesotrophic grasslands of the NVC.

In all but two endgroups, 90% of quadrats were from either the Scotland survey or from England and Wales survey (Table 6).

Comparison with the revision of the Calthion Alliance (Wallace & Prosser, 2017) suggests that the AgBp units come closest to the northern *Caltha-Bellis* subcommunity of *Cynosurus cristatus-Carex panicea-Caltha palustris* grassland (MG8d). The main discrepancy between the two Scottish noda and the MG8d is the generally lower frequency of *Caltha palustris, Anthoxanthum odoratum, Trifolium pratense, Cardamine pratensis, Poa trivialis* and *Agrostis capillaris* in the Scottish samples, whilst the Scottish vegetation is characterised by high frequency of *Potentilla anserina*.

The CaCn units retain some affinities with the dune slack SD17c subcommunity with occasional records for *Triglochin maritima, Sagina nodosa* and *Oenanthe lachenalii.* In earlier surveys many of these quadrats were classified by Dargie (1988), as MG8 or various forms of Mx and Mxt.

Table 6. Allocation of each vegetation community across the 20 endgroups from the combined England, Wales and Scottish Twinspan analysis. Values are % of each vegetation community in each end group. Total is the number of quadrats in each row/column._ For example: 51% of MG8a quadrats occurred in Endgroup 1, with a further 47% being in Endgroup 2. 89% of quadrats allocated to MG8d occurred in endgroup 8, the remainder of quadrats in that end group were allocated to forms of the Agrostis-Bellis Scottish vegetation. Reading down the columns there are few endgroups that have a mix of Scottish quadrats with those from the England & Wales data set.

ENDGROUP	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Total
Vegetation community																					
England and Wales Data																					
MG14a	.	.	.	.	.	0	.	.	1	0	.	.	.	1	0	47	24	3	13	10	245
MG14b	1	.	.	.	.	1	.	1	3	.	.	.	.	.	.	1	53	1	3	34	316
MG8a	51	47	1	.	.	0	.	0	.	.	.	.	.	.	.	.	.	0	0	1	398
MG8b	4	7	1	1	0	41	1	1	0	5	.	.	0	.	.	0	1	8	11	18	590
MG8c	16	.	0	2	.	2	.	.	51	.	.	.	1	0	.	1	5	1	.	20	352
MG8d	1	2	2	.	.	1	2	89	.	.	.	.	.	.	.	.	.	.	1	2	150
Scottish data																					
MG14c	.	.	.	.	.	.	.	.	.	4	29	.	7	.	39	.	7	.	14	.	28
CnPe	.	2	67	.	.	.	.	.	.	.	.	29	2	.	.	.	.	.	.	.	42
CaCn a	.	.	7	9	2	7	1	.	.	5	29	7	15	.	.	.	3	1	4	9	94
CaCn b	.	.	2	25	3	.	.	.	2	3	4	1	56	.	.	.	.	.	.	5	133
AgCf	1	1	11	19	57	1	2	1	.	.	2	.	3	.	.	.	.	.	1	2	183
AgBp a	.	.	1	.	15	5	55	11	.	.	4	.	3	.	1	.	1	.	1	3	80
AgBp b	.	.	2	.	24	2	62	10	.	.	.	.	.	.	.	.	.	.	.	.	42
Total	290	235	75	86	134	272	80	161	198	40	46	20	105	3	13	121	253	64	121	336	2653

The AgCf vegetation has greatest similarity with the Typical subcommunity of MG8.

Comparison of floristic tables for the English and Welsh communities (Wallace & Prosser, 2017) with the Scottish units highlighted several species that are common in the English and Welsh Calthion communities that were either absent or present at very low frequencies in the Scottish data, and vice versa (Table 7).

Some of these discrepancies may reflect differences in the northern distribution limits of species.

Table 7. Species less or more frequent in the floristic tables for the Scottish communities compared to the Calthion in England and Wales

Species absent or less frequent in the Scottish data	Species more frequent in the Scottish vegetation
Centaurea nigra	*Potentilla anserina*
Filipendula ulmaria	*Eriophorum angustifolium*
Sanguisorba officinalis	*Epilobium palustre*
Schedonorus pratensis	*Equisetum fluviatile*
Lysimachia nummularia	*Sagina procumbens*
Carex acuta	*Comarum palustre*
C. acutiformis	*Silene flos-cuculi*
C. disticha	*Carex flacca*
C. panicea	*Vicia cracca*
Alopecurus pratensis	*Euphrasia* agg.
Leontodon hispidus	*Poa pratensis*
Juncus acutiflorus	*Potentilla erecta*
J. effusus	
J. inflexus	
Lotus uliginosus	
Geum rivale	
Cirsium dissectum	

Comparison of the Scottish grasslands with the Irish vegetation classification
Seventeen Irish communities were highlighted as having affinities with the Scottish communities. Of the 775 Scottish quadrats, 57% were classed by ERICA as transitional and 43% were classed as assigned (with a maximum membership score > 50%).

Table 8. Percentage of quadrats in each Scottish community that were 'assigned' to an Irish community in the IVC

Scottish community	Assigned	Transitional
AgBpa	15.2	84.8
AgBpb	52.9	47.1
AgCfa	42.4	57.6
AgCfb	62.0	38.0
AgCfc	47.2	52.8
AgCfd	28.9	71.1
CaCna	40.0	60.0
CaCnb	49.2	50.8
CnPe	33.9	66.1
MG14c	71.9	28.1
Total Result	43.1	56.9

The highest proportion of transitional quadrats were in the *Ranunculus repens* subcommunity of *Agrostis-Bellis* AgBp a =84.8%), the *Succisa* subcommunity of AgCf (AgCf d=71.1%) and the CnPe (66.1%) vegetation units (Table 8). These values indicate that although the vegetation may fall within the scope of the IVC they do not clearly match a single IVC community.

