Phytocoenologia Vol. 47 (2017), Issue 1, 13–32
Published online November 2016

Research Paper

Plant community ecology of petrifying springs (*Cratoneurion*) – a priority habitat

Melinda D. Lyons* & Daniel L. Kelly

Abstract

Aims: To investigate the floristic and abiotic characteristics of the Habitats Directive priority habitat 'Petrifying springs with tufa formation (*Cratoneurion*)'. **Location:** The island of Ireland, north-western Europe. **Methods:** Vascular plants, bryophytes and abiotic variables were recorded in a field survey of 186 relevés (4 m²). Relevés were assigned to groups based on species composition, using fuzzy clustering and Indicator Species Analysis. Eight plant communities were described. **Results:** Group 1 *Eucladium verticillatum-Pellia endiviifolia* Tufa Cascades, of steep slopes, are related to Continental *Eucladietum verticillati* and *Adiantion* communities. Group 2 *Palustriella commutata-Geranium robertianum* Springheads and Group 3 *Brachythecium rivulare-Platyhypnidium riparioides* Tufaceous Streams and Flushes are woodland communities related to the *Equiseto telmatejae-Fraxinetum* and the *Pellio endiviifoliae-Cratoneuretum commutati*. Groups 1 to 3 fall broadly within the *Brachythecio rivularis-Cratoneuretum* forest spring vegetation type. Group 4 *Palustriella commutata-Agrostis stolonifera* Springheads are intermediate between Groups 1 to 3 and Groups 5 to 8. Group 5 *Schoenus nigricans* Springs, Group 6 *Carex lepidocarpa* Small Sedge Springs and Group 7 *Palustriella falcata-Carex panicea* Springs are transitional to *Caricion davallianae* small-sedge fen communities. Group 8 *Saxifraga aizoides-Seligeria oelandica* Springs are ecologically distinctive, species-rich assemblages confined to montane cliffs, with a restricted distribution in upland limestone regions, containing a number of nationally and internationally rare taxa. Of our eight groups, Groups 7 and 8 have the closest affinities with *Cratoneuretum falcati* spring communities. Abiotic variables differ significantly among the eight groups. Slope, macronutrient levels and shading by tree canopies are highly significantly related to the main axes of variation in the floristic data. Species diversity is inversely related to phosphate levels. Group 8 communities are irrigated by water of the highest pH and lowest solute concentrations. **Conclusions:** Our eight groups characterise variation within the habitat, elucidate ecological gradients with related habitats and facilitate conservation of this ecologically distinctive habitat.

Keywords: Bryophyte; *Cratoneurion*; fuzzy clustering; Habitats Directive; Indicator Species Analysis; Non-metric Multidimensional Scaling; *Palustriella*; travertine; tufa.

Nomenclature: Stace (2010) for vascular plants and Hill et al. (2008) for bryophytes.

Abbreviations: ISA = Indicator Species Analysis (Dufrêne & Legendre 1997); MC = Membership Coefficient, a measure of how strongly a sample belongs to a particular fuzzy cluster group; MPA = Multi-level Pattern Analysis (De Cáceres et al. 2010); MRPP = Multi-response Permutation Procedure; NMS = Non-metric Multidimensional Scaling; NVC = National Vegetation Classification of Great Britain (Rodwell 1998a, 1998b, 1998c); SCS = Sorensen Coefficient of Similarity.

Submitted: 3 December 2015; first decision: 17 February 2016; accepted: 27 August 2016

Co-ordinating Editor: Monika Janišová

*Corresponding author's address: Department of Botany and Trinity Centre for Biodiversity Research, School of Natural Sciences, Trinity College, The University of Dublin, College Green, Dublin 2, D02 XR15, Ireland; lyonsm5@tcd.ie. Complete addresses of all authors can be found at the bottom of the paper.

DOI: 10.1127/phyto/2016/0101

www.borntraeger-cramer.de
0340-269X/2016/0101 $ 9.00

Introduction

Petrifying springs with tufa formation (*Cratoneurion*) constitute a priority habitat (7220) under Annex I of the European Union Habitats Directive (92/43/EEC) owing to their ecological significance, vulnerability and small spatial extent. Lime-rich spring water, on contact with the atmosphere, loses carbon dioxide and precipitates tufa (travertine), a porous calcium carbonate deposit. Plants, especially bryophytes, and microbial biofilms are intimately associated with the deposition process (Emeis et al. 1987; Pentecost 1996; Golubić et al. 2008; Pedley et al. 2009). Tufa can also form in other hydrogeological settings, for example on streams and at waterfalls (Arenas et al. 2014; Auqué et al. 2014).

Cratoneurion commutati Koch 1928 (commonly shortened to *Cratoneurion*) falls within the spring vegetation class *Montio-Cardaminetea* Br.-Bl. et Tx. 1943 and the order *Montio-Cardaminetalia* Pawlowski 1928. It takes its name from the pleurocarpous moss *Cratoneuron commutatum* (Hedw.) Roth, which was reclassified as *Palustriella commutata* (Hedw.) Ochyra in 1989. *Palustriella falcata* (Brid.) Hedenäs was not considered specifically distinct from the preceding taxon in many older floras (e.g. Smith 1978) and data for this segregate are lacking in some major vegetation studies (e.g. Rodwell 1998b).

Definition of *Cratoneurion* vegetation has from the outset been problematic and the ecological continuum between petrifying springs and other habitats remains widely acknowledged but poorly defined. Unusually for a phytosociological entity, this alliance was defined principally by abiotic attributes – lime-rich spring communities, which are moss-dominated and often tufa-forming – rather than species composition (Koch 1928; Braun-Blanquet 1949). However, the presence or absence of tufa is insufficient as a means of delimiting one habitat from another, and indeed tufa formation is not a prerequisite in *Cratoneurion* communities (Koch 1928; Braun-Blanquet 1949). The shortcomings of a definition based on tufa formation are illustrated by the British National Vegetation Classification (NVC): M37 *Cratoneuron commutatum-Festuca rubra* Springs and M38 *Cratoneuron commutatum-Carex nigra* Springs (the only British communities synonymous with the Annex I priority habitat, Commission of the European Communities 2013) are often – though not necessarily – tufa-forming, while so too is the British alkaline fen M10 *Carex dioica-Pinguicula vulgaris* mire (Rodwell 1998b). Thus, *Cratoneurion* communities are ecologically similar to, and often grade into, small sedge fen vegetation of the alliance *Caricion davallianae* Klika 1934 (Class *Scheuchzerio-Caricetea nigrae* (Nordh. 1936) Tx. 1937).

Similarly, the close floristic connection of bryophyte-rich waterfall communities with those of springs was noted in an Irish context by Ivimey-Cook & Proctor (1966). Irish *Adiantum capillus-veneris* Stands reported by those authors are indicative of the close association between *Adiantion* communities (which include the *Eucladietum verticillati* Allorge 1922) and *Cratoneurion* communities (e.g. Deil 1994; Philippi 1965). The *Adiantion* is included in an overview of priority habitat 7220 for Spain (Carcavilla Urquí et al. 2009), but is excluded from overviews for France (Anonymous 2002) and Italy (Biondi & Blasi 2009).

Petrifying springs in woodlands remain poorly described. The *Equiseto telmatejae-Fraxinetum* Oberd. ex Seib. 1987 is described as containing woodland flushes rather than strongly petrifying springheads (Oberdorfer 1992) and the British NVC lacks a woodland spring category altogether (Rodwell 1998a).

Revisions within the class *Montio-Cardaminetea* have been attempted but not widely adopted (Maas 1959; Zechmeister & Mucina 1994).

This detailed field survey of the vegetation of Irish petrifying springs aims to elucidate the variation in floristic composition within petrifying spring communities and their relationships with other kinds of vegetation. This bryophyte-dominated community is well represented in the mild Atlantic climate of Ireland, showing patterns of variation that are reflected in the wider European context. It also contains some species-rich assemblages with rare species of international importance. The present study combines a detailed analysis of both floristics and abiotic variables of this habitat; previous studies elsewhere have focused on only one or other of these aspects.

Methods

In total, 186 relevés were recorded between April 2011 and September 2013 from 110 separate water sources spread across the island of Ireland (including Northern Ireland). Most samples (90.3%) were from semi-natural, tufa-forming springheads, seepages and flushes with *Cratoneurion*-type vegetation; 18 samples (9.7%) were from tufa-forming streams, waterfalls or anthropogenically-modified hydrogeological settings. Plant species (vascular plants and bryophytes) were recorded in 4 m^2 quadrats by per cent cover. Woody species occurring > 2 m above ground level over the quadrat were recorded as tree canopy cover. Tufa was recorded as per cent of surface area within each quadrat, classified according to Pentecost & Viles (1994) and Pentecost (1995, 2005): cascade tufa (consolidated, often massive deposits of steep slopes), paludal tufa (on low gradients, accumulating around the bases of plants and often poorly consolidated), stream crust tufa (sheet-like deposits beneath flowing water), oncoids/ooids (coated grains) and tufa dams (impounding water on streams). Paludal tufa was recorded in three categories: (1) weakly formed, discontinuous, inconspicuous tufa forming traces on soil or at base of plants, (2) intermediate, (3) strongly formed tufa, often crunchy underfoot, coating the ground with a conspicuous white layer, often with detached chunks of consolidated tufa. Hydrological characteristics (flowing/trickling water, dripping water, pools and damp ground) were estimated as percentage areas in each quadrat, as were bare (unvegetated) tufa, stone, soil, etc. Water samples were collected from 91 individual water sources (115 samples in total) and analysed for pH, alkalinity (bicarbonate), calcium, magnesium, potassium, sodium, chloride, nitrate, phosphate (as soluble reactive phosphate) and sulphate using standard laboratory procedures (Lyons 2015).

Data were analysed using R (Version 3.0.3) and PC-ORD Version 5.33 (McCune & Mefford 2006). A square root transformation was performed on relevé data to reduce the skewness of species distributions and to reduce overall variance. The Sørensen (Bray-Curtis) coefficient was used to create a distance matrix. Relevés were assigned to fuzzy cluster groups using the 'fanny' function in the R package Cluster, a non-hierarchical clustering method based on the differences between objects (Kaufman & Rousseeuw 2005). The membership exponent was set at 1.1. Membership coefficients (MC) are a measure of how strongly a sample belongs to a particular fuzzy cluster group. Indicator Species Analysis (ISA) of fuzzy cluster outputs led to the selection of eight groups as the optimal arrangement of relevés into clusters, with 108 statistically significant indicator species and a mean p-value of 0.0092 (Dufrêne & Legendre 1997). Multi-level Pattern Analysis of species was carried out using the 'multipatt' function in the R package Indicspecies (Version 1.7.1) to investigate the association between species patterns and combinations of groups of sites, rather than just the single groups tested by ISA (De Cáceres et al. 2010).

The differences among groups were tested using Multi-response Permutation Procedure (MRPP) in PC-ORD, on ten environmental characteristics (relating to tufa formation types, hydrological characteristics, slope, tree canopy cover and the proportion of ground surface covered by tufa) and ten water chemistry parameters (listed above). Variables were relativised (by column total) before analysis and the distance measure used was the Sørensen coefficient. MRPP produces a statistic A that describes within-group homogeneity compared to random expectation.

Ordinations of relevé data were produced by Nonmetric Multidimensional Scaling (NMS) in PC-ORD. Species occurring in less than four samples were removed from the data set to reduce noise caused by incidental species (leaving a total of 162 species) and a square-root transformation was performed on relevé data (McCune & Grace 2002). The ordinations were produced in 'slow and thorough autopilot' mode using the distance measure Sørensen (Bray-Curtis). An NMS ordination of our groups along with previously published communities was produced by the same method; the data used were species frequencies.

