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A comparison of distribution patterns in British and Irish mosses and liverworts

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We classified 747 species of British and Irish mosses into 10 clusters, based on their recorded distribution in 10 × 10 km grid squares (hectads). We generated the clusters in a two-stage process using the CLUSTASPEC program, by the same method as we had earlier used for British and Irish liverworts and hornworts. The clusters are named after the species with distributions which are most similar to those of the clusters as a whole. Clusters of widespread species (*Bryum capillare*), southern, lowland species (*Rhynchostegium confertum*), widespread calcifuges (*Pleurozium schreberi*), upland species (*Blindia acuta*) and montane calcifuges (*Kiaeria falcata*) closely match clusters recognised in the liverworts. The remaining clusters (*Tortella flavovirens*, *Weissia longifolia*, *Mnium stellare*, *Encalypta alpina*, *Mnium lycopodioides*) are less similar. The classification of mosses into 15 and 20 clusters generates additional clusters of hyperoceanic and montane mosses which also resemble liverwort clusters. The influence of calcareous bedrock has a more marked effect in determining moss distributions and, unlike the liverworts, the 10 moss clusters include one which is predominantly coastal. Mosses tend to be a less upland group than liverworts; a smaller proportion of their species have northern and western distributions and the lowland clusters are characterised by more extreme environmental conditions. As with the liverworts, geographically restricted clusters of species with predominantly Mediterranean-Atlantic, Arctic-montane and Boreo-arctic Montane world ranges include marked concentrations of threatened species, and species which are not recorded as fruiting in the British Isles.

Keywords: Climate, Cluster analysis, Geology, Nested distributions, Phytogeography, Threat

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Introduction

The delimitation of biogeographical regions (areas characterised by a similar biota) and biogeographical elements (groups of species with similar distributions) has long been a central aim of biogeography. Such studies have traditionally been carried out by the laborious accumulation, assessment and synthesis of evidence by individual experts and, although evidence-based, they have inevitably been essentially subjective. However, as Kreft & Jetz (2010) remark, "the recent availability of global species range maps, novel multivariate techniques and enhanced computational power now enable a quantitative scrutiny and extension of biogeographical regionalizations". This has led to a number of recent papers exploring such questions. At the European scale there have been, for example, studies of the distribution of mammals (Heikinheimo *et al*., 2007), plants (Finnie *et al*., 2007), a comparison of mammals and plants (Heikinheimo *et al*., 2012) and a comparison of amphibians, birds, butterflies, mammals, reptiles and trees (Rueda *et al*., 2010).

Similar opportunities for new analytical studies have also become available at the national level. Since 1960, members of the British Bryological Society (BBS) have systematically collected records of the occurrence of British and Irish bryophytes which can be summarised at the 10 × 10 km ('hectad') scale of the Ordnance Survey national mapping grids. These detailed records from a bryophyte-rich and climatically and geologically diverse region represent an invaluable resource for examining the geographical patterning of bryophyte distributions and the ecological factors underlying them. In a recent paper (Preston *et al*., 2011), we described a method which could be used to detect recurring distribution patterns and we used it to classify records of liverworts and hornworts at the hectad scale. In this paper, we use the same techniques to classify the equivalent records of British mosses into 10 patterns ('clusters') and compare these to the 10 liverwort clusters described in our earlier paper. By comparing the clusters, we aim to highlight the phytogeographical and ecological similarities, and differences, between the two groups. We also outline the results of a classification of the mosses into 15 or 20 clusters.

Data

Records of mosses were derived from the British Bryological Society database held by the Biological Records Centre. Details of the sources of the records in this database are provided by Hill *et al*. (1991) and Preston *et al*. (2009). Records for mosses were extracted at the same time as those for liverworts, so that the geographical coverage of the two groups is strictly comparable.

The available data were summarised as the occurrence of species in hectads. Records of infraspecific taxa were included with those of the appropriate species. In some cases where a species aggregate consists of one rare and one common species, records of the aggregate were assumed to refer to the commoner segregate unless otherwise stated, e.g. records of *Ceratodon purpureus sens. lat.* were assumed to refer to *C. purpureus* unless they were explicitly reported as the extremely rare *C. conicus*. The taxonomy and nomenclature follow Hill *et al*. (2008), with a few exceptions. We recognised nine well-recorded aggregates in place of their less adequately recorded component species: *Acaulon muticum* (*A. mediterraneum*, *A. muticum*), *Anomobryum julaceum* (*A. concinnatum*, *A. julaceum*), *Campylium stellatum* (*C. protensum*, *C. stellatum*), *Dichodontium pellucidum* (*D. flavescens*, *D. pellucidum*), *Dicranum fuscescens* (*D. flexicaule*, *D. fuscescens*), *Ephemerum serratum* (*E. minutissimum*, *E.*

serratum), *Grimmia trichophylla* (*G. dissimulata*, *G. lisae*, *G. muehlenbeckii*, *G. trichophylla*), *Palustriella commutata* (*P. commutata*, *P. falcata*) and *Seligeria trifaria* (*S. patula*, *S. trifaria*). *Fissidens curnovii*, *Hymenostylium insigne* and *Syntrichia ruraliformis* were treated as species rather than varieties of *F. bryoides*, *H. recurvirostrum* and *S. ruralis*, and *Bryum stirtonii*, *Ephemerum stellatum* and *Plagiothecium ruthei* as species rather than synonyms of *B. elegans*, *E. serratum sens. lat.* and *P. denticulatum*. For simplicity, the aggregates and segregates included in the study are all referred to as species in the text. Data for 747 species (in this sense) and 3651 hectads were included in the analysis, giving a total of 388,405 species/hectad records.

Ecological and phytogeographical data on species, and information on the recorded presence of sporophytes, were taken from the BRYOATT spreadsheet, updated from Hill *et al*. (2007) and downloadable from www.brc.ac.uk.

Methods

The program CLUSTASPEC was used to classify the hectad distribution of British and Irish mosses into distribution patterns or clusters. We set the program to recognise 10 moss clusters (k=10) to match the number recognised for liverworts and thus facilitate comparison between the two groups. CLUSTASPEC is described by Preston *et al.* (2011); it uses a two-stage clustering procedure which first constructs a predetermined number of clusters and then checks each species against these clusters, reassigning misfits until all species are placed in the cluster they fit best. The similarity of species to clusters is assessed by a metric S, the cosine of the angle between species and cluster centroids. Each cluster is named after the species which has the greatest similarity to the cluster, i.e. the species with maximum S value in the cluster. The same metric S was used to compare the moss clusters to the liverwort clusters described by Preston *et al*. (2011). We also used the CLUSTASPEC program to identify 15 and 20 moss clusters.

Nestedness between two clusters, a ‘focal cluster’ and a ‘comparison cluster’, is measured by a metric N, also described by Preston *et al.* (2011). A value of N>1 for the focal cluster indicates that the members of that cluster have a greater probability of being found where members of the comparison cluster are found than they have of being found where members of their own cluster are present. Focal clusters with N>1 are thus regarded as being nested within the comparison cluster.

The 10 moss clusters

The 10 clusters identified in the analysis are summarised as coincidence maps (Figure 1). The number of species in each cluster is given in Table 1, which also includes their average range size and some of their ecological attributes. Their phytogeographical affinities are illustrated in Figure 2, following Hill & Preston (1998). In this system each species is classified by the major biome(s) in which it grows, from Arctic-montane to Southern-temperate, and by its eastern limit, from Hyperoceanic to Circumpolar; there are also two additional categories for species with major biome ranges which are wider in the west than further east, Mediterranean-Atlantic and Submediterranean-Subatlantic. The proportions of threatened species and of species which have not been recorded with sporophytes are provided in Table 2. The clusters are described individually below, and their component species are listed in the Appendix.

Bryum capillare *cluster (85 species)*
The characteristic members of this group are bryophytes which are virtually ubiquitous at the 10-km square scale in Britain and Ireland (Figure 1A); only in a few areas (reclaimed land south of The Wash; Outer Hebrides; Shetland) is the absence of more than half the species likely to be the result of genuine absence rather than under-recording. They have correspondingly large world ranges, with many having Circumpolar distributions and spanning the Boreal and Temperate or Temperate and Southern biomes (Figure 2A). Similarity (S) measures in this cluster are very high, exceeding 0.75 for 60 species; the remaining species (especially seven very rare species with S<0.11) are simply placed in the group for want of any more appropriate cluster. The ecological parameters indicate that the species in the cluster inhabit slightly warmer, drier, more base-rich and more nutrient-rich habitats than the majority of mosses. Almost all species are known to fruit in our area and few are threatened; the only non-fruiting and threatened species belong to the group of very rare and poorly matched species.

Tortella flavovirens *cluster (66 species)*
These species are concentrated on the coasts of S.W. England and Wales and most of them have Mediterranean-Atlantic or Submediterranean-Subatlantic ranges (Figures 1B, 2B). This is reflected in their climatic parameters: they grow in areas with notably mild winters, moderately warm summers and relatively low rainfall; their habitats are less shaded than those of any other cluster and they are also more base-rich than average. The cluster also includes a few more widespread halophytes, including *Hennediella heimii* and *Schistidium maritimum*, and the predominantly coastal *Syntrichia ruraliformis*. Although sporophytes are known for all the species in the group except *Didymodon cordatus* and *Ditrichum cornubicum*, 26% of the species have not been found fruiting in our area. The species have more limited ranges than those of any other lowland cluster, and only two of the montane groups include a higher proportion of threatened species.

Weissia longifolia *cluster (46 species)*
The distribution of this small group of species reflects the familiar pattern of the English chalk and softer limestones (Figure 1C). They grow in lowland, base-rich habitats; some of the species are saxicolous but most grow in grassland or on disturbed calcareous soil. Unlike the *Tortella flavovirens* cluster, they are not necessarily found in well-illuminated sites. The mean Ellenberg L value is similar to that of the bryophytes as a whole, reflecting the presence in the group of species of unshaded sites (e.g. *Abietinella abietina*, *Entodon concinnus*) and of shaded places (e.g. *Seligeria calcarea*, *Tortella inflexa*). The range of these species is not only characterised by the highest summer temperatures and the lowest rainfall, but the mean Ellenberg F value is low, indicating a preference for dry microhabitats. The group is drawn primarily from species with European Temperate and broadly Mediterranean-Atlantic affinities (Figure 2C).