The best 'fitting' Irish communities for each Scottish community are given in Table 9a, and for each Scottish subcommunity in Table 9b.

Values in the final column of Tables 9a & b indicate the percentage of the quadrats that were assigned to each of the listed IVC communities from the Scottish community or sub community. The most frequently assigned IVC communities were GL1B (*Agrostis stolonifera-Filipendula ulmaria* marsh grassland) and DU3D (*Festuca rubra-Bellis perennis* grassland) (See Table 9b).

Table 9a. Allocation of Scottish communities to the communities of the IVC. This table is restricted to those quadrats that were 'assigned' in ERICA, i.e. had a membership score of=> 0.5. The IVS communities listed in this table are restricted to those where >25% of Scottish quadrats for that community were assigned to IVC community

Scottish community	IVC code	IVC name	Percentage of quadrats assigned to this community
AgBp	GL2	*Juncus effusus-Holcus lanatus*	45.3
	GL3	*Cynosurus cristatus-Plantago lanceolata*	42.2
AgCf	DU3	*Agrostis stolonifera-Carex arenaria*	49.5
	GL1	*Juncus articulatus-Molina caerulea*	23.4
CaCn	FE3	*Agrostis stolonifera-Carex arenaria*	58.1
	GL1	*Juncus articulatus-Molina caerulea*	27.4
CnPe	GL4	*Nardus stricta-Galium saxatile*	94.7
MG14c	FE3	*Agrostis stolonifera-Carex nigra*	47.8

Table 9b. Best fitting Irish communities for the Scottish subcommunities.

Scottish community	IVC Code	IVC name	Percentage of quadrats assigned to this community
AgBpa	GL2A	*Agrostis stolonifera-Ranunculus repens* marsh-grassland	30.0
	GL2C	*Holcus lanatus-Lolium perenne* grassland	30.0
AgBpb	GL2C	*Holcus lanatus-Lolium perenne* grassland	31.5
	GL3B	*Lolium perenne-Trifolium repens* grassland	25.9
AgCfa	DU3D	*Festuca rubra-Bellis perennis* grassland	64.3
AgCfb	DU3D	*Festuca rubra-Bellis perennis* grassland	67.7

AgCfc	DU3D	*Festuca rubra-Bellis perennis* grassland	45.2
	GL1C	*Molinia caerulea -Succisa pratensis*	28.6
AgCfd	GL1B	*Agrostis stolonifera-Filipendula ulmaria* marsh grassland	33.3
	FE3D	*Carex nigra-Calliergonella cuspidata* fen	25.0
CaCna	GL1B	*Agrostis stolonifera-Filipendula ulmaria* marsh grassland	33.9
	FE3B	*Carex nigra-Potentilla anserina* fen	26.8
CaCnb	FE3A	*Carex nigra-Ranunculus flammula* fen	32.8
	FE3D	*Carex nigra-Calliergonella cuspidata* fen	34.2
CnPe	GL4D	*Agrostis canina/vinealis-Rhytidiadelphus squarrosus* grassland	89.5
MG14c	FE3B	*Carex nigra-Potentilla anserina* fen	39.1

NMDS ordination was conducted using the vegan package in R. The data set comprised 5369 quadrats including all the 775 Scottish quadrats and Irish data from the IVC for the 17 communities highlighted. Mean abundance-weighted Ellenberg values were fitted as Environmental vectors (Fig. 5). At the Scottish community level fertility (N) and reaction (R) were strongly and positively correlated with Axis 2, soil moisture (F) and salinity (S) were strongly and positively correlated with axis 1 (Table 10).

Table 10. Correlation coefficients between NMDS-axis scores and Ellenberg-indicator scores.

Ellenberg	NMDS Axis 1	NMDS Axis 2	r^2	Probability
Light (L)	0.98419	-0.017710	0.0446	0.001 ***
Soil moisture (F)	0.81119	-0.58478	0.7635	0.001 ***
Reaction (R)	0.36979	0.92912	0.5267	0.001 ***
Fertility (N)	0.04430	0.99902	0.7939	0.001 ***
Salinity (S)	0.82928	0.55883	0.3832	0.001 ***