Synoptic tables (Electronic Supplement 1) contain frequency data in classes to facilitate comparison with other syntaxa described in the literature: Class I = up to 20%, Class II = 21% to 40%, Class III = 41% to 60%, Class IV = 61% to 80% and Class V = 81% to 100%. All species in Classes V, IV and III (and all that are significant indicator species of the group) are included for the relevant fuzzy cluster group in each table; species in Classes V and IV for the published communities with which our group is being compared are also shown. Percentage frequencies for all species are given in Electronic Supplement 2 and the full data set has been submitted to the Irish National Biodiversity Data Centre. In general, 'constant' indicates species in Classes V or IV, 'frequent' indicates Class III and 'occasional' Class II (Rodwell 1998a, 1998b, 1998c). The statistical significance of the results of Indicator Species Analysis and Multi-level Pattern Analysis is denoted as *** p-value < 0.001; ** p-value < 0.01; * p-value < 0.05.

Results

The eight plant communities of Irish petrifying springs, derived from fuzzy cluster analysis of floristic data, are summarised in Table 1. MRPP showed a highly statistically significant difference among groups based on abiotic characteristics ($A = 0.2347$, $p < 0.001$; for pairwise comparisons of Groups, see Electronic Supplement 3 (a)). An NMS ordination indicating the relationship of the Irish communities to selected published communities can be found in Electronic Supplement 4 (a).

Tufa formation type and extent in each group is shown in Fig. 1.

Group 1 *Eucladium verticillatum-Pellia endiviifolia* Tufa Cascades

This group contains massive, steep cascade tufa deposits and exemplifies extreme tufa-forming habitats in which few plant species can survive (Fig. 2). The calcicole moss *Eucladium verticillatum* is constant along with the liverwort *Pellia endiviifolia*, frequently accompanied by *Didymodon tophaceus;* all three are highly significant indicators of Group 1 (see Electronic Supplement 1 for synoptic table). *E. verticillatum* is the most abundant species (mean cover 25%), typically colonising vertical tufa surfaces and often somewhat shaded by aspect, microtopography or overhanging vegetation (*cf*. Pentecost & Zhaohui 2006). *Palustriella commutata* is constant and almost as abundant as *E. verticillatum*. Bryophytes dominate the vegetation more than in any other group (Elec-

Table 1. The eight plant communities of Irish petrifying springs (n = 186). Mean silhouette width (S_i) is a measure of similarity among samples within our fuzzy cluster groups; high S_i values indicate well-clustered groups.

Group	Name and Description	n	Mean S_i
1	***Eucladium verticillatum-Pellia endiviifolia* Tufa Cascades**: Bryophyte-dominated, strongly tufa-forming spring communities on steep slopes (both coastal and inland) with low species diversity.	18	0.20
2	***Palustriella commutata-Geranium robertianum* Springheads**: Woodland springhead tufa cascades, dominated by *P. commutata*, on moderately steep slopes.	26	0.16
3	***Brachythecium rivulare-Platyhypnidium riparioides* Tufaceous Streams and Flushes:** Woodland communities with flowing water, typically forming in hydrological sequence below Group 2 springheads.	29	-0.01
4	***Palustriella commutata-Agrostis stolonifera* Springheads**: A group of moderately steep slopes, intermediate between Group 1-3 and Groups 5-8.	28	0.04
5	***Schoenus nigricans* Springs**: Springs on level ground forming paludal tufa amongst *Schoenus nigricans* tussocks, with an underlayer of 'brown mosses'.	22	0.17
6	***Carex lepidocarpa* Small Sedge Springs**: Weakly tufaceous springs with high species diversity, on level ground, associated with small-sedge fens.	30	0.09
7	***Palustriella falcata-Carex panicea* Springs**: Springs of level or gently sloping ground, especially characteristic of karst landscapes, and often with bare, unvegetated tufa or exposed bedrock; *P. falcata*-dominated.	20	0.08
8	***Saxifraga aizoides-Seligeria oelandica* Springs**: Species-rich springs with *S. aizoides* and a suite of rare bryophyte species; weakly tufa-forming, on steep slopes, centred on the Benbulbin Range of NW Ireland.	13	0.17

tronic Supplement 4 (b)). The most frequently occurring vascular plants are *Agrostis stolonifera* and *Festuca rubra*; these have low cover values (mean 1% each) and total graminoid cover is at its lowest in Group 1. This group has the lowest overall species diversity (mean 8.7 species per 4 m² relevé, Electronic Supplement 4 (c)). It is a cohesive group, with the highest mean silhouette width (0.20, Table 1).

This group is strongly tufa-forming. Tufa cascades occupy, on average, 89% of surface area – the highest proportion for any group (Fig. 1). Bare, unvegetated patches of tufa are often present (mean 24% of ground surface), sometimes with stalactites or intricate assemblages of 'petrified' plant fragments. Group 1 occurs on the most steeply sloping sites (mean slope 70°, Electronic Supplement 4 (c)). Dripping water is characteristic and, occasionally, thin sheets of water flow over the surface of the tufa. Samples are divided almost equally between springs on coastal spray zone cliffs and at inland (mostly wooded) locations. Accordingly, canopy cover is variable: absent from coastal cliffs but often dense at inland sites. Most samples were recorded at springheads but one sample with highly typical vegetation (MC 99%) occurred at a tufa-forming waterfall.

The Central European *Eucladietum verticillati* Allorge 1922 of steep, irrigated rock faces (Philippi 1965; Braun 1968; Anonymous 2002), is similar to our Group 1. *E. verticillatum* is constant in both and *P. commutata* is frequent, but *Pellia endiviifolia*, constant in Group 1, was seldom reported from the Continental European community. Our Group 1 also has affinities with Hadač's lowland *Lycopo-Cratoneurion commutati* Alliance (*Pellio endiviifoliae-Cratoneurion commutati* Rivola 1982 community), but *Campylium stellatum* – constant in Hadač's community – is absent from our Group 1 and occurs instead in our fen-related communities. *E. verticillatum*, although named as a characteristic species of Hadač's community, occurs in ≤ 40% of his samples (Hadač 1983). Furthermore, *Scrophularia umbrosa* and *Lycopus europaeus*, characteristic of Hadač's community, are absent from all our groups. Both species occur in less base-rich communities in Ireland.

Eucladium verticillatum-Pellia endiviifolia Tufa Cascades are intermediate between *Adiantion* communities (bryophyte-rich communities of damp calcareous rock faces with *Adiantum capillus-veneris*, especially characteristic of the Mediterranean region, Deil 1994, de Foucault 2015) and the Central European *Cratoneuretum filicino-commutati* (Oberdorfer 1977). The *Adiantion* communities of southern France include *E. verticillatum* as a characteristic species (de Foucault 2015). The author makes no mention of tufa; he notes that the *Adiantion* is found largely on base-rich substrata but that a variant is found on more acid substrata. *A. capillus-veneris* has a very limited biogeographical range in Ireland and was not recorded in Group 1 samples.

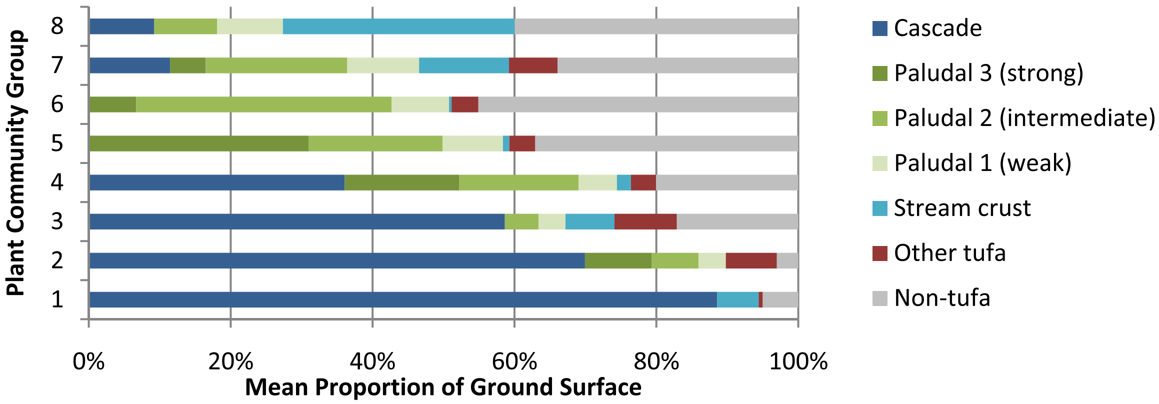


Fig. 1. Tufa formation type in plant communities (after Pentecost & Viles 1994 and Pentecost 1995, 2005).

Fig. 2. Group 1 *Eucladium verticillatum-Pellia endiviifolia* Tufa Cascade on coastal cliff at Ardmore Pt, Co. Wicklow (Sept. 2013). *Palustriella commutata* is abundant (centre top) along with the less conspicuous acrocarps *E. verticillatum* and *Didymodon tophaceus*.

Fig. 4. Group 3 *Brachythecium rivulare-Platyhypnidium riparioides* Tufaceous Stream and Flush community on a wooded hillside at Glenasmole, Co. Dublin (April 2013). Shoots of *Equisetum telmateia* are emerging on the stream margins. Bare tufa and flowing water are characteristic of this community.

Fig. 3. Group 2 *Palustriella commutata-Geranium robertianum* Springhead (centre) in woodland at Moneyduff, Co. Leitrim (May 2010). *P. commutata* dominates this large tufa cascade; *G. robertianum, Hedera helix, Rubus fruticosus* and *Asplenium scolopendrium* are occasional. *Fraxinus excelsior* is the most frequent tree species.

Fig. 5. Group 4 *Palustriella commutata-Agrostis stolonifera* Springhead on the lower slopes of the Benbulbin Range, Co. Sligo (Sept. 2012). *P. commutata* is dominant on this springhead tufa cascade. *A. stolonifera, Festuca rubra, Carex flacca, C. panicea* and *Bryum pseudotriquetrum* are occasional

Group 2 *Palustriella commutata-Geranium robertianum* Springheads

This group is characterised by large mounds of *Palustriella commutata* at woodland springheads (Fig. 3). *P. commutata* – constant/frequent in all eight groups – is at its most abundant here (ISA***, mean cover 61%). *Geranium robertianum* is also constant but rarely covers large areas (mean cover 4%, ISA***). It is one of the few vascular plant species found rooting in consolidated tufa or within mounds of *P. commutata*. The following are also statistically significantly linked to this group: *Rubus fruticosus* (small shoots rooted on tufa, seldom thriving), *Hedera helix, Carex remota, Equisetum telmateia* and *Asplenium scolopendrium*. The Group 1 indicator species *Pellia endiviifolia* and *Eucladium verticillatum* are frequent but much less abundant in Group 2, with mean covers of 2% and 1% respectively. *Fraxinus excelsior* seedlings are also frequent (mean cover 0.4%). They are absent from the most strongly tufaceous microhabitats and, even on weakly formed tufa, they seldom survive beyond the seedling stage. This is a cohesive group with a high mean silhouette width (0.16, Table 1).

Bryophytes dominate the vegetation, with total cover of 69% (joint highest with Group 6). Dominance by *Palustriella commutata* results in relatively low species diversity (mean 14.1 species per relevé). Graminoids and forbs cover 9% and 8% respectively. Woody plants make a bigger contribution to the field layer in this group than in any other, albeit only 3% of total ground cover.

These samples are strongly tufa-forming. Tufa cascades occupy on average 70% of the ground surface (second only to Group 1; Fig. 1). Cascades are sometimes massive, measuring 100 m^2 or more. Elsewhere, smaller, more fragmented cascades are combined with paludal tufa or oncoids/ ooids. Slope is very variable (mean 36°). Water sometimes trickles or drips over the tufa, but mostly (81% of surface area, on average) the surface is damp without obvious surface water. Where dripping water is plentiful, *Palustriella commutata* mounds are sometimes irrigated from above, as in the '*Cratoneuron* Drip-Zone' facies of Ferreira (1978). Tree canopy cover is high (mean 51%) and only Group 3 has a comparable level of shading.