Rhynchostegium confertum *cluster (116 species)*
The large group of southern and eastern species includes some of the most frequent mosses in south-east England, such as *Bryum rubens*, *Orthotrichum diaphanum*, *Phascum cuspidatum* and *Syntrichia montana* (Gardiner, 1981; Bates, 1995a; Sanford & Fisk, 2010). However, they are plants of nutrient-rich and moderately base-rich

sites, and are largely absent from the acidic, nutrient-poor habitats of the north and west (Figure 1D). As might be expected of a group of common species, the percentage of species which are not known to fruit is low and the percentage of threatened species is very low. Over half the species (53%) have Temperate ranges; there are also substantial numbers of species with Southern-temperate (15%), Submediterranean-Subatlantic (12%) and Boreo-temperate (10%) distributions (Figure 2D).

Mnium stellare *cluster (60 species)*
This group of calcicoles is a northern equivalent to the *Weissia longifolia* cluster; its range is centred on the Carboniferous limestone areas of Wales and northern England, with prominent outliers in areas of Carboniferous limestone in Counties Sligo and Leitrim, Ireland, and of other base-rich rocks in Scotland (Figure 1E). The species include many saxicolous plants, and in particular plants of shaded calcareous rocks. The mean maximum altitude (471 m) is significantly lower than that of mosses as a whole and it suggests that members of the group, although they may ascend into the uplands, are not montane plants. Similarly, although the species in the cluster have very varied wider distributions, most belong to the Boreal (21%), Boreo-temperate (20%) or the Temperate (33%) phytogeographical elements (Figure 2E).

Pleurozium schreberi *cluster (96 species)*
Only the species of the *Bryum capillare* cluster are more widespread than those in this group of species (Figure 1F). The mean Ellenberg R value is lower than that of any other group and the distribution of the group is determined by their requirement for acidic, nutrient-poor and in many cases moist or wet substrates. In areas where such habitats are available some members of this group are frequent and often abundant; these include *Pleurozium schreberi* itself and *Hypnum jutlandicum*, *Philonotis fontana*, *Plagiothecium undulatum*, *Pogonatum aloides* and *Polytrichum commune* (Wigginton, 1995; Bosanquet *et al*., 2005; Woods, 2006). The species have a wide altitudinal range in our area and extensive world distributions; most have Boreo-arctic (14%), Wide-boreal (13%), Boreo-temperate (40%) or Temperate (19%) ranges (Figure 2F). Most fruit in the British Isles and few are threatened.

Blindia acuta *cluster (123 species)*
This is the largest group of mosses and one that is widespread in the upland areas of Britain and Ireland (Figure 1G). Their ecological parameters show that they are species which characteristically grow in areas of high rainfall and favour acidic, nutrient-poor substrates. The species are drawn from two main phytogeographical groups. The majority have Boreo-arctic, Boreal or Boreo-temperate ranges, but the cluster also includes another concentration of species with Hyperoceanic Temperate, Hyperoceanic Southern-temperate and Oceanic Temperate distributions (Figure 2G). There are even four species with Mediterranean-Atlantic and Submediterranean-Subatlantic ranges in the group, but only two fit well ($S>0.6$), *Entosthodon attenuatus* and *E. obtusus*, species with British and Irish ranges which contrast with their European distributions. Although 20% of the species in the *Blindia acuta* cluster are not known to fruit in the British Isles, few are threatened.

Encalypta alpina *cluster (41 species)*
The ranges of the species in this relatively small group are concentrated in areas of Highland Scotland with base-rich rocks (Figure 1H), especially the calcareous

Dalradian schists of the Breadalbane mountains and Caenlochan which are known hotspots for rare montane species (Ratcliffe, 1977). There are outlying concentrations in other upland areas such as the Carboniferous limestone of the Craven Pennines and Co. Sligo, and of other base-rich rocks in Upper Teesdale and Skye. Many species are saxicolous but some grow on thin soil on rock ledges or in basic flushes. The climatic preferences of the species are less extreme than those of the following two montane clusters, and their mean maximum altitude (744 m) is much lower, but this may in part reflect the distribution of calcareous rocks in upland areas in Britain and Ireland. Arctic species (7%) are less well represented in this than in the following clusters and the majority of species in the *E. alpina* cluster have Boreo-arctic (46%) or Boreal (32%) ranges (Figure 2H). Both the proportions of non-fruiting species and of threatened species in this group are high.

Kiaeria falcata *cluster (70 species)*
This is the largest of the three montane groups; it is concentrated in areas of high altitude in Scotland with outliers in the Lake District and North Wales (Figure 1I). Unlike the *Encalypta alpina* cluster, its component species are plants of very acidic substrates. They occur in areas of more extreme climate than the *E. alpina* cluster (colder winters, colder summers, higher rainfall) and ascend to much higher altitudes. The seven species with the highest similarity values are all strongly associated with areas of late snow-lie (Hill *et al*., 1992, 1994). All but one of the species in the cluster have Arctic (34%), Boreo-arctic (17%) or Boreal (47%) ranges (Figure 2I); the exception is the Hyperoceanic Temperate *Andreaea megistospora*. The cluster resembles the *E. alpina* cluster in having similarly high proportions of non-fruiting and of threatened species.

Mnium lycopodioides *cluster (44 species)*
Like the members of the *E. alpina* cluster, these species grow on basic rocks, in rock crevices and on soil on rock ledges in the mountains. They have almost identical mean Ellenberg values to those in the *Encalypta alpina* cluster but a much more restricted distribution; the only areas with high proportions of the species are the Breadalbanes (especially Ben Lawers), Ben Alder and Caenlochan (Figure 1J). The mean January temperate for these species is lower than that of any other group. Arctic species (32%) are much more richly represented in this cluster than in the *Encalypta alpina* group; the other major phytogeographical groups are the Boreo-arctic (18%) and Boreal (45%) elements (Figure 2J). The Mediterranean-Atlantic species in this group is *Bartramia stricta* and, not surprisingly, it has the lowest similarity value of any member of the group; its presence in this group is due to its disjunct distribution with a single record from Glen Lyon. The group has a remarkably high proportion of species which are not known to fruit in the British Isles (48%) and an even higher proportion of threatened species (57%).

Nested patterns
Six clusters are nested within the virtually ubiquitous *Bryum capillare* cluster (Table 3), and two more are nearly nested within it, those characterised by *Pleurozium schreberi* (N=0.999) and *Blindia acuta* (N=0.993). The *Weissia longifolia* cluster of southern calcicoles is nested within the widespread, lowland *Rhynchostegium confertum* cluster but there are no other cases of nestedness in the lowland clusters. There are more marked relationships in the northern and upland clusters. Four northern clusters (*Blindia acuta*, *Kiaeria falcata*, *Encalypta alpina* and *Mnium*

lycopodioides) are nested within the more widespread *Pleurozium schreberi* cluster, and the three least widespread of these four are in turn nested within the most widespread, the *Blindia acuta* cluster. The *Mnium lycopodioides*, *Encalypta alpina* and *Mnium stellare* clusters of calcicoles form a nested series with the more restricted clusters nested within the more widespread. More surprisingly, the rarest, *Mnium lycopodioides*, cluster is also nested within the *Kiaeria falcata* cluster of montane calcifuges, presumably reflecting the presence of both acidic and calcareous rocks in the high-altitude hectads in which it occurs.

Comparison with liverwort clusters

Distribution patterns

Table 4 compares the moss clusters defined above to the 10 liverwort clusters identified using the same methods by Preston *et al*. (2011). Five of the moss clusters are very similar to liverwort groups. These include the widespread *Bryum capillare* and *Pellia epiphylla* groups, the *Rhynchostegium confertum* and *Lophocolea heterophylla* groups of species concentrated in lowland England and Wales and the complementary *Pleurozium schreberi* and *Scapania undulata* groups of acidic, nutrient-poor soils which are concentrated in the north and west. There is a larger percentage of the total moss flora in the southern and eastern *Rhynchostegium confertum* cluster than there is of liverworts in the equivalent *Lophocolea heterophylla* group; conversely the moss percentage is smaller than that of liverworts in the *Pleurozium schreberi/Scapania undulata* clusters. The other similar pairs are the more restricted, upland *Blindia acuta* and *Anastrepta orcadensis* groups and the montane calcifuge clusters typified by *Kiaeria falcata* and *Moerckia blyttia*. There is a less close relationship between two south-western groups, the coastal mosses in the *Tortella flavovirens* cluster and the less coastal, *Phaeoceros laevis* group of liverworts. The montane calcicoles of the *Encalypta alpina* cluster and the more restricted *Mnium lycopodioides* group are both closest to the *Scapania degenii* cluster of liverworts, although the cosine measures do not indicate a very close similarity. The groups which are essentially unmatched are two more groups of calcicole mosses, the lowland *Weissia longifolia* and the northern *Mnium stellare* clusters, the *Cladopodiella fluitans* cluster of bog liverworts, the hyperoceanic liverworts in the *Harpalejeunea molleri* cluster and the *Marsupella condensata* cluster of liverworts which is concentrated in the Cairngorms.

Ecological correlates

The results of a Principal Components Analysis of the ecological characteristics of the moss clusters (Table 1) and the equivalent characteristics of the liverwort clusters (Preston *et al*. 2011, Table 1, with the addition of Ellenberg S) are shown in Figure 3. The first component, which accounts for 57% of the variance, separates the species of base-rich, nutrient-rich, warm, dry, lowland habitats from those of acidic, nutrient-poor, cold, wet, upland sites. The second component accounts for a further 13% and separates species of open and saline habitats from those of shaded sites. The most extreme lowland clusters are all mosses, the *Rhynchostegium confertum*, *Tortella flavovirens* and *Weissia longifolia* groups; by contrast the most extreme of the upland clusters are two liverwort groups, characterised by *Harpalejeunea molleri* and *Scapania degenii*.

Classification of mosses into 15 and 20 clusters

In the above analysis we chose to use the CLUSTASPEC program to define 10 groups, thus matching both the method and the number of groups with our earlier classification of liverworts. As there are only 300 liverworts compared to 747 mosses, it is arguable that one might obtain a better classification of mosses by recognising more groups, especially as the moss distributions reflect a greater range of ecological factors than those of the liverworts (as discussed above). We have therefore explored the result of classifying the mosses into 15 and 20 clusters.