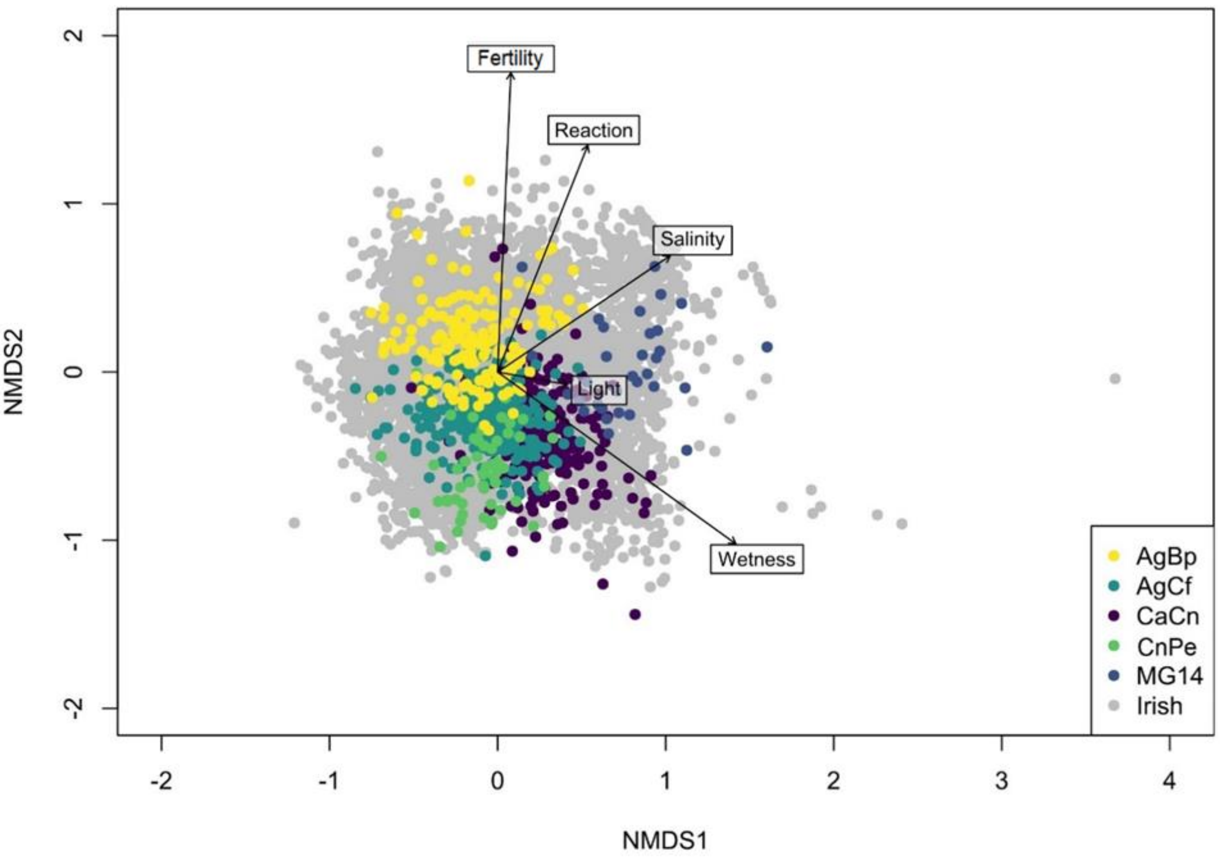


Figure 5. Plot of NMDS scores for axis 1 and 2. All Irish quadrats are represented by grey dots; the 5 Scottish communities are distinguished by different coloured dots.

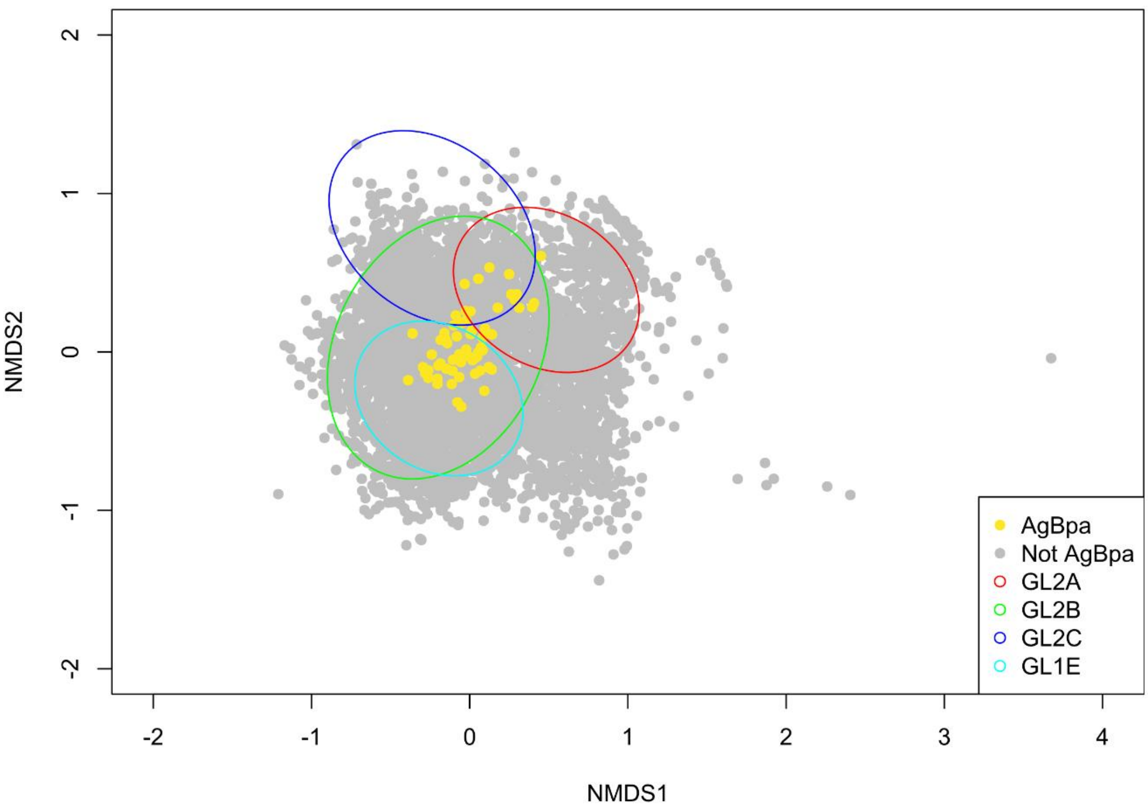
For each of the 10 Scottish categories, the NMDS plots have ellipses encompassing plots from the 17 selected IVS communities. Ellipses are only shown for those IVS categories which matched to 10% or more of the plots from the Scottish category in the ERICA analysis, hence many IVS communities do not feature as ellipses on the plots.