Group 2 *Palustriella commutata-Geranium robertianum* Springheads falls between the *Cratoneuretum filicino-commutati* (Kuhn 1937) Oberd. 1977 and the *Equiseto telmatejae-Fraxinetum* Oberd. ex Seib. 1987. The former lacks woodland species and the latter is characteristic of woodland flushes rather than spring heads (Oberdorfer 1977, 1992). Group 2 falls within the *Brachythecio rivularis-Cratoneuretum* Dierßen 1973 (Hájková & Hájek 2011), which broadly encompasses our Groups 1, 2 and 3. However, *Brachythecium rivulare, Bryum pseudotriquetrum* and *Philonotis calcarea* (diagnostic of Dierßen's community) are infrequent in our Group 2, but are significant indicators of other groups in our study. Group 2 also has affinities with the *Pellio endiviifoliae-Cratoneuretum commutati* Rivola 1982 community (Hadač 1983), but the Group 2 woodland species are lacking in that community.

Group 3 *Brachythecium rivulare-Platyhypnidium riparioides* Tufaceous Streams and Flushes

This group is characterised by the presence of trickling water in tufa-forming streams, waterfalls, flushes and seepage zones, with the mosses *Brachythecium rivulare*, *Palustriella commutata*, *Cratoneuron filicinum* and *Platyhypnidium riparioides*. *B. rivulare* and *P. riparioides* are highly significant indicators, along with *Ranunculus repens* (ISA***). *C. filicinum* and *P. riparioides* sometimes dominate the vegetation. They are more tolerant of intermittent dry periods than *P. commutata* and their abundance is positively correlated with increased macronutrient levels (*P. riparioides* is favoured by eutrophication, Blockeel et al. 2014). Forbs, of which *Ranunculus repens*, *Geranium robertianum* and *Mentha aquatica* are most frequent, make an important contribution to the vegetation. Bryophyte cover is at its lowest in this group; the ratio of forb to bryophyte cover, 1:2.1, is higher than in any other group. Overall, species diversity is relatively low (mean 13.8 species per relevé).

Trickling water is present in 90% of samples, flowing over more gently sloping ground (mean slope 27°). Tufa formation is variable both in type and extent: tufa cascades are most frequent, but paludal tufa, stream crust tufa, oncoids/ooids and dams are also present. Bare tufa is characteristic (mean 29% of ground surface); it is especially prevalent below flowing water (Fig. 4). Most samples are situated in woodland and mean canopy cover (50%) is comparable to Group 2. This somewhat disparate group has the lowest mean silhouette width (-0.01, Table 1; negative values can occur when several samples lie between two or more groups, rather than having clear affinities with a single group). The group contains three poorly clustered samples (7% of the total) from locations where the hydrology had been strongly modified by anthropogenic activities: two tufa cascades located below pipe outfalls and a third in the overflow from a golf-course pond. Other samples are semi-natural, with no indications of human interference; several of these have affinities with Group 2 and/or Group 4.

Group 3, like Group 2, lies between the *Equiseto telmatejae-Fraxinetum* Oberd. ex Seib. 1987 and the *Cratoneuretum filicino-commutati* (Kuhn 1937) Oberd. 1977 in terms of species composition (Oberdorfer 1977, 1992). Physiognomically, Group 3 comes closer to the *Equiseto telmatejae-Fraxinetum,* woodland flushes being a feature of both. Of our eight groups, Group 3 comes closest to the *Pellio endiviifoliae-Cratoneuretum commutati* Rivola 1982 community (Hadač 1983) with close agreement of constant species – apart from *Campylium stellatum* which is almost exclusive to our fen-related groups.

Group 4 *Palustriella commutata-Agrostis stolonifera* Springheads

This group consists of hillside springheads, seepages and flushes, usually in unshaded places, dominated by *Palustriella commutata*. The grasses *Festuca rubra* and *Agrostis stolonifera* are constant (Fig. 5). After Group 2, this is the group in which *P. commutata* is most frequent and abundant (mean cover 37%). Accompanying species are varied but most often consist of wetland generalists such as *Filipendula ulmaria, Mentha aquatica, Juncus articulatus, Carex flacca*, *Calliergonella cuspidata, Cratoneuron filicinum* and *Bryum pseudotriquetrum*. This is a somewhat disparate group with a low mean silhouette width of 0.04 (Table 1, n = 28). The statistically significant indicators of the group, *Agrostis stolonifera* and *Filipendula ulmaria* (ISA **), have relatively broad ecological ranges and the group lacks a distinctive set of characteristic species. Overall, Group 4 is more diverse in species composition than Groups 1 to 3, with a mean of 19.7 species per relevé; bryophytes contribute the greatest amount of cover (56%), but graminoids are also prominent (33% cover).

Within this group, a subset of samples consists of *Palustriella commutata*-dominated springheads (Fig. 5); these are, in effect, the unwooded equivalent of Group 2, lacking the woodland plants of that group, and instead containing *Festuca rubra*. The remaining samples consist of diffuse seepages and flushes. In these, *Filipendula ulmaria*, *Eupatorium cannabinum*, *Crepis paludosa*, *Agrostis stolonifera*, *Carex flacca*, *Equisetum telmateia*, *Brachythecium rivulare* and *Calliergonella cuspidata* are more abundant, along with smaller amounts of *Palustriella commutata*.

The extent of tufa formation in Group 4 samples is variable: 39% of samples contain tufa over the entire relevé surface area, but several have very low tufa cover (in two cases only a trace). Paludal and cascade tufa are present in approximately equal quantities (mean cover 38% and 36% respectively, Fig. 1). Slope is variable, ranging from 0° to 80°, with a mean of 26°. In most cases, the ground surface is damp, as water seeps through the soil just below the surface (damp ground occupies 75% of surface area, on average). Occasionally, the water emerges above the ground surface, as small rivulets or pools. Most samples have no tree canopy cover, but five samples (18%) are situated in woodland. Four samples (14%) are in the coastal spray zone and a further three (11%) are within 100m of the high tide mark.

Sorensen coefficients of similarity (SCS) between pairs of communities indicate that, of our eight groups, Group 4 comes closest to the British M37 *Cratoneuron commutatum-Festuca rubra* Springs (SCS 40%, Lyons 2015; Rodwell 1998b). M37 constant species are constant/frequent in Group 4. Group 4 contains the same bryophyte species as the *Cratoneuretum filicino-commutati* but differs somewhat for vascular plants. It has closest affinities with the *Molinia*-rich facies of that community (Oberdorfer 1977) and is indicative of the shift away from *Brachythecio rivularis-Cratoneuretum* communities towards small-sedge vegetation of the *Caricion davallianae*.

Group 5 *Schoenus nigricans* Springs

Schoenus nigricans is conspicuously dominant in Group 5 vegetation, colonising unshaded springs on level ground, typically with strongly-formed paludal tufa (Fig. 6). Graminoids and bryophytes cover the surface in equal measure, often forming a hummock-hollow pattern. *Campylium stellatum* is the most abundant bryophyte (mean cover 22%). *Scorpidium cossonii* and *S. scorpioides* are frequent, sometimes with high cover values, up to 50% and 65% respectively – the latter species is especially typical of shallow pools. *Ctenidium molluscum* is constant but seldom occupies large areas (mean cover 4%); it typically occurs in drier places, e.g. on the tops of hummocks. *Molinia caerulea* is frequent, but with mean cover only 9%. All of the above-named species are highly significant indicators of this group (ISA***). This is a cohesive group, with a high mean silhouette width (0.17, Table 1).

The flora is relatively diverse, with 21.7 species per relevé on average. *Palustriella commutata* and *P. falcata* each occur in approximately half the samples (mean cover values 8% and 1% respectively). *S. nigricans*, *M. caerulea*, *Festuca rubra*, *Carex panicea* and *C. lepidocarpa* are frequent in the graminoid layer. Forbs and other non-graminoid vascular plants make a small contribution: the most frequent are *Selaginella selaginoides, Pinguicula vulgaris, Anagallis tenella, Potentilla erecta* and *Succisa pratensis*, with occasional *Pinguicula lusitanica, Cirsium dissectum, Potamogeton coloratus, Samolus valerandi* and *Dactylorhiza fuchsii*. Two calcifuge species, *Calluna vulgaris* and *Drosera rotundifolia*, are present infrequently; they colonise microhabitats (such as hummock tops) which have least contact with the calcareous spring water.

Paludal tufa is at its most abundant in this group (Fig. 1) and is often heavily precipitated, forming a conspicuous white, crunchy layer on the ground surface. Cascade tufa is absent. Tufa covers 63% of the ground surface on average, but the degree of tufa formation is highly variable. Two samples which are highly characteristic of this group (both with MC 100%) are almost devoid of tufa, yet in other characteristic samples (also MC 100%) the surface consists almost entirely of strongly precipitated paludal tufa. These springs nearly always occur on level ground. The mean slope is 5°, joint lowest with Group 6.

Fig. 6. Group 5 *Schoenus nigricans* Springs at Corhawnagh, Co. Sligo (Sept. 2012). *S. nigricans* is dominant, strongly-formed paludal tufa is conspicuous and the 'brown moss' underlayer contains *Palustriella commutata, P. falcata, Campylium stellatum*, *Scorpidium cossonii* and *Ctenidium molluscum*.

Fig. 8. Group 7 *Palustriella falcata-Carex panicea* Springs on Moneen Mtn, Burren, Co. Clare (detail of 2x2m quadrat, May 2012). Spring water deposits thin, stream crust tufa on limestone pavement. *C. panicea* and *Pinguicula grandiflora* grow amongst a mat of *P. falcata* (centre, foreground).

Fig. 7. Group 6 *Carex lepidocarpa* Small-sedge Springs at Louisa Bridge, Co. Kildare (Oct. 2010). The mixed sward includes *C. lepidocarpa, Molinia caerulea* and *Juncus inflexus*. Paludal tufa (intermediate in strength) forms amongst the bryophytes – *Palustriella commutata* is the dominant species. Forbs include *Anagallis tenella* and *Parnassia palustris*.

Fig. 9. Group 8 *Saxifraga aizoides-Seligeria oelandica* Springs near Eagle's Rock, Benbulbin Range, Co. Leitrim (July 2013). *S. aizoides* and the red pleurocarp, *Orthothecium rufescens* (centre), grow on flushed cliff faces. Thin stream crust tufa forms on rock surfaces, amongst which the tiny moss *S. oelandica* grows.

Pools are characteristic, occupying, on average, 19% of ground surface, the highest mean cover by pools. Conversely, trickling water is at its lowest in this group. All sites are open, lacking any woody canopy cover.

This group conforms to the alkaline fen association *Schoenetum nigricantis* (Allorge 1922) Koch 1926 in the alliance *Caricion davallianae* Klika 1934 *(Ó Críodáin & Doyle 1997; Rodwell 1998b; Hájek & Hájková 2011b; Jiménez-Alfaro et al. 2014)*. Group 5 vegetation lies at the calcicole extreme of this association, with a well-developed 'brown moss' layer and an abundance of base-rich indicator species, such as *Campylium stellatum, Scorpidium cossonii* and *Selaginella selaginoides.* Group 5 stands correspond to 'short-fen' vegetation indicative of main seepage tracks which feed into taller fen vegetation (Boyer & Wheeler 1989). Taller graminoids, such as *Juncus subnodulosus* and *Phragmites australis*, are infrequent and never dominate the vegetation.