The 15 clusters recognised by CLUSTASPEC are compared to the 10-cluster classification in Table 5. In essence, the 10 clusters are maintained (although somewhat modified in one case) and the five new clusters include two which are completely new and three which are nested within existing clusters but comprise species with more restricted ranges. There are two south-western clusters rather than one (Figures 4A, B), a coastal *Scleropodium tourettii* cluster (a modified version of the k=10 *Tortella flavovirens* cluster, from which it takes almost all its members) and an essentially new, inland, more upland *Fontinalis squamosa* cluster (drawn primarily from the *Pleurozium schreberi*, *Blindia acuta* and *Tortella flavovirens* clusters of the k=10 analysis). The other new cluster (*Syntrichia ruraliformis*) comprises species of soft coasts (especially sand dunes); these are widespread but distinctly less frequent in the south than elsewhere (Figure 4C). One of the three nested clusters is the hyperoceanic *Hylocomiastrum umbratum* group of 30 species (Figure 4D), 27 of which come from the oceanic *Blindia acuta* cluster of the k=10 analysis. The other two are montane clusters, a *Pseudoleskea incurvata* cluster (Figure 4E) which takes some of its members from the k=10 *Kiaeria falcata* cluster but rather more from the northern calcicoles in the *Mnium stellare* cluster, and a *Polytrichastrum sexangulare* cluster (Figure 4F) which is composed almost entirely of rarer members of the *K. falcata* cluster.

The clusters in the k=15 classification remain recognisable in the k=20 classification and the five additional clusters are all small, including only 8–16 species. A *Pleurochaete squarrosa* cluster includes species which are highly localised, usually on coastal limestone, in S. England and Wales (e.g. *Bryum canariense*, *B. kunzei*, *B. torquescens*, *Entosthodon pulchellus*, *Grimmia orbicularis*, *Plasteurhynchium striatulum*). A cluster characterised by *Tortella flavovirens* differs from the *T. flavovirens* cluster of the k=10 analysis in being composed primarily of very widespread coastal species (*Bryum algovicum*, *Hennediella heimii*, *Schistidium maritimum*). The additional clusters are characterised by *Hygroamblystegium fluviatile* (this is concentrated on the England-Wales border, and includes some species of major rivers such as *Hennediella stanfordensis*, *Myrinia pulvinata*, *Orthotrichum rivulare*, *O. sprucei*), *Buxbaumia aphylla* (the smallest group and one which has no ecological coherence, the next two most characteristic species being *Tortula leucostoma* and *Ditrichum pusillum*) and *Cratoneuron curvicaule* (calcicolous montane rarities such as *Hypnum revolutum*, *Sciuro-hypnum starkei* and *Syntrichia norvegica*, concentrated in two 10-km squares which reflect two hotspots, the Beadalbane mountains of Ben Lawers and Meall nan Tarmachan).

Discussion

Comparison of mosses and liverworts

The classification of moss and liverwort distributions by the same method into 10 clusters reveals striking similarities between their distributions. Five clusters of mosses and liverworts have essentially the same pattern, although there are differences in the proportions of species in some of the comparable clusters, with a higher proportion of liverworts than of mosses in the northern and western groups and a higher proportion of mosses in the southern and eastern *Rhynchostegium confertum* and *Lophocolea heterophylla* groups (Table 4). A group of mosses have ranges which are moderately similar to those of the *Harpalejeunea molleri* cluster of hyperoceanic liverworts (S=0.85) is recognised as the *Hylocomiastrum umbratum* cluster when the number of moss clusters is increased to 15; these species include *Campylopus setifolius*, *Hageniella micans*, *Paraleptodontium recurvifolium* and *Philonotis cernua*. Similarly, the *Polytrichastrum sexangulare* moss cluster of the k=15 analysis includes species such as *Andreaea alpestris*, *A. blyttii*, *Hygrohypnum molle* and *H. styriacum* and is close to the *Marsupella condensata* cluster of liverworts with distributions centred on the Cairngorms (S=0.79). There are also a few liverworts which are confined to the lowland limestones like the mosses in the *Weissia longifolia* cluster (e.g. *Cephaloziella baumgartneri*, *Lophozia perssonii*) and some with distributions which approximate to those of the mosses in the *Mnium stellare* cluster (e.g. *Cololejeunea rossettiana*, *Metzgeria pubescens*, *Pedinophyllum interruptum*, *Scapania aspera*) but clearly there are not enough in either group to form the basis for a distinct liverwort cluster. An alternative analysis which included all bryophyte species together might help identify mosses which occurred as a minority in predominantly liverwort clusters, and *vice versa*, although unless the mosses were subsampled the larger number of mosses than liverworts in such a combined analysis might act against the recognition of predominantly liverwort clusters.

Clusters which reflect the distribution of calcareous bedrock are a particular feature of the classification of mosses. Only one group of liverworts has an Ellenberg R value of 6.0 (the montane, *Scapania degenii* cluster) whereas six of the k=10 moss groups exceed this value. The lowland *Weissia longifolia* cluster (7.3), the upland *Mnium stellare* cluster (6.8) and the montane *Encalypta alpina* cluster (6.3) have the highest mean R values and all have ranges which clearly match the pattern of occurrence of calcareous substrates at appropriate altitudes. The tendency of mosses to occur on more calcareous substrates than liverworts has been shown in more detailed studies of epilithic bryophytes on treeless cliffs in the Czech Republic (Kubešová & Chytrý, 2005) and in 10 m^2 plots in eastern North America (Cleavitt *et al*., 2009). A single k=10 moss cluster, *Tortella flavovirens*, has a predominantly coastal distribution and includes some halophytic species. The scarcity of halophytic bryophytes is well-known feature of the bryophyte flora of the British Isles. Distribution patterns for flowering plants, analysed in the same way, show a much more pronounced coastal influence (Preston *et al*., unpublished).

Scale of the analysis

Although the results of cluster analyses, unlike classifications by expert judgement, are not subjective, they do not provide a single objective classification of distribution patterns. They rather provide a range of solutions depending on factors such as the method of analysis, the number of clusters defined, the size of the study area and the size of the sample unit (‘grain size’) used in the analysis. A single method is used in the classifications of liverworts and mosses discussed in this paper, and the effect of varying the number of moss clusters is discussed below. Our analysis is based on records from hectads in a climatically and geologically diverse area but one which represents only a small area (<3%) of Europe. The combination of climatic, geological and coastal variables which are reflected in the patterns described here are almost certainly a reflection of the scale of our analysis. Bates' (1995b) analysis of a smaller study area, a southern English county of subdued topography, showed that geology and habitat were much more important determinants of distribution than climate. It seems very likely that an analysis of the distribution of European bryophytes using 50 × 50-km grid cells would be less affected by geological factors. This is certainly true of vascular plants, where a European classification reflects climate, topography and perhaps historical factors (Heikinheimo *et al*., 2012) whereas patterns shown by vascular plants at the hectad scale in Britain and Ireland (Preston *et al*., unpublished) are determined by a similar mixture of factors, including geology, to those reported here for mosses. It is by analysing mosses and liverworts at the same scale, using the same survey data, that we have been able to compare the ecological factors which lie behind the patterns of the two groups, and show that, at least in the lowlands, mosses have a wider ecological amplitude, and therefore have distribution patterns governed by a wider range of ecological factors than liverworts.

Comparison with other studies of bryophytes

There are few comparable analyses of bryophytes at the scale of this project. At the continental scale, Stevenson *et al*. (2012) noted a similarity between the species-richness patterns of Australian hornworts, liverworts and mosses, suggesting that all might be controlled by similar environmental variables, especially moisture availability. In a pioneer study, an association analysis based on the distribution of British bryophytes in vice-counties, Proctor (1967) found that the presence or absence of *Anastrepta orcadensis* and *Blindia acuta* represented the first division of the analyses for liverworts and mosses respectively, and marked the division between 'Highland' and 'Lowland' Britain previously identified by A.G. Tansley. Remarkably, these two bryophyte species also characterise large clusters in this study. Hill & Dominguez Lozano (1994) studied the British distribution of a sample of 37 liverwort species occurring in at least 50 hectads, concluding that "large-scale pattern is determined mainly by climate … In future analyses at the scale of Britain, it would probably be better simply to ignore geological and edaphic variables". This conclusion is not borne out by our studies of all British and Irish mosses and liverworts, which show national patterns which reflect both climatic and geological and edaphic factors, as well as in one case (the *Cladopodiella fluitans* cluster of bog liverworts) the distribution of a particular habitat. At the regional scale, the importance of geological/edaphic and habitat factors has been demonstrated by Bates (1995b) and Vanderpoorten & Engels (2002) in lowland areas, and Callaghan & Ashton (2008) added altitude to these factors in a region which included both lowland and upland habitats.

We have already noted the higher proportion of liverworts than mosses in comparable northern and western clusters (Table 4). The greater affinity of the liverworts clusters as a group to the more extreme, northern and western habitats and of mosses to the more extreme lowland habitats is also apparent from Figure 3. Judging by other published studies, there seems to be no consistent difference between the altitudinal relationship of mosses and liverworts. In Nepal, mosses reach a maximum richness at 2500 m and liverworts at 2800 m (non-endemic liverworts at 2700 m; endemic liverworts at 3300 m) which suggests that liverworts are a more upland group (Grau *et al*., 2007). However, in the Canary Islands of Gomera and Tenerife, which rise to 1484 m and 3717 m respectively, liverworts are a more lowland group than mosses and have a narrower altitudinal range. The mean maximum altitude for liverwort species is 1117 m (Gomera) and 1174 m (Tenerife), compared to 1222 m and 1620 m for mosses (Lloret & González-Mancebo, 2011). Altitude does not affect plants directly but is correlated with temperature and habitat availability, and the differing relationships doubtless reflect variation in the occurrence of liverwort-rich habitats with altitude in different climatic regimes. In Scotland the complex of habitats associated with late-lying snow beds and summit plateaux at high altitude includes some communities dominated by liverwort crusts (Woolgrove & Woodin, 1994; Paton, 1999).

Phytogeography, reproductive biology and threat

In addition to the geographical similarity of several moss and liverwort clusters, both analyses reveal the presence of relatively small clusters which are dominated by species which are outside their core range in the British Isles, including Mediterranean-Atlantic species in the *Phaeoceros laevis* and *Tortella flavovirens* clusters and Arctic-montane and Boreo-arctic montane species in the *Encalypta alpina, Marsupella condensata, Mnium lycopodioides, Moerckia blyttii* and *Scapania degenii* clusters. All these clusters contain a high proportion of species which have not been known to fruit in Britain or Ireland, and a high proportion of threatened species. The analysis is a useful way of highlighting such hotspots of species which are at the limits of their range.