These figures largely confirm the results of the ERICA analyses. On this diagram the 5 Scottish communities are distinguished by different colours whilst all the Irish quadrats are grey.

In the plots for the individual communities, all quadrats not assigned to the select community are in grey. The bivariate ellipses for each community provide an indication of the exclusivity of the Scottish data to each of the 17 selected Irish Communities. In most cases the affinities are restricted to only a few of the Irish communities. So, for quadrats assigned to the *Ranunculus repens* subcommunity of *Agrostis-Bellis* (AgBpa) (Fig. 6a), the best overall association is with GL2B, but the quadrats can be segregated between GL2A and GL1E.

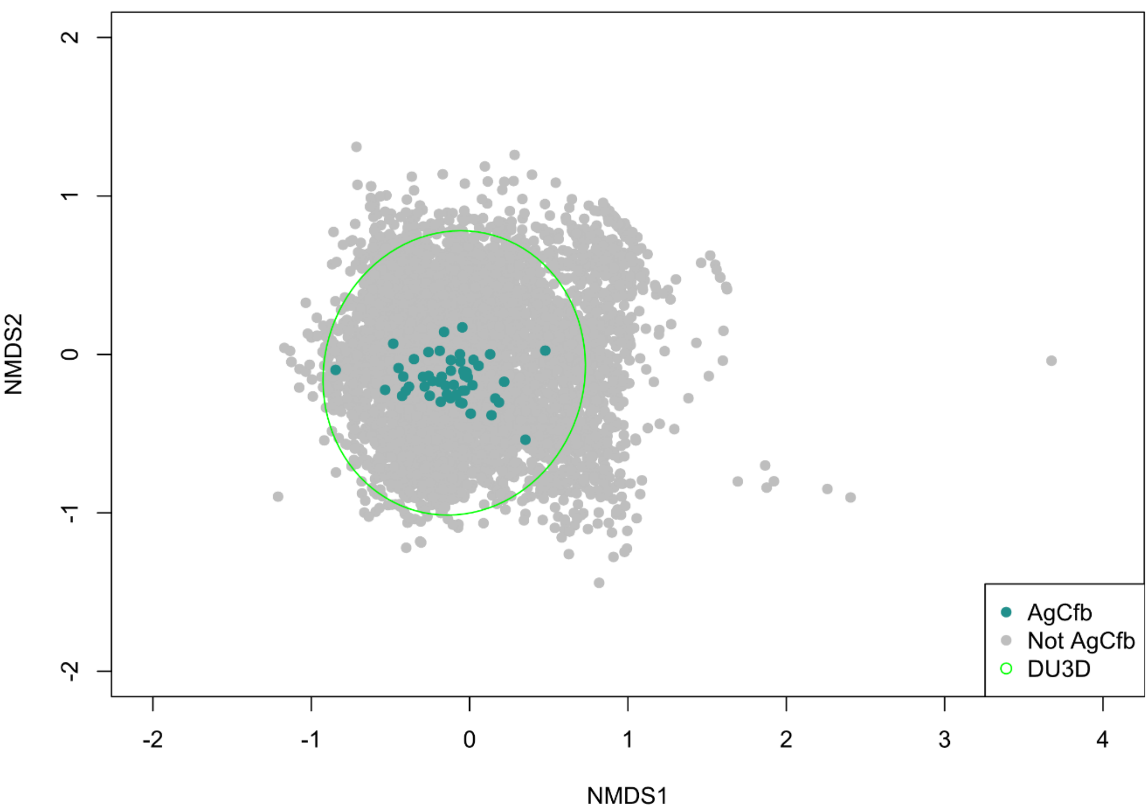
In contrast all the quadrats assigned to the Typical subcommunity of AgCf (AgCfb) (Fig. 6b) fall within the bounds of the DU3D community. For the *Succisa pratensis* subcommunity of *Agrostis-Carex flacca* (AgCfd) (Fig. 6c) all the quadrats are enclosed in the DU3D ellipse, but most are actually aggregated within the ellipse for the GL1B unit with a few outliers.

A)



NMDS2
NMDS1
2
1
0
-1
-2
-2
-1
0
1
2
3
4
AgBpa
Not AgBpa
GL2A
GL2B
GL2C
GL1E

B)



NMDS2
NMDS1
2
1
0
-1
-2
-2
-1
0
1
2
3
4
AgCfb
Not AgCfb
DU3D

C)