Group 6 *Carex lepidocarpa* Small Sedge Springs

The vegetation in this group consists of a sward of small sedges with a 'brown moss' underlayer. *Carex lepidocarpa* is often conspicuous amongst the sedges and *Palustriella commutata* and *Calliergonella cuspidata* are the dominant bryophyte species (Fig. 7). Samples have high species diversity and are, on the whole, only weakly tufaceous. *Succisa pratensis, C. lepidocarpa* and *Calliergonella cuspidata* are constant and highly significant indicators (ISA ***). *Anagallis tenella, Triglochin palustris, Pedicularis palustris, Mentha aquatica, Festuca rubra, Carex panicea, C. flacca, Eriophorum angustifolium, Juncus articulatus, Equisetum palustre* and *Bryum pseudotriquetrum* are also characteristic (constant and/or significant indicators, $p < 0.01$). Species composition is more diverse than in Groups 1 to 5 (mean 26.8 species per relevé). Overall, graminoids and bryophytes provide similar levels of cover (means of 60% and 69% respectively). Bryophytes can be locally dominant with few sedges or, conversely – in the absence of grazing – sedges and rushes can dominate, reducing bryophyte cover and diversity.

Paludal tufa – mostly of intermediate strength – is the dominant form in *Carex lepidocarpa* Small Sedge Springs, occupying on average 51% of ground surface (Fig. 1). Overall, tufa cover is lowest in this group (only 55% of ground surface on average is tufa-covered); four samples (13%, with MCs 35%–93%) are almost entirely devoid of tufa. Group 6 samples are located, for the most part, on level ground and, jointly with Group 5, have the lowest mean slope (5°). Shallow, almost static pools of water are characteristic on these level sites, occupying 11% of surface area on average. Canopy cover is absent in all but one (lightly shaded) sample. Cohesion of the group is intermediate (mean silhouette width 0.09, Table 1). With 30 samples, this is the best-represented group in our survey.

Group 6 consists of small-sedge *Caricion davallianae* vegetation equivalent to the British M10 *Carex dioica-Pinguicula vulgaris* Mire and the mainland European *Carici flavae-Cratoneuretum filicini* Kovács et Felföldy 1960 (Rodwell 1998b; Hájek & Hájková 2011a). *Carex davalliana* is absent from Ireland, and *Carex flava* agg. is represented in Group 6 by *C. lepidocarpa* (ISA ***), the most strongly calcicole member of the *C. flava* group. Group 6 is also the group that comes closest to M38 *Cratoneuron commutatum-Carex nigra* Springs (SCS 49%, Lyons 2015), but the prevalence of species such as *Carex nigra, C. demissa* and *Philonotis fontana* in that community suggest that it is less strongly calcicole than Group 6. Group 6 (like Group 5) is indicative of localised areas of intense seepage which, at many sites, irrigate larger expanses of less species-rich wetland vegetation (Boyer & Wheeler 1989).

Group 7 *Palustriella falcata-Carex panicea* Springs

This group is dominated by *Palustriella falcata,* which is accompanied by small sedges, most notably *Carex panicea*. The group occurs on level or gently sloping, unshaded sites and typically forms paludal tufa of intermediate strength. Bryophytes occupy almost twice as much of the ground surface as graminoids. Cover values of *P. falcata* greatly exceed those of all other species (mean cover 23%). *Palustriella commutata* is frequent but never abundant (mean cover 4%). *Philonotis calcarea* (ISA**), *Bryum pseudotriquetrum, Calliergonella cuspidata* and *Aneura pinguis* are frequent, while *Campylium stellatum, Ctenidium molluscum, Breutelia chrysocoma, Cratoneuron filicinum, Fissidens adianthoides, Jungermannia atrovirens* and *Pellia endiviifolia* occur occasionally, sometimes with high cover values. The rare moss, *Catoscopium nigritum* (on the candidate Red List for European bryophytes, Hodgetts 2015), was found in one sample.

Graminoids comprise a diverse mix: *Carex panicea, C. lepidocarpa* and *C. flacca* are constant (mean cover 6%, 5% and 4% respectively). Other graminoids include *Briza media* (ISA**), *Agrostis stolonifera, Festuca rubra, Juncus articulatus* and *Eriophorum angustifolium* (mean cover ≤ 2%). Forbs are infrequent: they include the rare species *Pinguicula grandiflora* (ISA***, Fig. 8), also *P. vulgaris*, *P. lusitanica, Anagallis tenella, Parnassia palustris, Samolus valerandi, Potamogeton coloratus, Polygala vulgaris, Leontodon saxatilis, Linum catharticum, Bellis perennis* and *Prunella vulgaris* (mean cover of each ≤ 2%). Species diversity in this group is relatively high (mean 22.1 species per relevé) and the group is moderately cohesive (mean silhouette width 0.08, Table 1).

Bare, unvegetated ground is characteristic of Group 7 (45% of surface area on average, comparable only to Group 8, 44%). Forty percent of samples are from the ecologically distinctive Burren region of Co. Clare (Fig. 8), at sites where spring water issues over karst limestone pavement, forming thin, unvegetated, stream crust tufa, and species-rich vegetation is confined to pockets of soil in grykes. Across Group 7 as a whole, paludal tufa is the most abundant form (mean cover 35%, usually of intermediate strength, Fig. 1). Cascade tufa is occasionally present. Overall tufa cover is low (mean 66%); one sample contained only a faint trace of tufa even though its vegetation was highly characteristic of the group (MC 90%). Trickling water is plentiful, occupying 16% of the ground surface on average; small pools occupied 11% on average. All samples are unshaded, on level to gently sloping ground (mean slope 12°).

Group 7 is similar to Group 6 in many respects; the most significant floristic difference lies in the relative proportions of *Palustriella falcata* and *P. commutata*. The two groups are also separated biogeographically in Ireland: Group 7 has a westerly distribution, (best represented in the Burren, Co. Clare and in the Benbulbin Range, Counties Sligo and Leitrim) while Group 6 is most frequent on the plains of the midlands and east of the country. Like Group 6, Group 7 has affinities with the British NVC communities M10 *Carex dioica-Pinguicula vulgaris* Mires and M38 *Cratoneuron commutatum-Carex nigra* Springs (Rodwell 1998b). *Carex panicea* and *Bryum pseudotriquetrum* are constant in all three communities and there is a broad overlap in general species composition. As noted above, data for *Palustriella falcata* are lacking for the NVC communities, the taxon not being considered specifically distinct. However, again, M10 and M38 vegetation are both less calcicole in character than Group 7. Group 7 falls within the *Cratoneuretum falcati* Gams 1927 in the constancy and dominance of *Palustriella falcata*, although lacking the alpine specialists of that community.

Group 8 *Saxifraga aizoides-Seligeria oelandica* Springs

This community is exceptionally species-rich, and is characterised by the presence of *Saxifraga aizoides* and a suite of rare bryophyte species (Fig. 9). It is best exemplified on montane cliffs of the Benbulbin Range in the north-west of Ireland. *Saxifraga aizoides* (rare in Ireland, confined to uplands of the north-west and one coastal location in the north-east) and *Festuca rubra* are constant, very highly significant indicators of the group (ISA***). The rare bryophytes *Seligeria oelandica, S. patula, Hymenostylium recurvirostrum* var. *insigne* and *Orthothecium rufescens* are frequent and characteristic components (ISA***). Bryophytes occupy the greatest proportion of the vegetated area, but their cover is almost matched by graminoids, while forbs amount to only one-third of the area of bryophyte cover.

Seligeria oelandica colonises steep, flushed rock surfaces. It has a very limited biogeographical range in Ireland (confined to the north-west, in Counties Sligo, Leitrim and Fermanagh, Lockhart et al. 2012). It has only a single station in Britain (Bosanquet & Motley 2009) and is 'Vulnerable' throughout continental Europe (Hodgetts 2015). *Seligeria patula* often grows in close proximity to *S. oelandica*. It is endemic to Europe and is assessed as 'Vulnerable' throughout most of continental Europe (Hodgetts 2015). *Hymenostylium recurvirostrum* var. *insigne* is restricted in Ireland to spring-irrigated cliffs in the Benbulbin Range and its status is 'Near Threatened'. It is rare in Europe, occurring also in NW Scotland and Spain. Irish specimens are distinct from var. *recurvirostrum,* but plants with intermediate morphological characteristics have been found in Scotland and Canada (Lockhart et al. 2012). The pleurocarp *Orthothecium rufescens* is 'Near Threatened' in Ireland (Lockhart et al. 2012) but common in parts of the Scottish Highlands on base-rich ground (Porley & Hodgetts 2005).

These rare species are accompanied by a diverse range of more familiar plants. *Sesleria caerulea*, *Carex flacca*, *Palustriella commutata*, *Breutelia chrysocoma*, *Bryum pseudotriquetrum*, *Jungermannia atrovirens*, *Pellia endiviifolia* and *Aneura pinguis* are constant. Other frequent associates include *Parnassia palustris, Pinguicula vulgaris, Succisa pratensis, Bellis perennis, Prunella vulgaris, Campanula rotundifolia, Fissidens adianthoides* and *Palustriella falcata*. One non-native species, *Epilobium brunnescens*, is present in small amounts (constancy class II, mean cover 0.1%). Group 8 has the greatest diversity of species (33.8 species per sample on average), and the highest number of statistically significant indicator species. This group is one of the most strongly cohesive (mean silhouette width 0.17, Table 1). It is the smallest group, with just 13 samples from eight sites.

Group 8 occurs on sparsely vegetated montane cliffs (mean altitude 243 m); on average, 50% of the surface area is unvegetated, consisting of bare tufa and rocky outcrops. Stream crust tufa is predominant and is much more prevalent here than in any other group (mean cover 33%, Fig. 1). This tufa is here mostly devoid of vascular plants and bryophytes, but almost always associated with a thin algal film. Overall, tufa occupies only 60% of ground surface. Bare rock covers 13% of the surface area, second only to Group 7. Sites are steeply inclined, with a mean slope of 53°, second only to Group 1. Most of the ground surface is damp (74%). Dripping water irrigates 12% of the surface area and trickling water 8% on average. One sample was recorded at a waterfall (MC 89%). Canopy cover is almost entirely absent but the northerly aspect of most samples (85% of samples) moderates summer temperature and insolation.

The constancy of *Saxifraga aizoides* links this group to a number of described communities. The strongest affinities are with British *Saxifragetum aizoidis* communities, represented in the NVC classification by U15 *Saxifraga aizoides-Alchemilla glabra* Banks (Rodwell 1998c; Group 8 and U15 have SCS 46%, compared to 39% for M37 Springs, Lyons 2015). *S. aizoides* and *Festuca rubra* are constant in both Group 8 and the U15 community, and there is a broad overlap in species composition. However, apart from *Orthothecium rufescens*, the Group 8 rare bryophytes were not recorded in the British communities. *S. oelandica* is unknown within the biogeographical range of U15 samples in Britain, although ranges of *S. patula* and *Hymenostylium recurvirostrum* var. *insigne* potentially overlap with that community. *Seligeria oelandica* and *Saxifraga aizoides* were jointly recorded in a high-altitude community in Norway (Coker 1983), but there were few other species in common with Group 8. *Saxifraga aizoides* and *Palustriella falcata* are indicative of the Alpine *Cratoneuretum falcati* community (e.g. Koch 1928; Braun-Blanquet 1949, 1978), although the character taxon of that community, *Arabis soyeri* ssp. *subcoriacea,* is absent from Ireland.

Relationships among groups

Multi-level pattern analysis yielded 123 species significantly linked to a group or set of groups (compared to 108 species found by ISA to be significantly linked to a single group); these are summarised in Table 2 (see Electronic Supplement 2 for full synoptic table). Of the five most frequent species of Irish petrifying springs, *Palustriella commutata* and *Agrostis stolonifera* are constant across nearly all groups. *Festuca rubra* and *Carex flacca* are more abundant in the graminoid-rich Groups 4 to 8, while *Pellia endiviifolia* is most abundant in the steeply-sloping Groups 1 to 3 and Group 8. The remaining species in Table 2 illustrate the contrast between Groups 1 to 3 and Groups 5 to 7, also the intermediate position of Group 4. Groups 1 to 3 (*Brachythecio rivularis-Crato-*

Table 2. Synoptic table showing per cent frequencies of selected species, with Indicator Species Analysis (ISA; significant values shown by superscripts) and Multi-level Pattern Analysis (MPA; significant values within groups shown by shaded cells; significant values for 'All Groups' shown by superscripts). Species present in ≥ 40% of samples are listed at top of table; remainder are sorted by group. See Electronic Supplement 2 for full synoptic table.