Classification of mosses into 10, 15 and 20 clusters

The classification of mosses into 15 clusters arguably provides a more useful general-purpose classification of British and Irish moss distributions than the 10 clusters into which we divided the species for comparison with the liverworts. The subdivision of the *Tortella flavovirens* group into separate coastal and inland components and the additional clusters of hyperoceanic mosses and widespread coastal mosses are informative. However, we regard the 20 clusters as too many, as the additional clusters are all small, accounting in total for only 8% of species. Clusters such as the *Pleurochaete squarrosa* cluster might be of interest as hotspots for rare species, but this classification also contains the one virtually meaningless cluster generated in these analyses, characterised by *Buxbaumia aphylla*.

In a study of the European distributions of diverse groups of species, using grid squares of *c*. 50 × 50 km, Rueda *et al*. (2010) used an algorithm to determine the statistically optimum number of clusters, an approach we have not attempted. They concluded that groups characterised by narrower ranges and less dispersal ability tended to form more clusters, so that birds (3 clusters), butterflies (4), mammals (4) and trees (5) required fewer clusters than amphibians (7) and reptiles (8). Although the relationship between cluster number and range size is not unexpected, it seems doubtful whether the relationship to dispersal ability will have any relevance at the scale of Britain and Ireland. Even at the European scale, Heikinheimo *et al*. (2012) found a strong similarity between the distributions of mammals and plants, as both were strongly related to environmental factors. In Britain and Ireland there are few substantial barriers to dispersal except the Irish Sea, even for poorly dispersed groups, and as bryophytes are well dispersed by spores or vegetative propagules it is most unlikely that many species have ranges which are limited by dispersal ability. The patterns revealed in this study are strongly related to environmental factors and the clusters for any group are likely to result from the interaction of the ecological tolerances of the species in the group and the environment of the study area. Comparative studies of other taxonomic groups in Britain and Ireland ought to allow these relationships to be explored further.

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Appendix

The mosses assigned to each of the 10 moss clusters are listed here in order of decreasing similarity to the cluster pattern, as measured by the cosine measure of similarity (S). Nomenclature follows Hill et al. (2008) with the exceptions listed in the text.

Bryum capillare cluster (85 species): Bryum capillare (0.95), Plagiomnium undulatum (0.94), Calliergonella cuspidata (0.94), Hypnum cupressiforme (0.94), Kindbergia praelonga (0.94), Ceratodon purpureus (0.94), Rhytidiadelphus squarrosus (0.94), Mnium hornum (0.94), Tortula muralis (0.94), Brachythecium rutabulum (0.94), Pseudoscleropodium purum (0.94), Homalothecium sericeum (0.94), Atrichum undulatum (0.93), Dicranella heteromalla (0.93), Fissidens taxifolius (0.93), Dicranum scoparium (0.93),Thuidium tamariscinum (0.92), Barbula convoluta (0.92), Grimmia pulvinata (0.92), Cratoneuron filicinum (0.91), Bryum argenteum (0.91), Barbula unguiculata (0.91), Funaria hygrometrica (0.91), Eurhynchium striatum (0.91), Isothecium myosuroides (0.91), Polytrichastrum formosum (0.90), Rhizomnium punctatum (0.90), Amblystegium serpens (0.90), Fissidens bryoides (0.90), Bryum bicolor (0.90), Platyhypnidium riparioides (0.89), Didymodon insulanus (0.89), Thamnobryum alopecurum (0.89), Oxyrrhynchium hians (0.89), Polytrichum juniperinum (0.89), Brachythecium rivulare (0.88), Orthotrichum affine (0.87), Pseudotaxiphyllum elegans (0.86), Zygodon viridissimus (0.86), Bryoerythrophyllum recurvirostrum (0.86), Pohlia nutans (0.86), Ctenidium molluscum (0.86), Isothecium alopecuroides (0.86), Dicranoweisia cirrata (0.86), Didymodon fallax (0.85), Neckera complanata (0.85), Didymodon rigidulus (0.85), Rhytidiadelphus triquetrus (0.85), Dicranella varia (0.84), Plagiothecium succulentum (0.84), Campylopus introflexus (0.83), Orthotrichum anomalum (0.83), Fontinalis antipyretica (0.82), Cirriphyllum piliferum (0.82), Weissia controversa (0.81), Plagiothecium denticulatum (0.81), Ulota crispa (0.80), Ulota bruchii (0.80), Tetraphis pellucida (0.77), Plagiomnium rostratum (0.75), Fissidens dubius (0.75), Hypnum andoi (0.75), Encalypta streptocarpa (0.74), Ulota phyllantha (0.74), Trichodon cylindricus (0.71), Sciuro-hypnum populeum (0.69), Orthotrichum pulchellum (0.64), Tortula subulata (0.63), Trichostomum crispulum (0.63), Calliergon cordifolium (0.58), Cinclidotus fontinaloides (0.58), Neckera pumila (0.55), Orthotrichum stramineum (0.54), Orthotrichum striatum (0.51), Pogonatum nanum (0.43), Bryum archangelicum (0.43), Zygodon rupestris (0.41), Orthotrichum rivulare (0.38), Tortula freibergii (0.10), Micromitrium tenerum (0.07), Orthotrichum pumilum (0.06), Paludella squarrosa (0.03), Neckera pennata (0.02), Orthotrichum shawii (0.01), Thamnobryum maderense (0.01).

Tortella flavovirens cluster (66 species): Tortella flavovirens (0.67), Tortula viridifolia (0.63), Bryum donianum (0.62), Scleropodium touretii (0.61), Epipterygium tozeri (0.60), Tortula atrovirens (0.58), Syntrichia ruraliformis (0.57), Hennediella heimii (0.57), Schistidium maritimum (0.55), Rhynchostegium megapolitanum (0.54), Scorpiurium circinatum (0.54), Tortella nitida (0.53), Pleurochaete squarrosa (0.52), Microbryum starckeanum (0.51), Bryum sauteri (0.50), Bryum algovicum (0.49), Tortula wilsonii (0.49), Leptodon smithii (0.45), Weissia perssonii (0.42), Tortula canescens (0.41), Drepanocladus polygamus (0.40), Fissidens crispus (0.40), Gymnostomum viridulum (0.40), Weissia rutilans (0.40), Campylopus pilifer (0.36), Schistostega pennata (0.36), Grimmia laevigata (0.33), Grimmia orbicularis (0.32), Bryum canariense (0.29), Campyliadelphus elodes (0.29), Tortula cuneifolia (0.29), Drepanocladus sendtneri (0.28), Bryum warneum (0.28), Entosthodon pulchellus (0.27), Ditrichum subulatum (0.26), Fissidens rivularis (0.25), Sematophyllum substrumulosum (0.25), Bryum marratii (0.25), Bryum calophyllum (0.24), Weissia multicapsularis (0.24), Fissidens curvatus (0.24), Ephemerum sessile (0.23), Coscinodon cribrosus (0.23), Philonotis rigida (0.23), Bryum knowltonii (0.22), Pseudocalliergon lycopodioides (0.22), Pohlia andalusica (0.22), Bryum kunzei (0.21), Fissidens polyphyllus (0.20), Tortula solmsii (0.18), Bryum dyffrynense (0.18), Scopelophila cataractae (0.17), Leptophascum leptophyllum (0.17), Cheilothela chloropus (0.16), Acaulon triquetrum (0.16), Weissia levieri (0.14), Amblystegium radicale (0.14), Fissidens serrulatus (0.13), Achrophyllum dentatum (0.11), Plasteurhynchium meridionale (0.11), Didymodon cordatus (0.10), Calyptrochaeta apiculata (0.09), Ditrichum cornubicum (0.09), Leptotheca gaudichaudii (0.07), Bryum salinum (0.07), Bryum valparaisense (0.06).

Weissia longifolia cluster (46 species): Weissia longifolia (0.70), Campyliadelphus chrysophyllus (0.69), Microbryum rectum (0.68), Seligeria calycina (0.67), Microbryum curvicollum (0.64), Fissidens gracilifolius (0.64), Seligeria calcarea (0.63), Tortula lanceola (0.62), Entodon concinnus (0.58), Tortella inflexa (0.57), Microbryum floerkeanum (0.54), Tortula protobryoides (0.53), Abietinella abietina (0.52), Ephemerum recurvifolium (0.52), Oxyrrhynchium schleicheri (0.52), Thuidium assimile (0.51), Campylophyllum calcareum (0.50), Weissia sterilis (0.46), Aloina ambigua (0.45), Pterygoneurum ovatum (0.43), Didymodon acutus (0.43), Pottiopsis caespitosa (0.40), Rhynchostegiella curviseta (0.39), Aloina rigida (0.38), Herzogiella seligeri (0.37), Leptobarbula berica (0.37), Weissia condensa (0.35), Bryum torquescens (0.32), Rhynchostegiella litorea (0.28), Pterygoneurum lamellatum (0.27), Weissia squarrosa (0.26), Leptodontium gemmascens (0.24), Dicranum flagellare (0.24), Tortula vahliana (0.21), Atrichum angustatum (0.21), Tortella inclinata (0.20), Aloina brevirostris (0.20), Ceratodon conicus (0.16), Tortula cernua (0.12), Weissia mittenii (0.11), Physcomitrium eurystomum (0.10), Rhynchostegium rotundifolium (0.09), Ephemerum stellatum (0.08), Dialytrichia saxicola (0.06), Didymodon glaucus (0.06), Orthotrichum consimile (0.05).