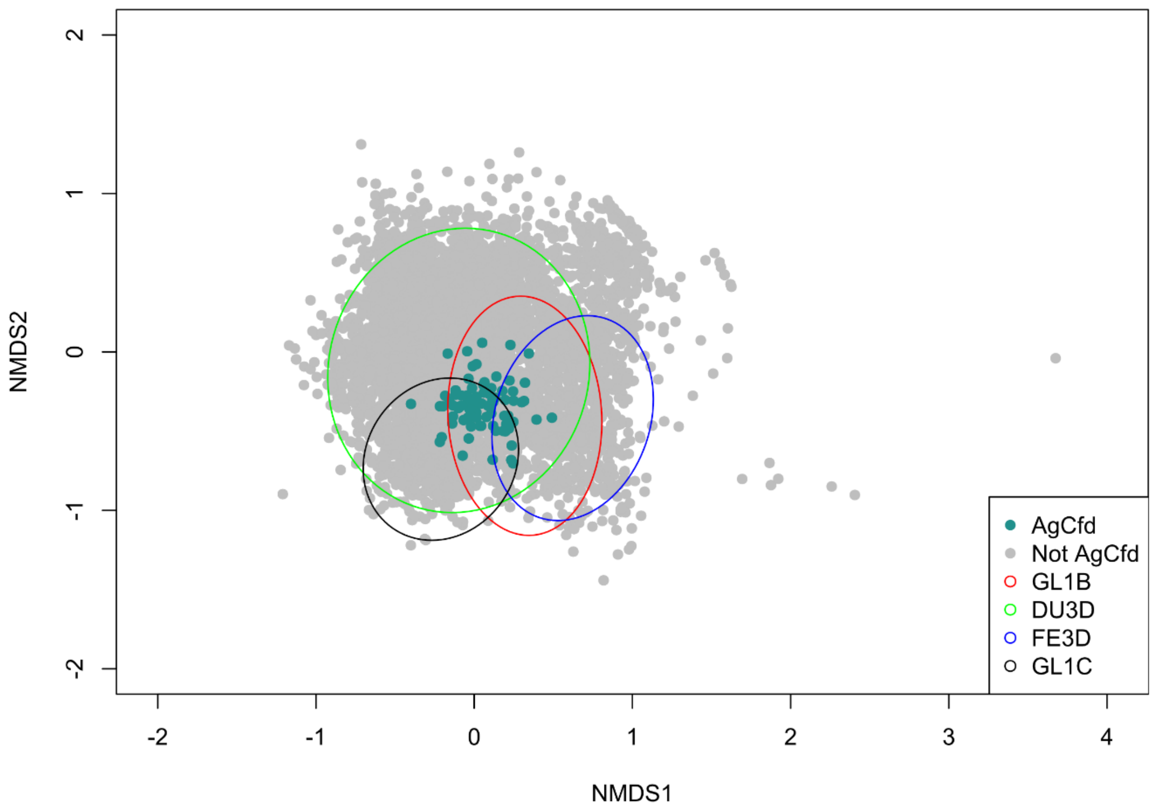


Figure 6. Bivariate ellipses for a) AgBpa, b) AgCfb, c)AgCfd.

Wider European perspective

The position of the Scottish units was compared against 102 noda from across Europe spanning 12 alliances.

The explained variance of the DCA is good with 78% of variance in the floristic data explained by the first 3 axes, R^2 values Axis 1=40%, Axis 2=17.9% and Axis 3 =19.6%.

The first axis of the ordination is clearly negatively related to soil fertility, high scores on Axis 1 indicating low fertility (Kendal Rank coefficient with Ellenberg N = r^2 0.670), whilst Axis 2 is strongly negatively correlated with soil moisture, high scores on Axis 2 indicating drier soil conditions (Kendal Rank coefficient with Ellenberg F = r^2 0.785). Axis two is also weakly correlated with soil reaction (Kendal Rank coefficient with Ellenberg R = r^2 0.286).

The bivariate ellipses plotted onto the DCA (Fig. 7) emphasise the relatively narrow spread of the Scottish noda (coded 13) across the fertility gradient (Axis 1); the outliers being the proposed new subcommunity of MG14, which has a generally higher fertility and the new CnPe wet grassland, which has a lower fertility. There is a greater spread along the hydrological gradient (Axis 2).

Table 11. The alliance names assigned to each nodum are those given by the authors (Wallace & Prosser, 2017)

Alliance number on Figure 7	Name	Number of examples.
1	Phragmition	2
2	Calthion	42
3	Caricion gracilis	2
4	Potentillion	12
5	Alopecurion	7
6	Cynosurion	14
7	Deschampsion	2
8	Molinion	6
9	Lolio-Potentillion	5
10	Caricion davallianae	4
11	Caricion fuscae	2
12	Elymo-Rumicion	4
13	Scottish Noda from 2020 analysis	14