	Gr. 1	Gr. 2	Gr. 3	Gr. 4	Gr. 5	Gr. 6	Gr. 7	Gr. 8	All Groups
	% ISA	% ISA	% ISA	% ISA	% ISA	% ISA	% ISA	% ISA	% MPA
Palustriella commutata	78	100 ***	66	96	45	73	60	69	75
Agrostis stolonifera	61	58	83	96 **	23	53	65	92	66 ***
Festuca rubra	50	12	10	89	45	83	60	100 ***	54 ***
Carex flacca	11	15	14	79	36	80	90	92 **	51 ***
Pellia endiviifolia	61 **	62	48	29	14	23	20	85	40 ***
Eucladium verticillatum	100 ***	50	10	11	9	3	.	15	23 ***
Didymodon tophaceus	56 ***	23	10	21	5	3	.	23	16 **
Rubus fruticosus	11	50 ***	21	7	.	.	.	.	12 ***
Geranium robertianum	22	77 ***	52	25	.	.	.	.	25 ***
Equisetum telmateia	.	42 *	34	32	.	7	10	.	18 ***
Carex remota	.	38 **	21	4	.	.	.	.	9 ***
Brachythecium rivulare	11	35	83 ***	36	5	10	.	.	26 ***
Platyhypnidium riparioides	.	4	28 ***	.	.	.	.	.	5 ***
Cratoneuron filicinum	17	31	69 *	43	.	37	10	38	33 **
Filipendula ulmaria	.	31	21	43 **	5	10	.	31	18 **
Schoenus nigricans	6	.	.	14	95 ***	30	20	.	21 ***
Campylium stellatum	.	.	.	14	86 ***	60	30	.	25 ***
Selaginella selaginoides	6	.	.	.	45 **	13	30	31	13 ***
Scorpidium cossonii	.	.	.	4	45 ***	33	5	.	12 ***
Scorpidium scorpioides	.	.	.	.	41 ***	.	5	.	5 ***
Ctenidium molluscum	.	4	.	7	68 ***	27	30	62	22 ***
Molinia caerulea	11	.	.	11	68 ***	60	35	15	25 ***
Carex lepidocarpa	6	.	.	36	55	80 ***	95	38	38 ***
Mentha aquatica	6	15	41	46	23	63 **	30	.	32 ***
Anagallis tenella	6	.	.	7	41	57 ***	40	.	20 ***
Eriophorum angustifolium	.	.	.	7	23	50 **	20	15	15 ***
Eleocharis quinqueflora	.	.	.	.	32	33	20	.	11 ***
Pedicularis palustris	.	.	.	.	5	23 ***	.	.	4 ***
Juncus subnodulosus	.	.	.	11	27	23 *	5	.	9 ***
Succisa pratensis	6	.	.	11	41	87 ***	60	46	31 ***
Calliergonella cuspidata	.	15	3	68	32	80 ***	50	62	39 **
Juncus articulatus	.	15	3	68	27	70 **	65	69	39 ***
Bryum pseudotriquetrum	11	4	17	54	23	70 *	65	62	38 ***
Palustriella falcata	11	.	.	11	41	30	90 ***	54	26 ***
Carex panicea	6	.	.	25	59	83	85 ***	31	36 ***
Philonotis calcarea	6	.	.	18	23	33	50 **	31	19 ***
Pinguicula grandiflora	.	.	.	.	.	.	25 ***	.	3 ***
Saxifraga aizoides	.	.	.	4	.	.	5	85 ***	7 ***

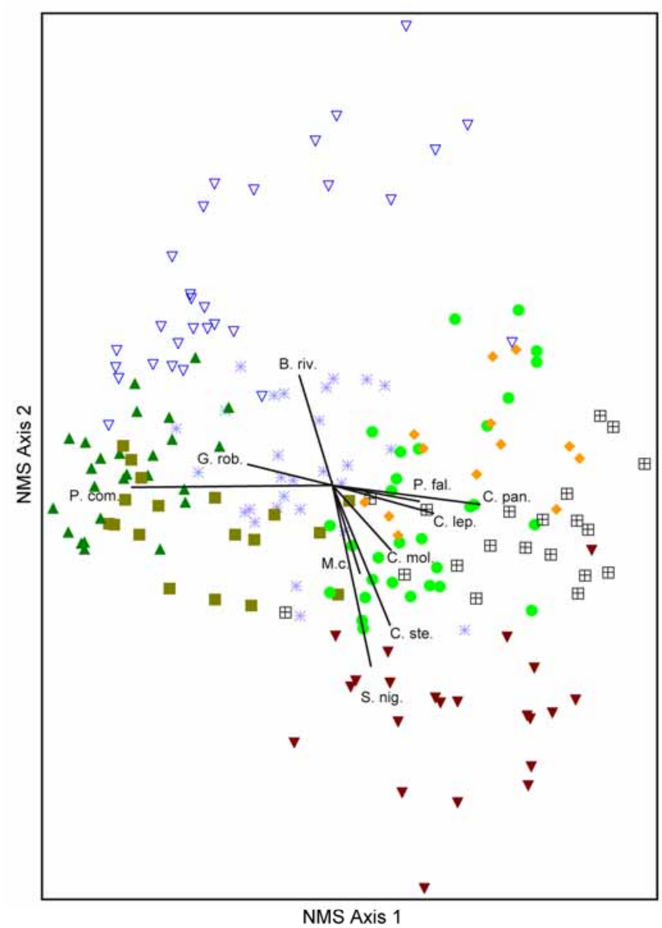
Table 2. cont.

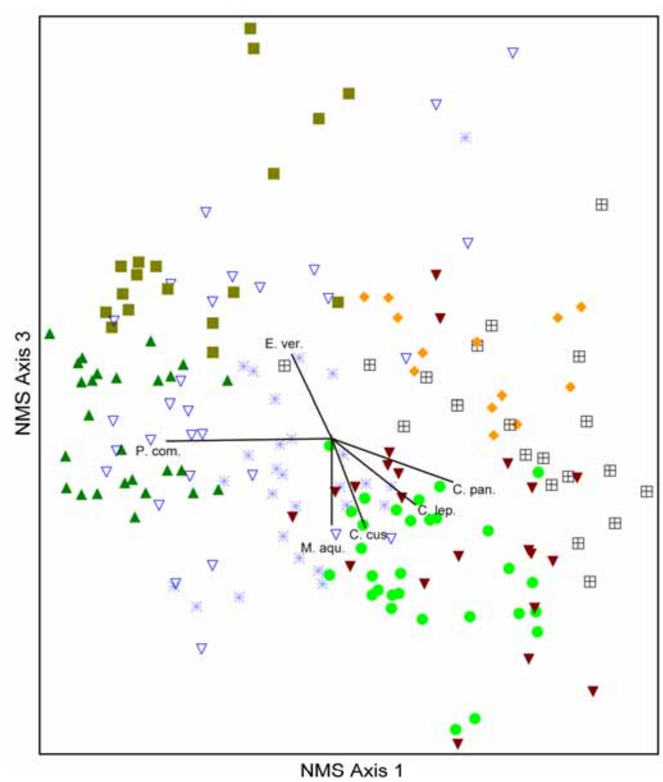
	Gr. 1	Gr. 2	Gr. 3	Gr. 4	Gr. 5	Gr. 6	Gr. 7	Gr. 8	All Groups
	% ISA	% ISA	% ISA	% ISA	% ISA	% ISA	% ISA	% ISA	% MPA
Jungermannia atrovirens	.	8	.	7	9	.	15	77 ***	10 ***
Aneura pinguis	11	4	.	14	55	47	55	77 ***	29 ***
Sesleria caerulea	11	4	.	4	14	3	10	69 ***	10 ***
Breutelia chrysocoma	6	.	.	4	23	7	35	62 *	13 ***
Pinguicula vulgaris	6	.	.	7	41	37	25	54 *	19 ***
Orthothecium rufescens	.	.	.	.	5	.	.	54 ***	4 ***
Seligeria oelandica	6	.	.	.	9	.	5	46 ***	5 ***
Bellis perennis	.	4	.	4	.	10	15	46 ***	8 ***
Parnassia palustris	.	.	.	.	9	30	25	46 **	12 ***
Seligeria patula	6	.	.	.	.	.	.	46 ***	4 ***
Campanula rotundifolia	.	.	.	4	.	.	.	46 ***	4 ***
Hymenostylium recurvirostrum var. *insigne*	.	4	.	.	.	.	.	46 ***	4 ***
Hymenostylium recurvirostrum var. *recurvirostrum*	6	4	.	.	5	.	5	31 ***	4 ***
Alchemilla glabra	.	4	.	.	.	.	.	31 ***	3 ***
Epilobium brunnescens	.	4	3	.	.	.	.	23 **	3 ***

neuretum communities) are characterised by the bryophytes *Eucladium verticillatum, Brachythecium rivulare, Cratoneuron filicinum, Didymodon tophaceus* and *Platyhypnidium riparioides*. In contrast, *Succisa pratensis, Anagallis tenella, Pinguicula vulgaris, Parnassia palustris, Carex lepidocarpa, C. panicea, Schoenus nigricans, Eriophorum angustifolium, Eleocharis quinqueflora, Selaginella selaginoides* and the bryophytes *Campylium stellatum, Palustriella falcata, Philonotis calcarea, Scorpidium cossonii, S. scorpioides* and *Aneura pinguis* are characteristic of Groups 5 to 7 (*Caricion davallianae*-related groups). Group 8 stands apart in having the greatest number of unique significant indicator species.

NMS of relevé data recommended a 3-dimensional ordination (representing 78.7% of total variance; final stress 16.34 (p = 0.004); final instability < 0.00001, Fig. 10). Group 4 occupies a central position, with Groups 1 to 3 opposed to Groups 5 to 7. Group 8 is, on the whole, more closely aligned with the unshaded, fen-type vegetation of Groups 5 to 7, but the vegetation is also influenced by the steep slopes on which it occurs, and in this respect it comes closer to Groups 1 to 3. *Palustriella commutata, Eucladium verticillatum, Brachythecium rivulare* and *Geranium robertianum* are most strongly associated with Groups 1 to 3; *Schoenus nigricans, Carex lepidocarpa, C. panicea, Molinia caerulea, Mentha aquatica, Campylium stellatum, Palustriella falcata, Ctenidium molluscum* and *Calliergonella cuspidata* are closely associated with Groups 5 to 8 (Fig. 10, Pearson correlation coefficients calculated in PC-ORD). Spearman rank correlation coefficients (r_s, not available in PC-ORD, but more statistically appropriate than Pearson correlation coefficients) were calculated separately for environmental variables (Electronic Supplement 3 (c)). Axis 1 (which represents the greatest amount of variance, r^2 = 0.303) is most strongly correlated with decreasing tree canopy cover (r_s = -0.685), decreasing cascade tufa (r_s = -0.530) and increasing species numbers (r_s = 0.521). Most wooded sites were located on hillsides, an artefact of anthropogenic influences, and species diversity was lower at wooded sites than in unshaded springs. We surmise that the combination of low light levels and extreme edaphic conditions makes for an environment to which few plants can adapt. Slope and cascade tufa are significantly opposed to paludal tufa on all three axes. Increasing slope is most strongly associated with Axis 3 (r_s = 0.753). Axis 2 is most strongly correlated with increasing phosphate levels (r_s = 0.530; water chemistry is discussed further below).