Rhynchostegium confertum cluster (116 species): Rhynchostegium confertum (0.88), Orthotrichum diaphanum (0.87), Bryum rubens (0.85), Pohlia melanodon (0.85), Brachytheciastrum velutinum (0.84), Syntrichia montana (0.84), Tortula truncata (0.84), Leptodictyum riparium (0.84), Syntrichia ruralis (0.82), Didymodon luridus (0.81), Rhynchostegiella tenella (0.81), Oxyrrhynchium pumilum (0.81), Plagiothecium nemorale (0.80), Pseudocrossidium hornschuchianum (0.80), Orthodontium lineare (0.80), Dicranella staphylina (0.79), Dicranella schreberiana (0.79), Didymodon sinuosus (0.78), Brachythecium albicans (0.78), Plagiomnium affine (0.78), Didymodon vinealis (0.77), Didymodon tophaceus (0.77), Syntrichia laevipila (0.77), Homalia trichomanoides (0.77), Rhynchostegium murale (0.76), Cryphaea heteromalla (0.75), Aulacomnium androgynum (0.74), Bryum caespiticium (0.74), Fissidens incurvus (0.73), Pleuridium acuminatum (0.73), Bryum ruderale (0.72), Pseudocrossidium revolutum (0.72), Cirriphyllum crassinervium (0.72), Bryum radiculosum (0.72), Orthotrichum lyellii (0.72), Syntrichia latifolia (0.71), Leskea polycarpa (0.71), Physcomitrium pyriforme (0.70), Anomodon viticulosus (0.70), Bryum klinggraeffii (0.69), Pseudephemerum nitidum (0.69), Homalothecium lutescens (0.68), Bryum moravicum (0.68), Plagiothecium curvifolium (0.68), Fissidens viridulus (0.67), Microbryum davallianum (0.67), Ephemerum serratum sens. lat. (0.66), Aloina aloides (0.64), Bryum subapiculatum (0.64), Zygodon conoideus (0.63), Leucodon sciuroides (0.63), Fissidens exilis (0.62), Leptobryum pyriforme (0.62), Gyroweisia tenuis (0.61), Scleropodium cespitans (0.61), Bryum violaceum (0.61), Hygroamblystegium tenax (0.61), Weissia brachycarpa (0.61), Drepanocladus aduncus (0.61), Orthotrichum cupulatum (0.59), Fissidens crassipes (0.59), Schistidium crassipilum (0.59), Tortula modica (0.57), Tortula marginata (0.56), Didymodon nicholsonii (0.56), Brachythecium glareosum (0.56), Pleuridium subulatum (0.55), Orthotrichum tenellum (0.55), Syntrichia papillosa (0.54), Pohlia lutescens (0.52), Dicranum tauricum (0.52), Bryum gemmiferum (0.52), Aphanorrhegma patens (0.51), Oxyrrhynchium speciosum (0.50), Fissidens pusillus (0.50), Dialytrichia mucronata (0.49), Encalypta vulgaris (0.49), Entosthodon fascicularis (0.48), Brachythecium mildeanum (0.48), Hygroamblystegium varium (0.48), Polytrichastrum longisetum (0.46), Plagiothecium latebricola (0.45), Rhodobryum roseum (0.45), Dicranum montanum (0.43), Acaulon muticum sens. lat. (0.43), Syntrichia virescens (0.40), Orthotrichum sprucei (0.33), Platygyrium repens (0.32), Bryum pallescens (0.32), Leucobryum juniperoideum (0.32), Bryum bornholmense (0.30), Bryum intermedium (0.30), Brachythecium salebrosum (0.30), Plagiothecium ruthei (0.29), Hygroamblystegium humile (0.27), Didymodon umbrosus (0.27), Hennediella stanfordensis (0.26), Pohlia lescuriana (0.25), Fissidens fontanus (0.25), Hennediella macrophylla (0.20), Weissia rostellata (0.19), Dicranum polysetum (0.18), Myrinia pulvinata (0.15), Orthotrichum obtusifolium (0.14), Didymodon tomaculosus (0.12), Bryum gemmilucens (0.12), Fissidens monguillonii (0.11), Dendrocryphaea lamyana (0.10), Zygodon forsteri (0.07), Cinclidotus riparius (0.07), Ephemerum cohaerens (0.06), Tortula amplexa (0.05), Sphagnum obtusum (0.04), Grimmia crinita (0.04), Gyroweisia reflexa (0.03), Timmia megapolitana (0.02).

Mnium stellare cluster (60 species): Mnium stellare (0.72), Neckera crispa (0.69), Eucladium verticillatum (0.67), Mnium marginatum (0.63), Didymodon spadiceus (0.61), Philonotis calcarea (0.58), Seligeria pusilla (0.58), Seligeria recurvata (0.58), Rhynchostegiella teneriffae (0.58), Seligeria donniana (0.57), Taxiphyllum wissgrillii (0.56), Plagiomnium cuspidatum (0.56), Ditrichum gracile (0.54), Didymodon ferrugineus (0.53), Platydictya jungermannioides (0.53), Plagiopus oederianus (0.51), Seligeria acutifolia (0.47), Schistidium platyphyllum (0.44), Gymnostomum calcareum (0.40), Ditrichum flexicaule (0.39), Amblyodon dealbatus (0.39), Brachydontium trichodes (0.38), Fissidens rufulus (0.38), Seligeria trifaria sens. lat. (0.38), Amblystegium confervoides (0.38), Entosthodon muhlenbergii (0.36), Discelium nudum (0.33), Plasteurhynchium striatulum (0.33), Distichium inclinatum (0.32), Plagiothecium laetum (0.32), Pylaisia polyantha (0.31), Tortella bambergeri (0.30), Tortella densa (0.27), Homomallium incurvatum (0.26), Campylostelium saxicola (0.24), Syntrichia princeps (0.24), Conardia compacta (0.23), Bryum creberrimum (0.20), Zygodon gracilis (0.19), Bryum uliginosum (0.18), Schistidium elegantulum (0.18), Rhytidiadelphus subpinnatus (0.17), Seligeria campylopoda (0.15), Bryum turbinatum (0.15), Physcomitrium sphaericum (0.14), Orthodontium gracile (0.13), Orthotrichum pallens (0.13), Thamnobryum angustifolium (0.12), Bryum gemmiparum (0.10), Grimmia tergestina (0.09), Anomodon attenuatus (0.08), Philonotis marchica (0.07), Encalypta brevicolla (0.07), Seligeria carniolica (0.07), Ephemerum hibernicum (0.06), Helodium blandowii (0.06), Grimmia anodon (0.06), Ephemerum spinulosum (0.03), Brachythecium erythrorrhizon (0.03), Calomnion complanatum (0.02).

Pleurozium schreberi cluster (96 species): Pleurozium schreberi (0.89), Polytrichum commune (0.89), Sphagnum palustre (0.89), Philonotis fontana (0.88), Plagiothecium undulatum (0.88), Sphagnum fallax (0.87), Hypnum jutlandicum (0.87), Pogonatum aloides (0.87), Sphagnum subnitens (0.87), Aulacomnium palustre (0.87), Racomitrium aciculare (0.87), Rhytidiadelphus loreus (0.87), Campylopus flexuosus (0.86), Sphagnum denticulatum (0.86), Sphagnum capillifolium (0.86), Polytrichum piliferum (0.86), Hylocomium splendens (0.86), Bryum pseudotriquetrum (0.85), Sciuro-hypnum plumosum (0.85), Dicranum majus (0.85), Sphagnum papillosum (0.85), Racomitrium lanuginosum (0.84), Dichodontium pellucidum sens. lat. (0.84), Pogonatum urnigerum (0.84), Racomitrium fasciculare (0.84), Fissidens adianthoides (0.82), Pohlia wahlenbergii (0.82), Leucobryum glaucum (0.81), Campylopus pyriformis (0.81), Hookeria lucens (0.81), Dichodontium palustre (0.80), Sphagnum cuspidatum (0.80), Campylium stellatum sens. lat. (0.80), Heterocladium heteropterum (0.79), Bryum pallens (0.78), Palustriella commutata sens. lat. (0.77), Pohlia annotina (0.77), Bartramia pomiformis (0.77), Hyocomium armoricum (0.76), Ditrichum heteromallum (0.76), Sphagnum tenellum (0.75), Tortella tortuosa (0.74), Ptychomitrium polyphyllum (0.74), Sphagnum inundatum (0.74), Straminergon stramineum (0.73), Grimmia trichophylla sens. lat. (0.71), Sphagnum compactum (0.71), Sarmentypnum exannulatum (0.70), Hygrohypnum ochraceum (0.70), Campylopus fragilis (0.70), Sanionia uncinata (0.70), Trichostomum brachydontium (0.70), Climacium dendroides (0.70), Dicranella rufescens (0.70), Sphagnum squarrosum (0.69), Hygrohypnum luridum (0.69), Sphagnum fimbriatum (0.68), Dicranum bonjeanii (0.67), Polytrichum strictum (0.65), Warnstorfia fluitans (0.63), Schistidium rivulare (0.60), Sphagnum magellanicum (0.58), Calliergonella lindbergii (0.57), Archidium alternifolium (0.56), Fontinalis squamosa (0.55), Plagiomnium elatum (0.52), Leptodontium flexifolium (0.52), Hygroamblystegium fluviatile (0.48), Calliergon giganteum (0.47), Rhizomnium pseudopunctatum (0.47), Cynodontium bruntonii (0.47), Plagiomnium ellipticum (0.44), Fissidens curnovii (0.44), Pohlia camptotrachela (0.44), Campylopus brevipilus (0.44), Fissidens celticus (0.43), Dicranella cerviculata (0.40), Schistidium apocarpum (0.39), Scorpidium cossonii (0.39), Atrichum crispum (0.37), Sphagnum flexuosum (0.35), Racomitrium affine (0.33), Hamatocaulis vernicosus (0.31), Philonotis arnellii (0.31), Philonotis caespitosa (0.29), Hypnum imponens (0.22), Bryum tenuisetum (0.21), Dicranum spurium (0.20), Dicranella crispa (0.20), Atrichum tenellum (0.19), Sphagnum pulchrum (0.15), Sanionia orthothecioides (0.12), Sphagnum balticum (0.07), Tetrodontium repandum (0.04), Bruchia vogesiaca (0.03), Grimmia sessitana (0.02).