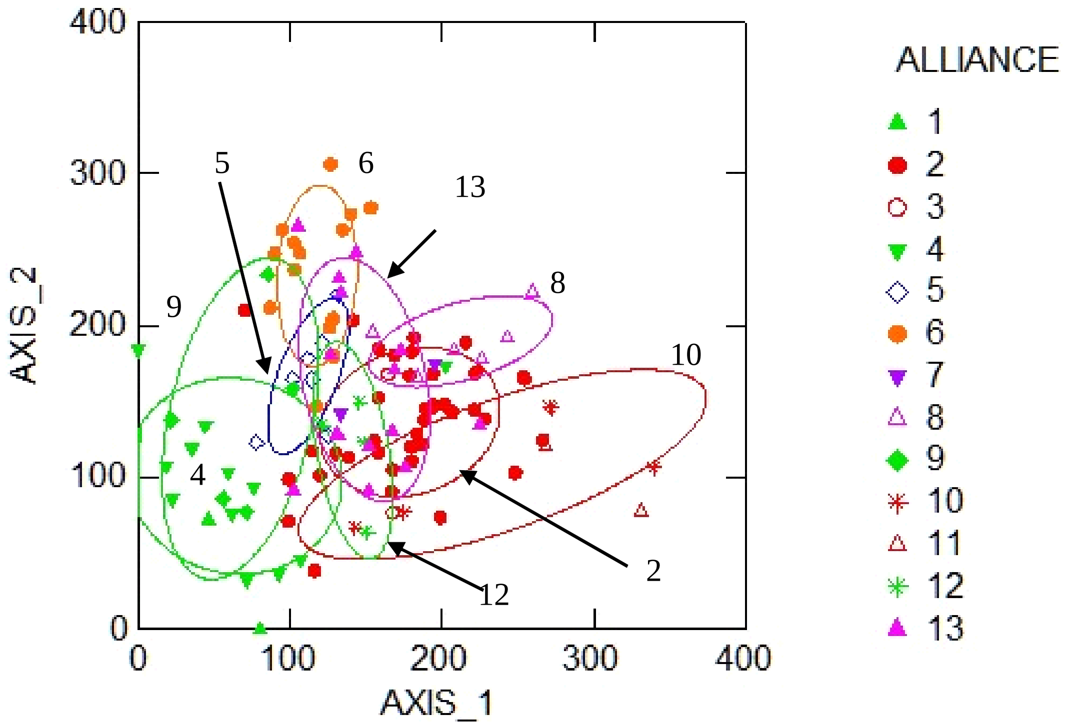


Figure 7. Bivariate ellipses for the 12 Alliances together with the Scottish noda. DCA diagram of the 116 noda coded by the Alliance given by the original author. Bivariate Ellipses are centred on the sample means of the two axis scores. The axes of the ellipses are determined by the sample standard deviation and orientation by sample covariance. Probability level set at 0.55 for determining size of ellipses. Four alliances have only 2 noda and ellipses are not plotted for these (1, 3, 7, 11)

Noda allocated to the Cynosurion (code 6) by previous workers tend to occupy the top LH sector of the DCA plot, with high fertility but low soil moisture, those of the Alopecurion (code 5) tend to occupy the same sector but with generally higher moisture tolerance. Those of the Calthion (code 2) are widely spread but tend to be concentrated in the upper RH sector of the diagram, representing low fertility and intermediate soil moisture. Only the Caricion davallianae (code 10) and Caricion fuscae (code 11) associations have higher Ellenberg F scores. The Molinion (code 8) tends to overlap with the Calthion but generally with lower soil moisture and lower fertility (i.e. lower Axis 2 and higher Axis 1 scores). In the lower LH sector are noda allocated to the Potentillion (code 4), Lolio-Potentillion (code 9) and Phragmition (code 1), all associations characteristic of wet but fertile conditions.

The Scottish noda presented (coded 13) form a relatively tight ellipse with the main spread being along axis 2 (moisture), with relatively little variation in terms of fertility (Axis 1).

In general, most of the Calthion noda from the United Kingdom and Ireland have higher fertility and higher moisture tolerance than their European counterparts, and relative to the Scottish oceanic wet grasslands.

Discussion

Uniqueness of the vegetation

The proposed new Oceanic wet grasslands show a floristic variation that is most strongly linked to the hydrological gradient from the relatively dry, sandy soils, near the dune ridge to the damp, peaty substrates towards the back drain which separates the grasslands from the peatlands beyond.

The floristic table clearly shows the shift from species of dry, slightly calcareous substrates to those of damp, less fertile and more acidic substrates.

When compared with the Calthion communities of England and Wales, the driest Scottish unit, the *Ranunculus repens* subcommunity of *Agrostis-Bellis* (AgBpa) subcommunity has similar soil moisture tolerance to the MG8a and MG8d subcommunities whilst the CaCn subcommunities have similar tolerances to the MG14 and MG8c units (Wallace & Prosser, 2017; Wallace *et al.,* 2020). When soil fertility levels are compared the CaCn subcommunities have low fertility, similar to the MG8d subcommunity, whilst the CnPe community has even lower fertility values. The subunits of MG14 remain the most fertile and some of the wettest subcommunities.

Comparison with the IVS (Perrin, 2021) indicates close alignment of only two of the Scottish units. The AgCf unit aligned well with DU3D of the Irish Classification. This is described as a low-growing community of agriculturally improved dune slacks, machair, and some inland wet grasslands. The sward is mostly comprised of *Festuca rubra, Carex flacca* and *Agrostis stolonifera* with *Trifolium repens, Prunella vulgaris, Bellis perennis, Lotus corniculatus, Plantago lanceolata* and *Hydrocotyle vulgaris* all constant as is *Calliergonella cuspidatum*.

The CnPe unit of the Scottish communities aligned closely with the GL4D - *Agrostis canina/vinealis-Rhytidiadelphus squarrosus* grassland of the IVS. This is described as a wet or humid sward found in infertile, acidic, organic gleys, and peats. The dominant graminoids include *Anthoxanthum odoratum, Holcus lanatus, Luzula multiflora, Juncus acutiflorus* and *Agrostis canina/vinealis*. Frequent sedges include *Carex echinata, Carex nigra* and *Carex panicea*. The only constant forb is *Potentilla erecta* accompanied by frequent *Succisa pratensis* and *Trifolium repens*. The vegetation has a good bryophyte layer which includes constant *Rhytidiadelphus squarrosus* and *Psuedoscleropodium purum*.

In the Scottish survey, this community was restricted to sites away from the machair, mainly on Shetland.

In a European context, the Scottish grasslands form a relatively tight group within the Calthion alliance, but spread, on a hydrological gradient towards the drier Cynosurion in the AgBp community and towards the Caricion-fuscae in the wetter CaCn stands. The drier stands have been retained in the wet oceanic grasslands rather than in the Cynosurion based largely on the high frequencies of damp tolerant species; notably *Agrostis stolonifera* (which is constant), and *Potentilla anserina* (which is frequent) together with occasional *Carex nigra, Caltha palustris, Equisetum fluviatile and Juncus articulatus*, all species that are more characteristic of the Calthion. In contrast, many of the character species of the British MG5 community in the Cynosurion are scarce in the Scottish data, notably *Dactylis glomerata, Centaurea nigra, Agrostis capillaris, Trifolium pratense* and *Lotus corniculatus* (Wallace *et al.,* 2020).