Two or more of the communities described sometimes occur in combination along ecological gradients within spring complexes. The most evident sequences are found on wooded hillsides: they consist of either Group 1 *Eucladium verticillatum-Pellia endiviifolia* Tufa Cascades





Species abbreviations:

B. riv. = *Brachythecium rivulare*
C. cus = *Calliergonella cuspidata*
C. lep. = *Carex lepidocarpa*
C. mol = *Ctenidium molluscum*
C. pan. = *Carex panicea*
C. ste. = *Campylium stellatum*
E. ver. = *Eucladium verticillatum*
G. rob. = *Geranium robertianum*
M. aqu. = *Mentha aquatica*
M.c. = *Molinia caerulea*
P. com = *Palustriella commutata*
P. fal = *Palustriella falcata*
S. nig. = *Schoenus nigricans*

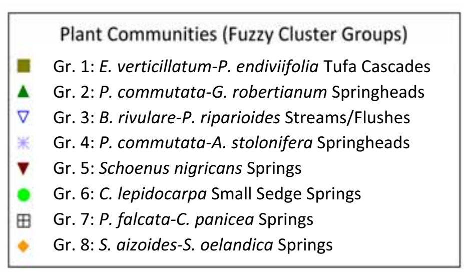


Fig. 10. Non-metric Multidimensional Scaling (NMS) ordination of relevés (n = 186) showing plant communities and strongly correlated plant species ($r^2 > 0.2$). Variance (r^2) represented by Axis 1 = 0.303, Axis 2 = 0.268 and Axis 3 = 0.216.

(on steep slopes) or Group 2 *Palustriella commutata-Geranium robertianum* Springheads (on moderate slopes) giving way below to Group 3 *Brachythecium rivulare-Platyhypnidium riparioides* Tufaceous Streams and Flushes. Often, the springhead vegetation occupies only a few square metres while the flush below extends over tens or even hundreds of square metres. The Group 3 community sometimes forms in the absence of a separate springhead community, but such instances often occur in settings which have been modified by anthropogenic activities, resulting in depauperate variants of the vegetation. Group 4 *Palustriella commutata-Agrostis stolonifera* Springheads are associated with Group 6 *Carex lepidocarpa* Small Sedge Springs at four separate sites studied; the former community occurs at discrete areas of upwelling ground water and the latter colonises a more dispersed seepage zone from which the spring water dissipates. Occasionally, in the Burren, discrete Group 7 *Palustriella falcata-Carex panicea* Springs flow out over limestone pavement, flanked by diffuse Group 5 *Schoenus nigricans* Springs.

In twelve relevés (6%), only a trace of tufa was found, sparsely deposited on the stems of plants or on the ground surface. These samples are not confined to a single community, but distributed across Groups 4 to 8. Several of them have high membership coefficients – eight samples (67%) have MC > 80% – indicating that their floristic composition is very similar to the other (more strongly tufa-forming) members of their respective groups.

Water chemistry

Analysis of Irish petrifying spring water shows that there is considerable variation in chemical composition but all samples have high pH values and high alkalinity and calcium concentrations compared to most naturally occurring waters (Table 3). On the whole, pH and alkalinity levels are slightly higher, while calcium, magnesium and potassium concentrations are slightly lower in Irish petrifying springs compared to data reported in other studies of this habitat (Pentecost 1999; Pentecost & Zhaohui 2002; Hájek et al. 2002; Keppel et al. 2011; Arenas et al. 2014). Sodium and chloride levels are very variable, in part due to the coastal influence at many sites, but the highest levels, both in Ireland and elsewhere, are usually associated with deep artesian (inland) springs (Pentecost 1999; Kuczynska & Bartley 2008; Keppel et al. 2011). Nitrate levels in Irish petrifying springs are comparable to levels elsewhere, but phosphate levels are lower and sulphate levels are especially low (e.g. Pentecost 2005; Arenas et al. 2014). Outlying values recorded in some Irish petrifying springs coincide with some of the more atypical manifestations of the habitat, in terms of both tufa type and vegetation composition. An exceptionally high pH value (11.38) was recorded at one unusual tufa cascade on the coast in Co. Clare; the tufa was almost entirely devoid of plants and the surface consisted of a 'honeycomb' pattern not seen elsewhere during our study (Electronic Supplement 4 (d)). The cause of this extreme pH value is unknown.

MRPP indicated that there are statistically significant differences in the composition of the spring waters of different plant communities ($A = 0.1749$, $p < 0.001$). Pairwise comparisons showed that the chemical composition of spring water in Group 8 *Saxifraga aizoides-Seligeria oelandica* Springs is highly significantly different to that of all other groups except Group 7 *Palustriella falcata-Carex panicea* Springs ($p < 0.01$ with Dunn-Šidák correction for multiple comparisons; Electronic Supplement 3 (b)). Compared to other groups, the spring water of

Table 3. Chemical composition of Irish petrifying spring waters (n = 115; extreme outliers excluded from means, standard deviations and medians; [a]geometric mean; [b]unexplained; [c]associated with road drainage waters; [d]inland artesian spring influence; [e]coastal site, probable evaporation; [f]unknown nutrient source; [g]golf course; [h]tufa being eroded).

Parameter		Mean (SD)	Median	Range	Outlying Values
pH		7.88[a]	7.97	7.00–8.47	11.38[b]
HCO_3^-	mg/l	293.7 (93.0)	292.8	109.1–644.2	
Ca^{2+}	mg/l	87.80 (29.10)	84.50	19.08–181.22	
Mg^{2+}	mg/l	10.11 (7.91)	8.15	0.22–30.56	
K^+	mg/l	1.75 (2.30)	0.91	0.14–10.40	22.97[c]
Na^+	mg/l	15.52 (15.27)	8.97	5.10–82.31	209.42[d], 210.92[d], 225.38[d], 265.88[e]
Cl^-	mg/l	24.16 (24.77)	14.61	6.98–131.89	258.54[e], 410.22[d], 413.89[d], 423.13[d],
NO_3^-	mg/l	5.09 (8.78)	1.56	< 0.07–44.05	64.70[f]
PO_4^{3-}	μg/l	16 (19)	13	2–140	991[g]
SO_4^{2-}	mg/l	14.27 (16.09)	8.28	< 0.06–96.25	142.22[c,h], 146.88[c,h]

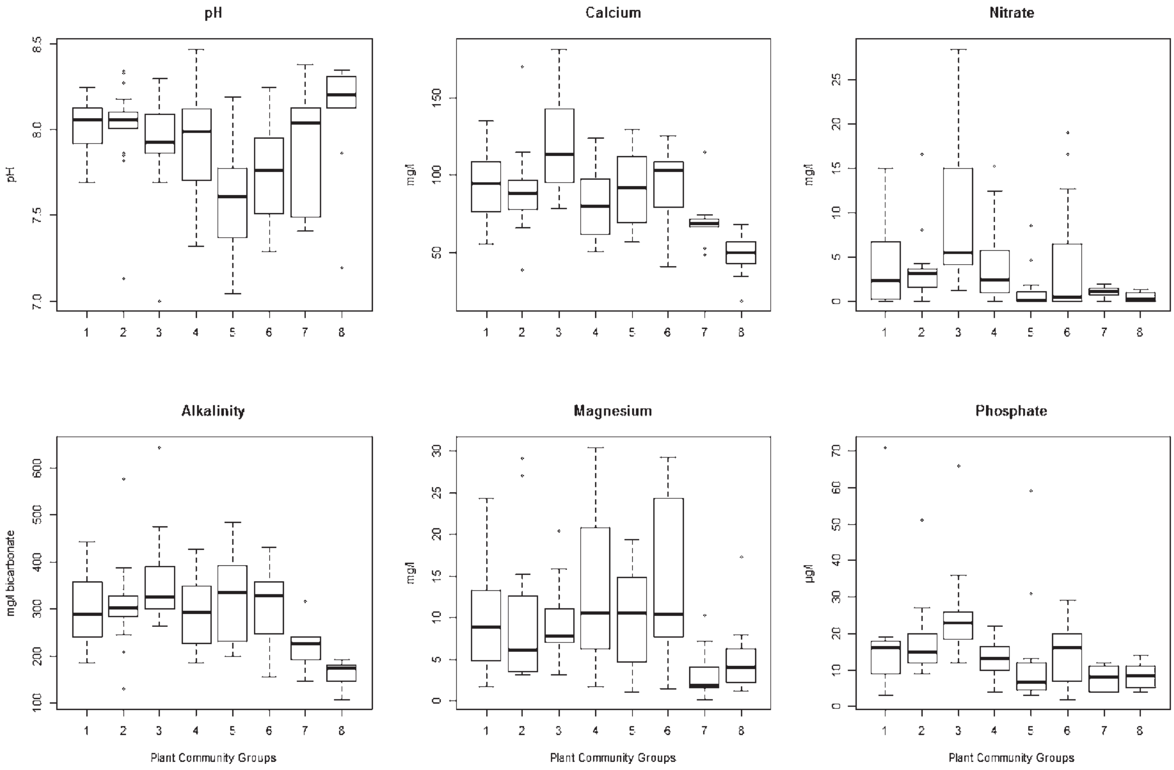


Fig. 11. Comparison of chemical composition of spring waters in plant communities (Groups 1 to 8) for pH, alkalinity, calcium, magnesium, nitrate and phosphate. Ten extreme outlying values were omitted for clarity of diagrams: pH Gr. 7 (11.38); Nitrate Gr. 1 (36 mg/l, 44 mg/l), Gr. 3 (46 mg/l), Gr. 4 (33 mg/l, 34 mg/l) Gr. 6 (65 mg/l); Phosphate Gr. 3 (115 µg/l, 140 µg/l, 991 µg/l).

Group 8 has high pH values and low concentrations of solutes (Fig. 11). The lowest pH values were recorded in Group 5 *Schoenus nigricans* Springs and Group 6 *Carex lepidocarpa* Small Sedge Springs (geometric means of 7.50 and 7.64 respectively). These two groups have relatively high alkalinity levels. Groups 1 to 4, the most strongly tufa-forming communities, have high pH values along with moderate to high alkalinity and calcium levels compared to other groups; they also contain somewhat higher levels of the macronutrients nitrate, phosphate and potassium. Phosphate levels were inversely related to species diversity ($r_s = -0.321$, $p < 0.001$; Lyons 2015). The highest phosphate concentrations occurred in Group 3 (Fig. 11).

Detailed data on the chemical composition of the spring waters irrigating plant communities are scanty, but the available data indicate that our communities are from waters of higher pH and calcium concentrations than closely related communities studied elsewhere (Table 4). Thus, Groups 4 and 8 have significantly higher pH and calcium levels than M37 *Cratoneuron commutatum-Festuca rubra* Springs, and the same is true of Groups 6 and 7 compared to M10 *Carex dioica-Pinguicula vulgaris* Mires ($p < 0.01$). Spring waters in Group 5 have pH and calcium levels which lie in the upper half of the range for those of Irish *Schoenetum nigricantis* communities.

Discussion

Irish petrifying springs have been shown to encompass a wide range of habitat and vegetation types. Slope exerts a dominant effect on community formation, influencing the rate of water movement and aeration, and the form of tufa deposition (notably cascade versus paludal tufa). The shading effect of tree canopy cover is also significant, and is inversely related to ground flora species diversity. Spring water composition, whilst highly distinctive for the habitat type as a whole, is less clearly differentiated amongst groups. Nevertheless, water composition in Group 8 is distinctive and the rare bryophytes characteristic of this group are confined to waters with high pH and very low concentrations of solutes.