Blindia acuta cluster (123 species): Blindia acuta (0.81), Amphidium mougeotii (0.81), Racomitrium aquaticum (0.81), Fissidens osmundoides (0.80), Anomobryum julaceum sens. lat. (0.80), Breutelia chrysocoma (0.79), Diphyscium foliosum (0.78), Anoectangium aestivum (0.78), Campylopus atrovirens (0.77), Sarmentypnum sarmentosum (0.77), Oligotrichum hercynicum (0.76), Trichostomum tenuirostre (0.75), Dicranum fuscescens sens. lat. (0.74), Sphagnum quinquefarium (0.74), Andreaea rupestris (0.73), Bryum alpinum (0.73), Polytrichastrum alpinum (0.73), Thuidium delicatulum (0.73), Isopterygiopsis pulchella (0.72), Gymnostomum aeruginosum (0.72), Hypnum callichroum (0.71), Scorpidium scorpioides (0.71), Andreaea rothii (0.70), Andreaea alpina (0.70), Sphagnum girgensohnii (0.69), Hylocomiastrum umbratum (0.69), Dicranodontium denudatum (0.69), Bartramia ithyphylla (0.69), Racomitrium ellipticum (0.67), Pohlia cruda (0.66), Pohlia elongata (0.66), Entosthodon obtusus (0.66), Grimmia ramondii (0.66), Splachnum sphaericum (0.66), Loeskeobryum brevirostre (0.66), Plagiobryum zieri (0.65), Racomitrium heterostichum (0.64), Racomitrium ericoides (0.64), Grimmia torquata (0.64), Rhabdoweisia crispata (0.63), Ptilium crista-castrensis (0.62), Entosthodon attenuatus (0.62), Bryoerythrophyllum ferruginascens (0.62), Grimmia funalis (0.61), Grimmia hartmanii (0.61), Distichium capillaceum (0.61), Ulota hutchinsiae (0.60), Antitrichia curtipendula (0.60), Sphagnum teres (0.60), Hygrohypnum eugyrium (0.60), Racomitrium sudeticum (0.59), Orthothecium intricatum (0.59), Tetraplodon mnioides (0.59), Schistidium strictum (0.58), Molendoa warburgii (0.57), Hymenostylium recurvirostrum (0.56), Campylopus gracilis (0.56), Dicranum scottianum (0.56), Sphagnum contortum (0.56), Pohlia drummondii (0.56), Ulota drummondii (0.55), Rhabdoweisia crenulata (0.55), Pterogonium gracile (0.55), Grimmia donniana (0.54), Scorpidium revolvens (0.53), Sphagnum strictum (0.53), Hedwigia stellata (0.52), Sphagnum russowii (0.52), Rhabdoweisia fugax (0.51), Bartramia halleriana (0.51), Sphagnum warnstorfii (0.50), Splachnum ampullaceum (0.48), Dicranodontium uncinatum (0.48), Tetrodontium brownianum (0.47), Orthotrichum rupestre (0.47), Sphagnum molle (0.47), Dicranella subulata (0.46), Campylopus setifolius (0.45), Trichostomum hibernicum (0.44), Pohlia flexuosa (0.44), Glyphomitrium daviesii (0.43), Isothecium holtii (0.41), Sphagnum fuscum (0.40), Campylopus subulatus (0.39), Racomitrium elongatum (0.39), Pohlia bulbifera (0.39), Hedwigia integrifolia (0.39), Ulota calvescens (0.39), Bryum riparium (0.37), Sphagnum platyphyllum (0.35), Sphagnum affine (0.34), Hageniella micans (0.33), Cynodontium jenneri (0.31), Campylopus shawii (0.31), Sphagnum angustifolium (0.31), Platyhypnidium lusitanicum (0.31), Grimmia longirostris (0.30), Grimmia decipiens (0.29), Sphagnum austinii (0.29), Sphagnum subsecundum (0.26), Pseudobryum cinclidioides (0.25), Ulota coarctata (0.25), Heterocladium wulfsbergii (0.24), Schistidium agassizii (0.23), Myurium hochstetteri (0.20), Grimmia arenaria (0.19), Sphagnum skyense (0.18), Habrodon perpusillus (0.18), Daltonia splachnoides (0.18), Hedwigia ciliata (0.16), Sematophyllum demissum (0.16), Grimmia montana (0.16), Philonotis cernua (0.15), Ditrichum pusillum (0.15), Ditrichum plumbicola (0.14), Campylopus subporodictyon (0.14), Bryum cyclophyllum (0.14), Cyclodictyon laetevirens (0.11), Schistidium flaccidum (0.10), Hypnum uncinulatum (0.09), Grimmia alpestris (0.06), Orthotrichum gymnostomum (0.05), Tortella limosella (0.05).

Encalypta alpina cluster (41 species): Encalypta alpina (0.65), Schistidium trichodon (0.65), Mnium thomsonii (0.64), Myurella julacea (0.64), Encalypta rhaptocarpa (0.63), Orthothecium rufescens (0.59), Meesia uliginosa (0.58), Pseudoleskeella rupestris (0.57), Cinclidium stygium (0.53), Bryum elegans (0.52), Stegonia latifolia (0.52), Schistidium robustum (0.50), Rhytidium rugosum (0.49), Thuidium recognitum (0.45), Dicranella grevilleana (0.43), Hypnum vaucheri (0.43), Schistidium atrofuscum (0.42), Didymodon icmadophilus (0.42), Hymenostylium insigne (0.40), Bryum mildeanum (0.40), Catoscopium nigritum (0.40), Tomentypnum nitens (0.38), Pohlia proligera (0.36), Cynodontium tenellum (0.35), Pohlia filum (0.34), Schistidium frigidum (0.32), Grimmia ovalis (0.32), Tortella fragilis (0.31), Orthotrichum speciosum (0.29), Eurhynchiastrum pulchellum (0.29), Racomitrium canescens (0.27), Schistidium confertum (0.27), Schistidium pruinosum (0.24), Dicranum undulatum (0.21), Seligeria oelandica (0.19), Didymodon maximus (0.18), Thamnobryum cataractarum (0.14), Buxbaumia viridis (0.13), Schistidium flexipile (0.12), Trematodon ambiguus (0.07), Meesia triquetra (0.02).

Kiaeria falcata cluster (70 species): Kiaeria falcata (0.78), Pohlia ludwigii (0.78), Kiaeria starkei (0.77), Conostomum tetragonum (0.74), Andreaea nivalis (0.70), Ditrichum zonatum (0.70), Arctoa fulvella (0.69), Herzogiella striatella (0.68), Amphidium lapponicum (0.67), Isopterygiopsis muelleriana (0.66), Philonotis seriata (0.66), Kiaeria blyttii (0.65), Kiaeria glacialis (0.65), Hylocomiastrum pyrenaicum (0.65), Hypnum hamulosum (0.64), Sciuro-hypnum reflexum (0.63), Sciuro-hypnum glaciale (0.63), Pseudoleskea patens (0.63), Bryum weigelii (0.61), Racomitrium macounii (0.61), Polytrichastrum sexangulare (0.59), Pterigynandrum filiforme (0.59), Dicranoweisia crispula (0.58), Pseudocalliergon trifarium (0.58), Rhizomnium magnifolium (0.55), Campylopus schimperi (0.55), Bryum muehlenbeckii (0.55), Andreaea mutabilis (0.54), Encalypta ciliata (0.54), Sphagnum lindbergii (0.54), Oncophorus wahlenbergii (0.54), Andreaea alpestris (0.52), Andreaea blyttii (0.51), Bryum dixonii (0.51), Tetraplodon angustatus (0.51), Oedipodium griffithianum (0.51), Aulacomnium turgidum (0.50), Paraleptodontium recurvifolium (0.49), Philonotis tomentella (0.49), Plagiothecium platyphyllum (0.48), Dicranodontium asperulum (0.47), Ditrichum lineare (0.42), Splachnum vasculosum (0.42), Plagiothecium cavifolium (0.41), Hygrohypnum molle (0.41), Grimmia incurva (0.41), Grimmia atrata (0.40), Pohlia obtusifolia (0.39), Cynodontium strumiferum (0.38), Andreaea sinuosa (0.37), Hygrohypnum duriusculum (0.35), Grimmia elongata (0.34), Andreaea megistospora (0.33), Andreaea frigida (0.31), Cynodontium polycarpon (0.30), Dicranum elongatum (0.29), Sphagnum riparium (0.25), Saelania glaucescens (0.24), Pohlia scotica (0.23), Mielichhoferia mielichhoferiana (0.23), Cynodontium fallax (0.21), Hygrohypnum polare (0.21), Hygrohypnum styriacum (0.18), Grimmia unicolor (0.16), Sphagnum majus (0.15), Seligeria brevifolia (0.13), Seligeria diversifolia (0.13), Mielichhoferia elongata (0.12), Grimmia elatior (0.10), Pohlia crudoides (0.05).

Mnium lycopodioides cluster (44 species): Mnium lycopodioides (0.81), Campylophyllum halleri (0.80), Mnium spinosum (0.77), Ptychodium plicatum (0.76), Myurella tenerrima (0.75), Plagiobryum demissum (0.71), Hypnum bambergeri (0.70), Cratoneuron curvicaule (0.70), Hypnum revolutum (0.70), Bryum arcticum (0.69), Racomitrium himalayanum (0.66), Plagiomnium medium (0.66), Plagiothecium piliferum (0.66), Syntrichia norvegica (0.66), Sciuro-hypnum starkei (0.65), Oncophorus virens (0.64), Heterocladium dimorphum (0.64), Palustriella decipiens (0.63), Timmia austriaca (0.63), Bryum stirtonii (0.62), Pseudoleskea incurvata (0.61), Hygrohypnum smithii (0.61), Tayloria lingulata (0.60), Timmia norvegica (0.59), Bryoerythrophyllum caledonicum (0.56), Lescuraea saxicola (0.54), Schistidium dupretii (0.47), Bryum schleicheri (0.46), Blindia caespiticia (0.44), Paraleucobryum longifolium (0.44), Brachytheciastrum trachypodium (0.44), Schistidium papillosum (0.44), Pseudocalliergon turgescens (0.40), Brachythecium cirrosum (0.40), Pseudoleskeella nervosa (0.38), Ctenidium procerrimum (0.38), Tayloria tenuis (0.38), Aplodon wormskioldii (0.34), Tortula leucostoma (0.33), Anomodon longifolius (0.32), Aongstroemia longipes (0.30), Buxbaumia aphylla (0.29), Dicranum leioneuron (0.27), Bartramia stricta (0.13).

Legends for figures

Figure 1 Distribution of species in the 10 moss clusters. The lightest symbols indicate hectads in which 10–25% of the species are recorded, and increasingly dark symbols denote hectads with 25–50% and >50% of the total. (A) *Bryum capillare* cluster, (B) *Tortella flavovirens* cluster, (C) *Weissia longifolia* cluster, (D) *Rhynchostegium confertum* cluster, (E) *Mnium stellare* cluster, (F) *Pleurozium schreberi* cluster, (G) *Blindia acuta* cluster, (H) *Encalypta alpina* cluster, (I) *Kiaeria falcata* cluster, (J) *Mnium lycopodioides* cluster.

Figure 2 The phytogeographical affinities of the species in the 10 moss clusters. The bars indicate the percentage of species in the group in the Arctic (Arc), Boreo-arctic (Bor-arc), Boreal (Bor), Wide-boreal (Wide-bor), Boreo-temperate (Bor-temp), Wide-temperate (Wide-temp), Temperate (Temp), Southern-temperate (S-temp) and Mediterranean-Atlantic (Med-Atl) Major Biome Categories, and the Hyperoceanic (Hyp), Oceanic (Oc), Suboceanic (Suboc), European (Eur), Eurosiberian (Eurosib), Eurasian (Euras) and Circumpolar (Circ) Eastern Limit Categories. (A) *Bryum capillare* cluster, (B) *Tortella flavovirens* cluster, (C) *Weissia longifolia* cluster, (D) *Rhynchostegium confertum* cluster, (E) *Mnium stellare* cluster, (F) *Pleurozium schreberi* cluster, (G) *Blindia acuta* cluster, (H) *Encalypta alpina* cluster, (I) *Kiaeria falcata* cluster, (J) *Mnium lycopodioides* cluster.