Fragility of the vegetation

These are managed systems that have evolved over many centuries and rely on regular hay cutting and/or grazing. The small scale of many of the fields renders the use of large machinery impractical, whilst the damp peat soils towards the back drain are likely to be sensitive to compaction by heavy machinery. Maintenance of good water management within the fields is essential to allow sufficiently aerated soils in the summer for hay to dry; any reduction in ditch management is likely to have a deleterious impact on the diversity of the vegetation.

Any changes in the frequency of cutting or failure to remove the annual biomass may lead to a loss of floristic diversity due to an increase in the pool of available nutrients. The crofting system is critical to the maintenance of these grasslands; so abandonment of crofting may put them at risk (Pakeman *et al*., 2011). Reduced grazing intensity may also have a negative impact on biodiversity (Pakeman *et al*., 2016). Field enlargement and large-scale changes to traditional drainage patterns is potentially another threat (Angus, 2020).

Changes in climate, especially wetter summers, are likely to have a direct impact on the vegetation and an indirect effect in terms of hay cutting and grazing. Of particular concern is the ability to dry the hay. If soils sit wet into late summer, then the evapotranspiration rate may not allow lying hay to dry effectively. In some cases, more effective ditch level management might lower water tables within the centre of fields, thus enhancing hay drying.

In addition, sea-level rise (Angus, 2018; Angus & Hansom, 2021) may promote saline ingress, affecting the floristic composition of the vegetation, whilst direct inundation of sea water from storm surges through breakdown of the sand ridge could change the nature of the vegetation entirely.

Future work

A better understanding of the ecohydrological processes that maintain these vegetation communities is required to adapt to changes in climate that could threaten their survival. Some factors, such as maintaining the traditional management practices of crofting and the existing infrastructure for water-level management, offer means of mitigating the threat from climate change.

Other threats, such as rising sea levels causing saline intrusion and saline inundation, are more challenging to address.

Currently most of these grasslands are outwith government conservation schemes, which have tended to focus on the drier machair grasslands, mainly in the cultivated strip.

The lack of a clear definition of these wetter communities may have hampered their inclusion Recognition of these species-rich communities in government policies could promote their survival (Pakeman, 2017).

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Appendix A

Table A1. Community composition of the two proposed subcommunities of AgBp and the existing MG5 community, arranged as a floristic table in the format used in British Plant Communities

	AgBp a	**AgBp b**	**MG5 NVC**
Number of samples	66	102	195
Mean species/quadrat	24	19	23
Min-Max species /quadrat	13-26	8-35	12 -38
Holcus lanatus	V	V	IV
Agrostis stolonifera	IV	IV	I
Trifolium repens	V	V	IV
Ranunculus acris	IV	IV	III
Anthoxanthum odoratum	IV	I	IV
Carex nigra	IV	I	.
Cynosurus cristatus	IV	IV	V
Potentilla anserina	III	III	.
Juncus articulatus	IV	II	I
Species preferential to AgBp			
Bellis perennis	*V*	*V*	*III*
Rumex acetosa	IV	III	III
Ranunculus repens	V	III	I
Rhinanthus minor	IV	III	II
Euphrasia spp.	IV	II	.
Juncus bufonius	II	I	.
Sagina procumbens	II	I	.
Trifolium dubium	II	I	II
Kindbergia praelonga	II	I	II
Brachythecium rutabulum	II	I	III
Myosotis discolor	I	I	.
Lolium perenne	III	IV	III
Cerastium fontanum	IV	IV	II
Poa pratensis	I	III	II
Odontites vernus	I	II	.
Heracleum sphondylium	I	II	II
Cirsium arvense	.	I	II
Species preferential to AgCf			
Carex flacca	I	I	I
Festuca rubra	II	IV	V
Plantago lanceolata	III	IV	V
Prunella vulgaris	I	II	III

Luzula campestris	I	I	III
Trifolium pratense	II	II	IV
Vicia cracca	III	II	
Dactylorhiza fuchsii	II	I	
Poa humilis	II	I	
Neottia ovata	I	I	
Jacobaea vulgaris	I	I	
Silene flos-cuculi	II	I	
Scorzoneroides autumnalis	II	II	III
Lathyrus pratensis	I	I	II
Plantago maritima	.	I	
Succisa pratensis	.	.	I
Molinia caerulea	.	I	
Lysimachia tenella	.	I	
Lotus corniculatus	.	I	V
Juncus balticus	.	I	.
Ophioglossum vulgare	.	I	I
Dactylorhiza incarnata	I	I	.
Equisetum arvense	I	I	.
Carex arenaria	.	I	.
Linum catharticum	.	I	.
Pinguicula vulgaris	.	.	.
Plagiomnium undulatum	I	I	.
Species preferential to CaCn			
Caltha palustris	IV	I	.
Calliergonella cuspidata	III	I	I
Cardamine pratensis	III	I	I
Epilobium palustre	I	I	I
Angelica sylvestris	I	I	I
Filipendula ulmaria	I	I	I
Phragmites australis	I	I	.
Juncus effusus	I	I	I
Ranunculus flammula	I	.	I
Hydrocotyle vulgaris	.	I	I
Carex panicea	I	I	I
Pedicularis palustre	.	.	I
Mentha aquatica	.	.	I
Sagina nodosa	.	I	I
Oenanthe lachenalii	.	.	I
Triglochin palustris	I	I	I
Species preferential to CnPe			
Rhytidiadelphus squarrosus	I	I	II
Potentilla erecta	.	I	I
Equisetum palustre	I	I	.
Comarum palustre	.	.	.
Eriophorum angustifolium	.	.	.
Equisetum fluviatile	IV	I	.