Elevated macronutrient levels (especially phosphates) are significantly correlated with one of the main axes of variation (Axis 2) within the vegetation of the habitat as a whole, and phosphate concentrations are inversely related to species diversity. Tufa-forming short-fen vegetation is phosphate-limited (Boyer & Wheeler 1989; Rozbrojová & Hájek 2008; Pawlikowski et al. 2013). On the whole, the spring waters of our species-rich Groups 5–8 (*Caricion davallianae* and *Cratoneuretum falcati* communities) contained very low phosphate levels, while Groups 1–3 (*Brachythecio rivularis-Cratoneuretum*

Table 4. Comparison of pH and calcium concentrations (mean (range)) between published communities and Irish petrifying spring communities. M-W U = Mann Whitney U test; a, b, c, x and y represent statistically significant differences. M37 *Cratoneuron commutatum-Festuca rubra* Spring samples are from the *Cratoneuron commutatum-Saxifraga aizoides* nodum (McVean & Ratcliffe 1962 (n = 3) and Birks 1973 (n = 4)). M10 *Carex dioica-Pinguicula vulgaris* mire samples are from the *Eriophorum latifolium-Carex hostiana* Association (n = 6) and *Carex panicea-Campylium stellatum* Association (n = 6) (Birks 1973). *S. nig.* = *Schoenetum nigricantis* (Ó Críodáin & Doyle 1997). [g] geometric mean; [m] median value; nd = no data. Outlying pH 11.38 omitted from Gr. 7 data.

	pH	M-W U $p < 0.01$	Ca^{2+} (mg/l)	M-W U $p < 0.01$	n
M37	7.2[g] (6.8–7.4)	a	21 (8–49)	a	7
Gr. 4	7.8[g] (7.3–8.5)	b	83 (51–124)	b	15
Gr. 8	7.9[g] (7.2–8.4)	b	48 (19–68)	c	10
M10	6.3[g] (5.6–7.2)	x	6 (2–15)	x	12
Gr. 6	7.6[g] (7.3–8.3)	y	91 (41–126)	y	17
Gr. 7	7.9[g] (7.4–8.4)	y	71 (49–115)	y	9
S. nig.	6.0[m] (5.0–8.1)	nd	nd	nd	22
Gr. 5	7.6[m] (7.0–8.2)		92 (57–129)		12

communities) tolerated higher phosphate levels. There was no evidence of high phosphate levels impeding tufa formation.

Group 8 *Saxifraga aizoides-Seligeria oelandica* Springs stands apart from the other seven groups in its floristic composition. The proportion of species which are rare, some in a European or even worldwide context, makes this a community of exceptionally high conservation value. In Ireland, its fullest expression is confined to permanently irrigated springs, usually on north-facing cliffs of the limestone uplands of north-western Ireland (Counties Sligo, Leitrim and Fermanagh). This community, though striking in its species richness, is not strongly tufa forming, and very often there is little more than a thin layer of soft, unconsolidated tufa over part of the ground surface. In contrast, spring communities which are spectacular in their ability to form tufa typically contain few species, the extreme chemical environment being hostile to most. Such springs are best exemplified in the Group 1 *Eucladium verticillatum-Pellia endiviifolia* Tufa Cascade community; in contrast to Group 8, the thickness and extent of tufa in Group 1 provides fewer microniches.

Most characteristic of lowland Atlantic *Cratoneurion* vegetation are the two communities in which *Palustriella commutata* is dominant. Group 4 *Palustriella commutata-Agrostis stolonifera* Springheads forms the central expression of the Irish petrifying spring habitat, from which other communities depart along various ecological gradients. This community has a wide geographical distribution but is somewhat lacking in distinctive species, encompassing both springhead *Palustriella commutata*-dominated vegetation and associated flushes with increased numbers of vascular wetland generalists. The samples show a continuous gradation from springhead to flush, contributing to a low mean silhouette width for the group as a whole; further sampling might show that division into separate spring and flush communities is warranted. The woodland counterpart, Group 2 *Palustriella commutata-Geranium robertianum* Springhead community, is a more tightly defined community; associated flushes usually constitute separate Group 3 *Brachythecium rivulare-Platyhypnidium riparioides* Tufaceous Stream and Flush communities. Like Group 1, the Group 3 community is often very strongly tufa-forming but low in species diversity. The presence of several atypical, anthropogenically modified samples within this group contributes to the disparate nature of the group and its low mean silhouette width. Woodland springs are poorly represented in the NVC; our Groups 2 and 3 confirm that recognition of a separate woodland community containing *Palustriella commutata* and *Equisetum telmateia* is warranted, as speculated by Rodwell (1998a) in relation to W7 *Alnus glutinosa-Fraxinus excelsior-Lysimachia nemorum* Woodland.

The small-sedge communities – Group 5 *Schoenus nigricans* Springs, Group 6 *Carex lepidocarpa* Small-Sedge Springs and Group 7 *Palustriella falcata-Carex panicea* Springs – correspond to the alkaline extremes of *Caricion davallianae* small-sedge vegetation. We regard these communities as being indicative of the zones of most intense seepage of highly calcareous groundwater which feed the broader fen habitats, and as characterising the ecological transition between petrifying spring and fen habitat types. The aeration of water in these seepages compared to often more extensive, adjacent tall-fen habitats gives rise to higher pH values, promotes tufa precipitation and limits peat formation (Hájková et al. 2006).

The biogeographic separation in Ireland of Group 6 (eastern, lowlands) and Group 7 (western, limestone uplands of Benbulbin and The Burren) and the corresponding shift in proportions of *Palustriella commutata* and *P. falcata* mirrors the separation of the low-altitude *Cratoneuretum filicino-commutati* from the alpine *Cratoneuretum falcati* (Oberdorfer 1977). The altitudinal differences are much less between Groups 6 and 7, but the presence of alpine species close to sea-level is a characteristic feature of the Burren (Webb & Scannell 1983). The Massenerhebung effect (Grubb 1971) is a likely factor at the Benbulbin Range: its maximum elevation is only 643 m but it occupies an isolated Atlantic position.

Specialists of base-rich fen which span the major European biogeographic regions (Jiménez-Alfaro et al. 2014) are well represented in our groups, especially Groups 5 to 8. However, there are no strong links between our groups (individually or combined) and the biogeographic fen types or vegetation clusters identified by those authors. Rather, species assigned in that study to alpine, montane and lowland vegetation clusters are distributed broadly among our groups.

The NVC spring communities corresponding to the Habitats Directive priority habitat, M37 *Cratoneuron commutatum-Festuca rubra* Springs and M38 *Cratoneuron commutatum-Carex nigra* Springs, are upland communities of limited biogeographical range in the north of Britain. There is no direct counterpart amongst our Irish samples, although there are clear affinities between those two communities and our Groups 4, 6, 7 and 8. Once again, our groups are on the whole more calcicole in floristic composition and more base-rich in their spring water composition. Our most montane community, Group 8 *Saxifraga aizoides-Seligeria oelandica* Springs (which clearly constitutes an important and distinctive facies of the Habitats Directive priority habitat) has more in common with U15 *Saxifraga aizoides-Alchemilla glabra* Banks than with M37 or M38 Springs. However, the U15 community – of continuously irrigated, calcareous cliffs and banks – has not hitherto been recognised as corresponding to the priority petrifying spring habitat (Commission of the European Communities 2013). The degree of tufa formation in this habitat may warrant further investigation.

Conclusions

The eight plant communities of Irish petrifying springs, in combination, represent a robust characterisation of the priority habitat. Individually, they illustrate and explain much of the variation within the habitat, and they elucidate the ecological gradients between the *Cratoneurion* vegetation of petrifying springs and the related *Adiantion*, *Equisetum telmatejae-Fraxinetum, Schoenetum nigricantis* and *Caricion davallianae* vegetation types.

Characteristic species of the Habitats Directive priority habitat 7220 *Petrifying springs with tufa formation (*Cratoneurion*) – *Pinguicula vulgaris, Saxifraga aizoides, Palustriella commutata, P. falcata*, *Cratoneuron filicinum, Eucladium verticillatum, Hymenostylium recurvirostrum, Philonotis calcarea, S. cossonii* and *Bryum pseudotriquetrum* (Commission of the European Communities 2013) – are well represented in and broadly spread across the eight Irish groups. In fact, with the exception of Group 4, every group was allocated one or more of the above species as a statistically significant indicator by ISA ($p < 0.05$). Clearly, the priority habitat is widely distributed across Europe, with a more or less constant suite of bryophyte species. *Cratoneurion* vegetation, however, is not necessarily confined to springs and seepages – typical examples were also found in flushes, at waterfalls and along streams – nor is it always tufa-forming. We suggest that the priority habitat should be interpreted in the broad sense to accommodate such hydrogeological variation, unless and until a wider range of more clearly defined habitats are designated for conservation under European legislation.

All eight groups described are worthy of conservation; they contain highly specialised and ecologically distinctive plant communities of very small spatial extent. Group 8 *Saxifraga aizoides-Seligeria oelandica* Springs are of the highest conservation value. The Irish populations of *Seligeria oelandica* are of significance on a world scale (Lockhart et al. 2012) and the co-occurrence of this species with other rare bryophytes – *S. patula, Hymenostylium recurvirostrum* var. *insigne* and *Orthothecium rufescens* – makes this a distinctive and ecologically important community.

Author contributions

The project was planned jointly by the authors. All fieldwork was carried out by MDL. All drafts were composed by MDL and revised by DLK.

Acknowledgements

We are grateful to Dr Deirdre Lynn and Dr Neil Lockhart (National Parks and Wildlife Service) for co-ordinating the project, Nick Hodgetts for assisting with fieldwork on the Benbulbin Range and for identifying rare bryophytes, Dr Declan Doogue for advice on Irish flora and habitats, Mark Kavanagh for assistance with laboratory analysis of water samples and Dr Philip Perrin for advice on statistical analysis. This project was funded by National Parks and Wildlife Service, Ireland, and the Irish Research Council.

References

Anonymous 2002. Sources pétrifiantes avec formation de tuf (*Cratoneurion*). In: Bensettiti, F., Gaudillat, V. & Haury, J. (eds.) *Cahiers d'habitats Natura 2000. Connaissance et gestion des habitats et des espèces d'intérêt communautaire. Tome 3 – Habitats humides*, pp. 383–388. La Documentation Française, Paris, FR.

Arenas, C., Vázquez-Urbez, M., Auqué, L., Sancho, C., Osácar, C. & Pardo, G. 2014. Intrinsic and extrinsic controls of spatial and temporal variations in modern fluvial tufa sedimentation: a thirteen-year record from a semi-arid environment. *Sedimentology* 61: 90–132.

Auqué, L., Arenas, C., Osácar, C., Pardo, G., Sancho C., & Vázquez-Urbez, M. 2014. Current tufa sedimentation in a changing-slope valley: The River Añamaza (Iberian Range, NE Spain). *Sedimentary Geology* 303: 26–48.

Biondi, E. & Blasi, C. (eds.) 2009. *Manuale Italiano di interpretazione degli habitat della Directiva 92/43/CEE.* Online at http://vnr.unipg.it/habitat/ Accessed 23.05.2016.

Birks, H.J.B. 1973. *Past and present vegetation of the Isle of Skye: a palaeoecological study*. Cambridge University Press, Cambridge, UK.

Blockeel, T.L., Bosanquet, S.D.S., Hill, M.O. & Preston, C.D. (eds.) 2014. *Atlas of British & Irish Bryophytes,* Vol. 2. Pisces Publications, Newbury, U.K.

Bosanquet, S.D.S. & Motley, G.S. 2009. *The bryophytes of Mynydd Llangatwg SSSI and Craig y Cilau NNR, Brecon Beacons National Park, Wales*. CCW Staff Science Report No. 09/7/1. Countryside Council for Wales, UK.

Boyer, M. & Wheeler, B. 1989. Vegetation patterns in spring-fed calcareous fens – calcite precipitation and constraints on fertility. *Journal of Ecology* 77: 597–609.