Figure 3 Principal Components Analysis biplot showing environmental characteristics of the 10 moss and liverwort clusters. Abbreviations of the names of the clusters are in bold for mosses and in italics for liverworts. For the unabbreviated cluster names, see Table 1 (mosses) and Table 4 (liverworts).

Figure 4 Distribution of species in six of the clusters generated in the classification of moss distributions into 15 clusters. The lightest symbols indicate hectads in which 10–25% of the species are recorded, and increasingly dark symbols denote hectads with 25–50% and >50% of the total. (A) *Scleropodium tourettii* cluster, (B) *Fontinalis squamosa* cluster, (C) *Syntrichia ruraliformis* cluster, (D) *Hylocomiastrum umbratum* cluster, (E) *Pseudoleskea incurvata* cluster, (F) *Polytrichastrum sexangulare* cluster.

Table 1. Distributional and ecological characteristics of the 10 moss clusters.

Cluster	No. spp.	Total hectads	Maximum altitude (m)	Mean January temperature (°C)	Mean July temperature (°C)	Mean annual precipitation (mm)	Ellenberg values				
							L	F	R	N	S
Bryum capillare	85	**1573 (89)**	**742 (34)**	**3.4 (0.0)**	**14.6 (0.0)**	**1105 (11)**	**5.6 (0.1)**	**5.3 (0.2)**	**5.7 (0.2)**	**4.1 (0.1)**	0.1 (0.0)
Tortella flavovirens	66	**84 (14)**	**211 (24)**	**4.9 (0.1)**	**15.3 (0.1)**	**1075 (20)**	**6.8 (0.2)**	5.2 (0.3)	**6.2 (0.2)**	3.2 (0.2)	**0.8 (0.2)**
Weissia longifolia	46	**94 (17)**	**308 (38)**	**3.7 (0.1)**	**15.9 (0.1)**	**794 (17)**	6.0 (0.3)	**4.3 (0.2)**	**7.3 (0.2)**	3.3 (0.2)	**0.0 (0.0)**
Rhynchostegium confertum	116	**541 (41)**	**404 (22)**	**3.7 (0.0)**	**15.4 (0.0)**	**914 (12)**	5.9 (0.2)	**5.4 (0.2)**	**6.2 (0.1)**	**4.7 (0.1)**	**0.0 (0.0)**
Mnium stellare	60	**98 (20)**	**471 (39)**	3.0 (0.1)	14.1 (0.1)	**1258 (29)**	**5.2 (0.3)**	5.7 (0.2)	**6.8 (0.2)**	3.2 (0.2)	**0.0 (0.0)**
Pleurozium schreberi	96	**816 (58)**	**878 (31)**	**3.1 (0.0)**	13.9 (0.0)	1319 (13)	**6.5 (0.1)**	**7.0 (0.2)**	**3.6 (0.2)**	**2.3 (0.1)**	0.1 (0.0)
Blindia acuta	123	**226 (18)**	**824 (30)**	**2.6 (0.1)**	**13.0 (0.0)**	**1747 (25)**	6.1 (0.1)	6.0 (0.2)	**4.0 (0.1)**	**2.1 (0.1)**	**0.0 (0.0)**
Encalypta alpina	41	**26 (4)**	744 (51)	**1.5 (0.2)**	**12.5 (0.1)**	**1555 (51)**	6.5 (0.2)	5.7 (0.4)	**6.3 (0.3)**	**2.3 (0.1)**	**0.0 (0.0)**
Kiaeria falcata	70	**28 (3)**	**1011 (32)**	**0.5 (0.1)**	**11.5 (0.1)**	**1936 (39)**	6.1 (0.1)	**6.3 (0.2)**	**3.8 (0.2)**	**2.0 (0.1)**	**0.0 (0.0)**
Mnium lycopodioides	44	**6 (1)**	**937 (42)**	**0.1 (0.2)**	**11.6 (0.2)**	**1764 (59)**	6.4 (0.2)	6.0 (0.3)	**6.2 (0.2)**	**2.3 (0.1)**	**0.0 (0.0)**
Mosses, all species	747	430 (23)	662 (14)	2.8 (0.1)	13.9 (0.1)	1341 (16)	6.1 (0.1)	5.8 (0.1)	5.3 (0.1)	3.0 (0.1)	0.1 (0.0)
Liverworts, all species	300	325 (27)	738 (22)	2.8 (0.1)	13.5 (0.1)	1500 (24)	5.5 (0.1)	6.6 (0.1)	4.0 (0.1)	2.3 (0.1)	0.0 (0.0)

Note: Values are means (standard errors) for the species in the groups. Temperature and precipitation values have been calculated for each species from the values for the hectads in which they occur (Hill *et al*., 2007). The Ellenberg values are for Light (L), Moisture (F), Reaction or pH (R), Nitrogen (N), and Salt tolerance (S), with low values indicating low levels of the relevant parameter (i.e. species characteristic of shaded, dry, acidic, nutrient-poor and non-saline sites). Values in bold are significantly different from those for the mosses as a whole ($p<0.05$, t-test). The values for all liverwort species are provided for comparison.

Table 2. Percentage of threatened species in the 10 moss clusters, and of species which have not been recorded with sporophytes in the British Isles.

Cluster	No. spp.	Sporophytes not recorded in British Isles (%)	Threatened species (%)
Bryum capillare	85	2	2
Tortella flavovirens	66	26	27
Weissia longifolia	46	11	17
Rhynchostegium confertum	116	15	3
Mnium stellare	60	17	17
Pleurozium schreberi	96	9	3
Blindia acuta	123	20	6
Encalypta alpina	41	27	27
Kiaeria falcata	70	29	23
Mnium lycopodioides	44	48	57
All species	747	18	14

Note: Threatened species are those classified as Critically Endangered, Endangered and Vulnerable by Hodgetts (2011).

Table 3. Nestedness N of comparison clusters (columns) within focal clusters (rows).

	Bryu cap	*Rhyn conf*	*Weis long*	*Tort flav*	*Mniu stel*	*Pleu schr*	*Blin acut*	*Kiae falc*	*Enca alpi*	*Mniu lyco*
Bryu capi	1.00	**1.07**	**1.08**	**1.00**	**1.11**	1.00	0.99	0.93	**1.03**	**1.03**
Rhyn conf	0.71	1.00	**1.13**	0.86	0.81	0.59	0.41	0.26	0.49	0.40
Weis long	0.29	0.45	1.00	0.38	0.39	0.19	0.11	0.10	0.27	0.26
Tort flav	0.33	0.43	0.48	1.00	0.37	0.32	0.26	0.13	0.26	0.14
Pleu schr	0.76	0.67	0.55	0.72	1.00	1.00	**1.18**	**1.28**	**1.15**	**1.28**
Blin acut	0.36	0.22	0.15	0.29	0.58	0.57	1.00	**1.49**	**1.04**	**1.44**
Mniu stel	0.39	0.42	0.52	0.39	1.00	0.46	0.56	0.68	**1.03**	**1.12**
Kiae falc	0.05	0.02	0.02	0.02	0.11	0.09	0.23	1.00	0.49	**1.20**
Enca alpi	0.09	0.06	0.09	0.07	0.25	0.13	0.24	0.75	1.00	**1.59**
Mniu lyco	0.01	0.01	0.01	0.01	0.04	0.02	0.05	0.30	0.26	1.00

Note: The order of the moss clusters has been rearranged to best demonstrate the patterns of nestedness. Values of N>1 are shown in bold and signify that the comparison cluster is nested within the focal cluster. Cluster names are abbreviated; for the full names, see Tables 1 and 2.

Table 4. Similarity of the moss clusters with the liverwort clusters described by Preston *et al*. (2011), measured by the metric S (see text).

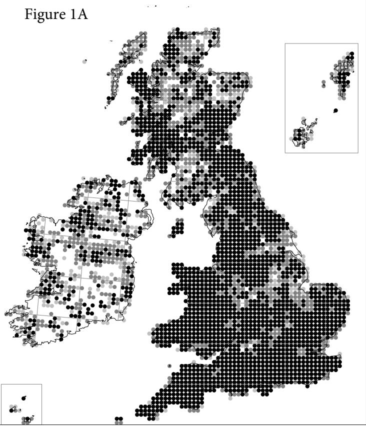
	Bryu capi (11)	*Tort flav* (9)	*Weis long* (6)	*Rhyn conf* (16)	*Mniu stel* (8)	*Pleu schr* (13)	*Blin acut* (16)	*Enca alpi* (5)	*Kiae falc* (9)	*Mniu lyco* (6)
Pellia epiphylla (10)	**0.96**	0.60	**0.48**	0.79	**0.68**	0.93	0.70	0.33	0.27	0.14
Phaeoceros laevis s.l. (8)	0.39	**0.71**	0.21	0.40	0.26	0.37	0.24	0.08	0.05	0.04
Cladopodiella fluitans (5)	0.39	0.26	0.19	0.32	0.28	0.48	0.39	0.19	0.17	0.10
Lophocolea heterophylla (10)	0.87	0.59	0.64	**0.94**	0.61	0.68	0.35	0.20	0.10	0.08
Scapania undulata (21)	0.76	0.40	0.24	0.49	0.67	**0.95**	0.90	0.44	0.42	0.21
Anastrepta orcadensis (12)	0.44	0.16	0.08	0.18	0.47	0.65	**0.91**	0.55	0.70	0.35
Harpalejeunea molleri (14)	0.42	0.27	0.08	0.18	0.34	0.57	0.76	0.22	0.29	0.07
Moerckia blyttii (12)	0.25	0.07	0.06	0.10	0.29	0.38	0.59	0.61	**0.92**	0.60
Scapania degenii (3)	0.18	0.04	0.07	0.08	0.34	0.26	0.39	**0.66**	0.52	**0.62**
Marsupella condensata (4)	0.07	0.01	0.01	0.02	0.07	0.12	0.21	0.25	0.58	0.33

Note: The proportion of species represented by each cluster is shown after the cluster name. S values in bold indicate the most similar liverwort group to each of the moss groups. The names of the moss clusters are abbreviated; for the full names, see Tables 1 and 2.