Carex echinata	.	.	.
Viola palustris	.	I	.
Luzula multiflora	I	I	.
Agrostis canina	.	I	.
<u>Species preferential to MG14a</u>			
Persicaria amphibia	III	I	.
Galium palustre	I	.	.
Poa trivialis	II	II	II
Jacobaea aquatica	I	.	.
Myosotis laxa	II	I	.
Glyceria fluitans	I	I	.
Alopecurus geniculatus	I	I	.
Calliergon cordifolia	I	.	.
Eleocharis palustris	I	I	.
Stellaria alsine	I	.	.
<u>Species preferential to MG5</u>			
Dactylis glomerata			IV
Centaurea nigra			IV
Agrostis capillaris			IV
Leucanthemum vulgare			II
Schedonorus pratensis			I
Knautia arvensis			I
Juncus inflexus			I
Galium verum			II
Trisetum flavescens			III
Achillea millefolium			III
Poterium sanguisorba			I
Koeleria macrantha			I
Festuca ovina			I
Danthonia decumbens			I
Pimpinella saxifraga			I
Betonica officinalis			I
Carex caryophyllea			I
Conopodium majus			I
Hypochaeris radicata			III
Ranunculus bulbosus			III
Taraxacum agg.			III

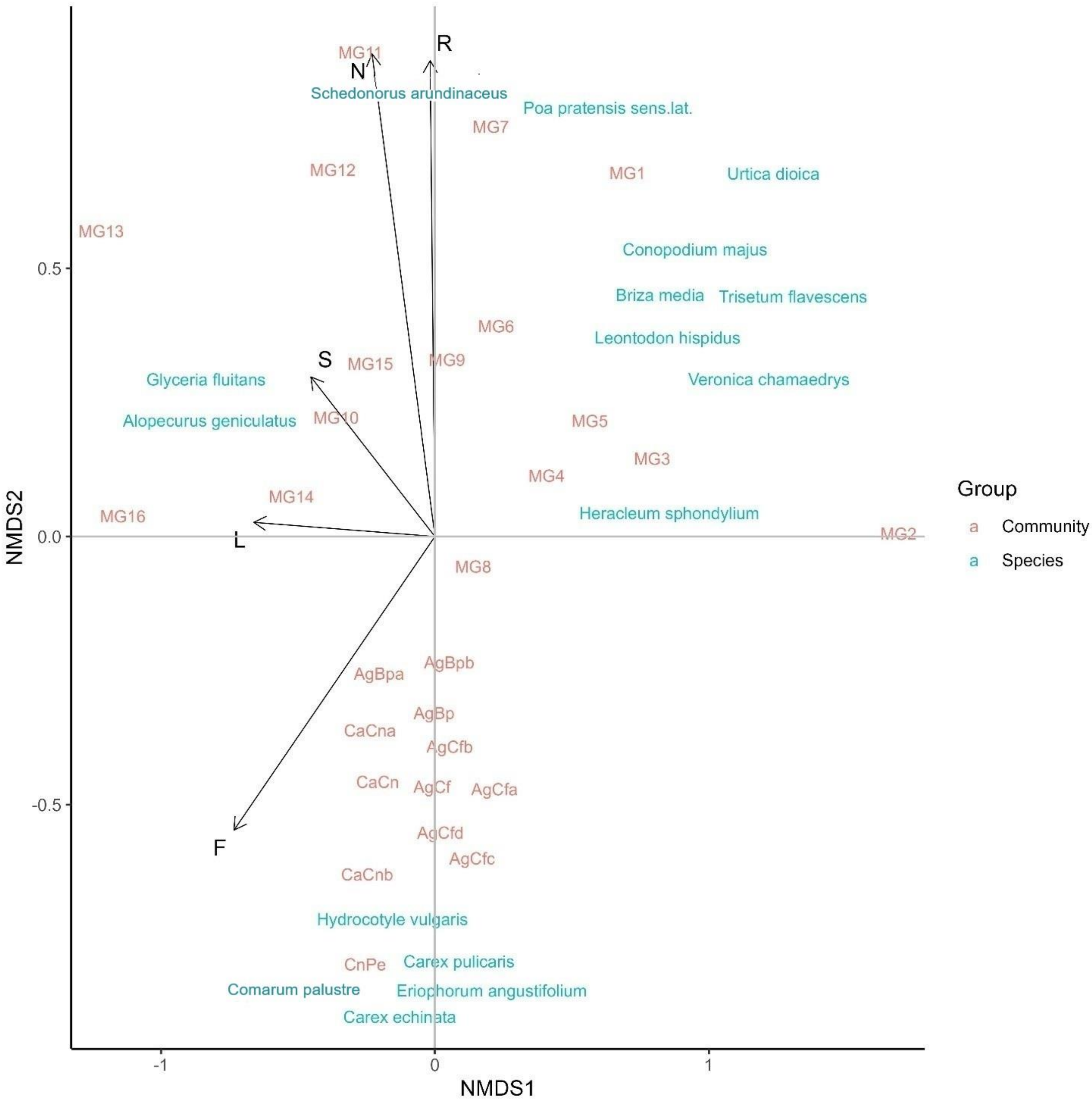

Figure A1. A non-metric multidimensional scaling (NDMS) ordination of the proposed oceanic wet grassland communities compared to all the Mesotrophic Grassland communities currently defined by the NVC. The arrows represent trends in Ellenberg indicator values. The names in blue show the position of individual species that help to differentiate the new communities from the existing ones.