Braun, W. 1968. Die Kalkflachmoore und ihre wichtigsten Kontaktgesellschaften im Bayerischen Alpenvorland. *Dissertationes Botanicae* 1: 1–135

Braun-Blanquet, J. 1949. Übersicht der Pflanzengesellschaften Rätiens (III). *Vegetatio* 1: 285–316.

Braun-Blanquet, J. 1978. Die Quellflur-Gesellschaft des *Cratoneuro-Arabidetum bellidifoliae* (Koch 1928) in der subalpinen Stufe Graubündens. *Vegetatio* 36: 115–117.

Carcavilla Urquí, L., de la Hera, A., Fidalgo, C. & González Martín, J.A. 2009. 7220 Formaciones tobáceas generadas por comunidades briofíticas en aguas carbonatadas. In: VV.AA., *Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España*. Ministerio de Medio Ambiente, y Medio Rural y Marino, Madrid, ES.

Coker, P.D. 1983. *Seligeria carniolica* (Breidl. & Beck) Nyh. and *S. oelandica* C. Jens. & Med.; two mosses new to Norway. *Lindbergia* 9: 81–85.

Commission of the European Communities 2013. *Interpretation manual of European Union habitats: EUR 28*. European Commission DG Environment, Brussels, BE.

De Cáceres, M., Legendre, P. & Moretti, M. 2010. Improving indicator species analysis by combining groups of sites. *Oikos* 119: 1674–1684.

de Foucault, B. 2015. Contribution au prodrome des végétations de France: les *Adiantetea capilli-veneris* Braun-Blanq. ex Braun-Blanq., Roussine & Nègre 1952. *Acta Botanica Gallica* 162: 375–403.

Deil, U. 1994. The class *Adiantetea* in the Mediterranean area – an approach from vegetation history and community evolution. *Colloques Phytosociologiques* 23: 241–258.

Dufrêne, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Emeis, K.C., Richnow, H.H. & Kempe, S. 1987. Travertine formation in Plitvice National Park, Yugoslavia: chemical versus biological control. *Sedimentology* 34: 595–609.

Ferreira, R.E.C. 1978. *A preliminary vegetation survey of selected cleuchs in Western Borders*. Nature Conservancy Council, Edinburgh, UK.

Golubić, S., Violante, C., Plenković-Moraj, A. & Grgasović, T. 2008. Travertines and calcareous tufa deposits: an insight into diagenesis. *Geologia Croatica* 61: 363–378.

Grubb, P.J. 1971. Interpretation of the 'Massenerhebung' effect on tropical mountains. *Nature* 229: 44–45.

Hadač, E. 1983. A survey of plant communities of springs and mountain brooks in Czechoslovakia. *Folia Geobotanica & Phytotaxonomica* 18: 339–361.

Hájek, M., Hekera, P. & Hájková, P. 2002. Spring fen vegetation and water chemistry in the Western Carpathian flysch zone. *Folia Geobotanica* 37: 205–224.

Hájek, M. & Hájková, P. 2011a. RBA02 *Carici flavae–Cratoneuretum filicini* Kovács et Felföldy 1960. In: Chytrý M. (ed.), *Vegetace České republiky. 3. Vodní a mokřadní vegetace* [*Vegetation of the Czech Republic 3. Aquatic and wetland vegetation*]. Academia, Praha, CZ.

Hájek, M. & Hájková, P. 2011b. RBA05 *Junco subnodulosi–Schoenetum nigricantis* Allorge 1921. In: Chytrý, M. (ed.), *Vegetace České republiky. 3. Vodní a mokřadní vegetace* [*Vegetation of the Czech Republic 3. Aquatic and wetland vegetation*]. Academia, Praha, CZ.

Hájková, P., Hájek, M. & Apostolova, I. 2006. Diversity of wetland vegetation in the Bulgarian high mountains, main gradients and context-dependence of the pH role. *Plant Ecology* 184: 111–130.

Hájková, P. & Hájek, M. 2011. RAB01 *Brachythecio rivularis-Cratoneuretum* Dierßen 1973. In: Chytrý, M. (ed.), *Vegetace České republiky. 3. Vodní a mokřadní vegetace* [*Vegetation of the Czech Republic 3. Aquatic and wetland vegetation*]. Academia, Praha, CZ.

Hill, M.O., Blackstock, T.H., Long, D.G. & Rothero, G.P. 2008. *A checklist and census catalogue of British and Irish bryophytes*. British Bryological Society, Middlewich, UK.

Hodgetts, N.G. 2015. Checklist and country status of European bryophytes – towards a new Red List for Europe. Irish Wildlife Manuals, No. 84. National Parks and Wildlife Service, Department of Arts, Heritage and the Gaeltacht, Dublin, IE.

Ivimey-Cook, R.B. & Proctor, M.C.F. 1966. The plant communities of the Burren, Co. Clare. *Biology and Environment: Proceedings of the Royal Irish Academy* 64B: 211–302.

Jiménez-Alfaro, B., Hájek, M., Ejrnaes, R., Rodwell, J., Pawlikowski, P., Weeda, E. J., Laitinen, J., Moen, A., Bergamini, A., … & Díaz, T. E. 2014. Biogeographic patterns of base-rich fen vegetation across Europe. *Applied Vegetation Science* 17: 367–380.

Kaufman, L. & Rousseeuw, P.J. 2005. *Finding groups in data: an introduction to cluster analysis*. Wiley, New Jersey, US.

Keppel, M.N., Clarke, J.D.A., Halihan, T., Love, A.J. & Werner, A.D. 2011. Mound springs in the arid Lake Eyre South region of South Australia: a new depositional tufa model and its controls. *Sedimentary Geology* 240: 55–70.

Koch, W. 1928. Die höhere Vegetation der subalpinen Seen und Moorgebiete des Val Piora. *Zeitschrift für Hydrologie* 4: 131–175.

Kuczynska, A. & Bartley, P. 2008. *Hydrological report for Leixlip Spa, Co. Kildare.* Report to Kildare Co. Council, Naas, IE.

Lockhart, N., Hodgetts, N. & Holyoak, D. 2012. *Rare and threatened bryophytes of Ireland.* National Museums Northern Ireland, Holywood, UK.

Lyons, M.D. 2015. *The flora and conservation status of petrifying springs in Ireland.* Ph.D. thesis, The University of Dublin, Trinity College, Dublin, IE.

Maas, F.M. 1959. Bronnen, bronbeken en bronbossen van Nederland, in het bijzonder die van de Veluwezoom. *Mededelingen Landbouwhogeschool Wageningen* 59: 1–166.

McCune, B. & Grace, J. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon, US.

McCune, B. & Mefford, M.J. 2006. *PC-ORD Multivariate analysis of ecological data.* Version 5.33. MjM Software Design, Gleneden Beach, Oregon, US.

McVean, D.N. & Ratcliffe, D.A. 1962. *Plant communities of the Scottish Highlands: a study of Scottish mountain, moorland and forest vegetation*. H.M.S.O. London, UK.

Oberdorfer, E. 1977. *Süddeutsche Pflanzengesellschaften*. Gustav Fischer, Stuttgart, DE.

Oberdorfer, E. 1992. *Süddeutsche Pflanzengesellschaften Teil IV. Wälder und Gebüsche*. Gustav Fischer, Jena, DE.

Ó Críodáin, C. & Doyle, G.J. 1997. *Schoenetum nigricantis*, the *Schoenus* fen and flush vegetation of Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* 97B: 203–218.

Pawlikowski, P., Abramczyk, K., Szczepaniuk, A. & Kozub, L. 2013. Nitrogen: phosphorus ratio as the main ecological determinant of the differences in the species composition of brown-moss rich fens in north-eastern Poland. *Preslia* 85: 349–367.

Pedley, M., Rogerson, M. & Middleton, R. 2009. Freshwater calcite precipitates from in vitro mesocosm flume experiments: a case for biomediation of tufas. *Sedimentology* 56: 511–527.

Pentecost, A. & Viles, H. 1994. A review and reassessment of travertine classification. *Géographie physique et Quaternaire* 48: 305–314.

Pentecost, A. 1995. The quaternary travertine deposits of Europe and Asia Minor. *Quaternary Science Reviews* 14: 1005–1028.

Pentecost, A. 1996. Moss growth and travertine deposition: the significance of photosynthesis, evaporation and degassing of carbon dioxide. *Journal of Bryology* 19: 229–234.

Pentecost, A. 1999. The origin and development of the travertines and associated thermal waters at Matlock Bath, Derbyshire. *Proceedings of the Geologists' Association* 110: 217–232.

Pentecost, A. & Zhaohui, Z. 2002. Bryophytes from some travertine-depositing sites in France and the UK: relationships with climate and water chemistry. *Journal of Bryology* 24: 233–241.

Pentecost, A., 2005. *Travertine*. Springer, Berlin, DE.

Pentecost, A. & Zhaohui, Z. 2006. Response of bryophytes to exposure and water availability on some European travertines. *Journal of Bryology* 28: 21–26.

Philippi, G. 1965. Die Moosgesellschaften der Wutachschlucht. *Mitteilungen des Badischen Landesvereins für Naturkunde und Naturschutz* 8: 625–668.

Porley, R. & Hodgetts, N.G. 2005. *Mosses and liverworts; The New Naturalist Library*. Collins, London, UK.

Rodwell, J.S. (ed.) 1998a. *British plant communities; Vol. 1, Woodlands and scrub.* Cambridge University Press, Cambridge, UK.

Rodwell, J.S. (ed.) 1998b. *British plant communities; Vol. 2, Mires and heaths.* Cambridge University Press, Cambridge, UK.

Rodwell, J.S. (ed.) 1998c. *British plant communities; Vol. 3, Grasslands and montane communities.* Cambridge University Press, Cambridge, UK.

Rozbrojová, Z. & Hájek, M. 2008. Changes in nutrient limitation of spring fen vegetation along environmental gradients in the West Carpathians. *Journal of Vegetation Science* 19: 613–620.

Smith, A.J.E. 1978. *The moss flora of Britain and Ireland*. 1st ed. Cambridge University Press, Cambridge, UK.

Stace, C.A. 2010. *New flora of the British Isles*. Cambridge University Press, Cambridge, UK.

Webb, D.A. & Scannell, M.J.P. 1983. *Flora of Connemara and the Burren*. Royal Dublin Society & Cambridge University Press, Cambridge, UK.

Zechmeister, H. & Mucina, L. 1994. Vegetation of European springs: high-rank syntaxa of the *Montio-Cardaminetea*. *Journal of Vegetation Science* 5: 385–402.

Author addresses

Lyons, M.D. (Corresponding author, lyonsm5@tcd.ie)[1], **Kelly D.L.** (dkelly@tcd.ie)[1]

[1] Department of Botany and Trinity Centre for Biodiversity Research, School of Natural Sciences, Trinity College, The University of Dublin, College Green, Dublin 2, D02 XR15, Ireland

Electronic supplements

Supplementary material associated with this article is embedded in the article's pdf. The online version of Phytocoenologia is hosted at the journal's website www.schweizerbart.com/journals/phyto. The publisher does not bear any liability for the lack of usability or correctness of supplementary material.

Supplement 1: Individual synoptic tables for Groups 1 to 8
Supplement 2: Synoptic table for all species and groups.
Supplement 3: Additional tables.
  MRPP results for differences between pairs of groups using 10 abiotic variables.
  MRPP results for differences between pairs of groups using 10 water chemistry parameters.
  Spearman rank correlation coefficients (r_s) for environmental variables, including chemical composition of spring water (and number of species per sample), with NMS axes.
Supplement 4: Additional figures.
  NMS ordination of selected previously published communities along with the plant communities of Irish petrifying springs.
  Ground cover by plant type in plant communities.
  General attributes of plant communities
  Tufa at Spanish Point, Co. Clare with unusual 'honeycomb' surface

Please save the electronic supplement contained in this pdf-file by clicking the blue frame above. After saving rename the file extension to .zip (for security reasons Adobe does not allow to embed .exe, .zip, .rar etc. files).