Table 5. The 15 moss clusters defined by CLUSTASPEC. The equivalent clusters when k=10 clusters is given, as measured by the metric S; clusters are regarded as equivalent if S>0.9.

Group	No. species	Similar k=10 group		Description of clusters if differ from those in k=10 analysis
		Name (no. species)	S	
Bryum capillare	82	*Bryum capillare* (85)	1.00	
Scleropodium tourettii	47	*Tortella flavovirens* (66)	0.95	More coastal than k=10 *Tortella flavovirens* cluster (Figure 4A)
Fontinalis squamosa	36		-	Wales, S.W. England, widespread in uplands, no coastal affinity (Figure 4B); unlike any k=10 cluster
Weissia longifolia	43	*Weissia longifolia* (46)	1.00	
Rhynchostegium confertum	109	*Rhynchostegium confertum* (118)	1.00	
Syntrichia ruraliformis	26		-	Widespread, soft coasts, least frequent in S. England, S. Ireland (Figure 4C) ; unlike any k=10 cluster
Mnium stellare	52	*Mnium stellare* (62)	0.99	
Pleurozium schreberi	84	*Pleurozium schreberi* (96)	1.00	
Amphidium mougeotii	88	*Blindia acuta* (124)	1.00	
Hylocomiastrum umbratum	30		-	Hyperoceanic areas of Wales, NW Scotland, W Ireland (Figure 4D); nested within *Amphidium mougeotii* cluster (N=1.16)
Schistidium trichodon	30	*Encalypta alpina* (42)	0.96	
Pseudoleskea incurvata	19		-	Rare species of base-rich mountains (Ben Lawers, Glen Clova) (Figure 4E); nested within *Schistidium trichodon* cluster (N=1.39)
Kiaeria falcata	41	*Kiaeria falcata* (70)	0.98	
Polytrichastrum sexangulare	24		-	Rare montane species centred on Cairngorms (Figure 4F); nested within *Kiaeria falcata* cluster (N=1.24)
Mnium lycopodioides	36	*Mnium lycopodioides* (45)	0.97	

Figure 1A



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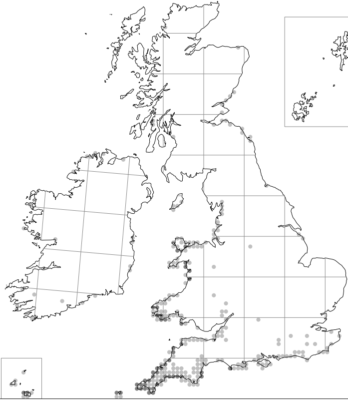


Figure 1C

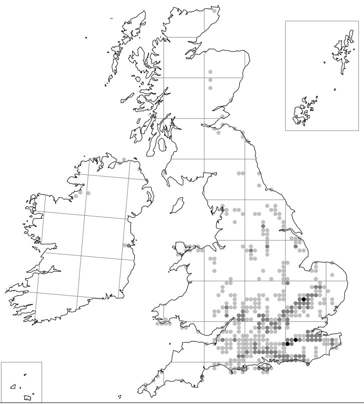


Figure 1D

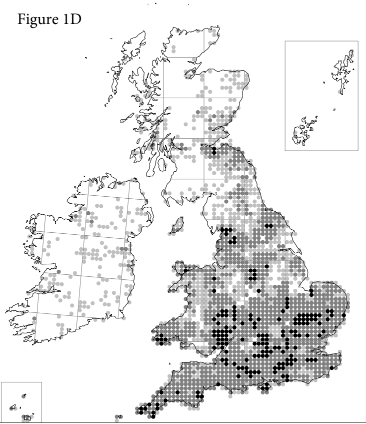
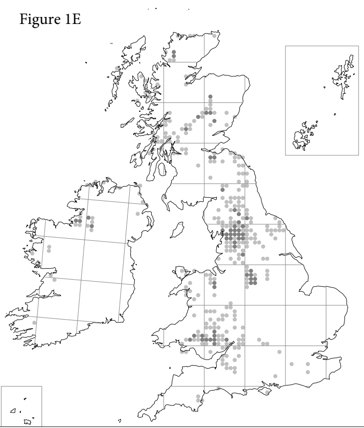


Figure 1E



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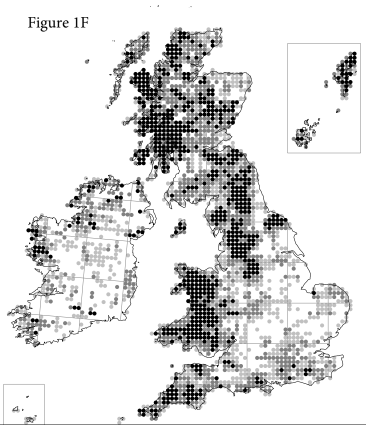


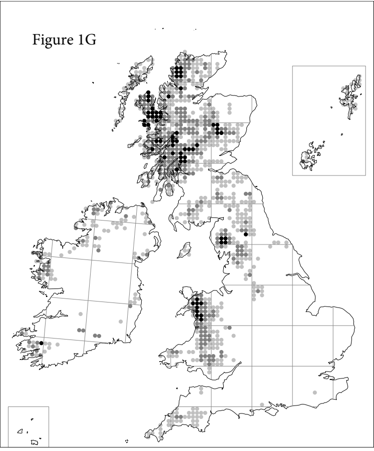
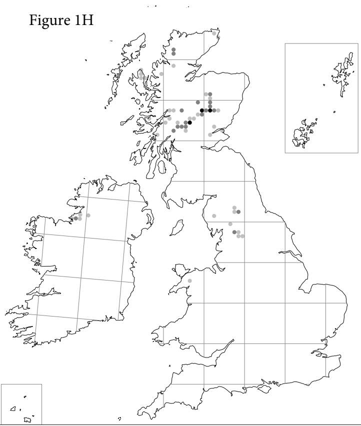


Figure 1G

Figure 1H



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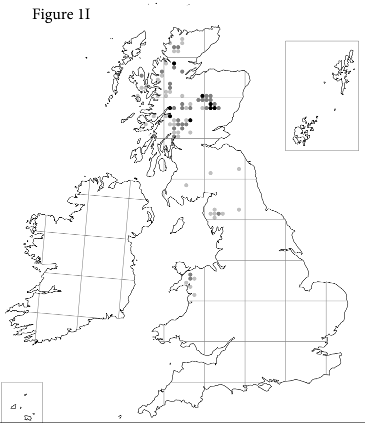

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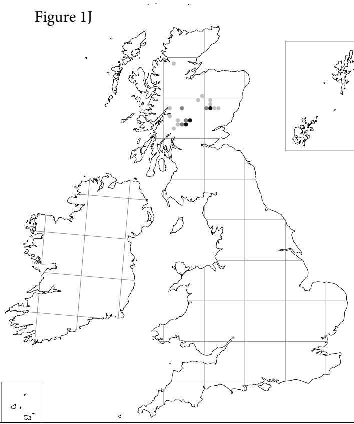

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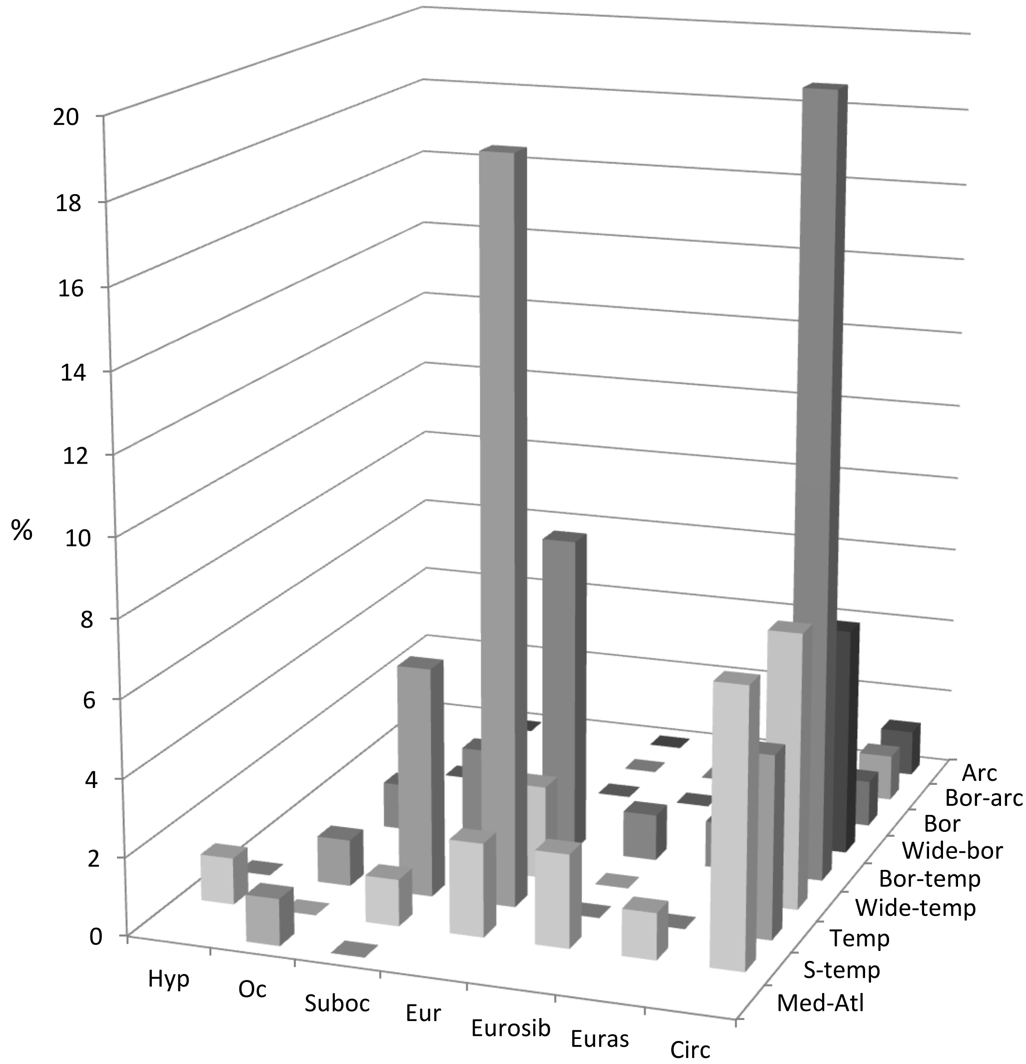

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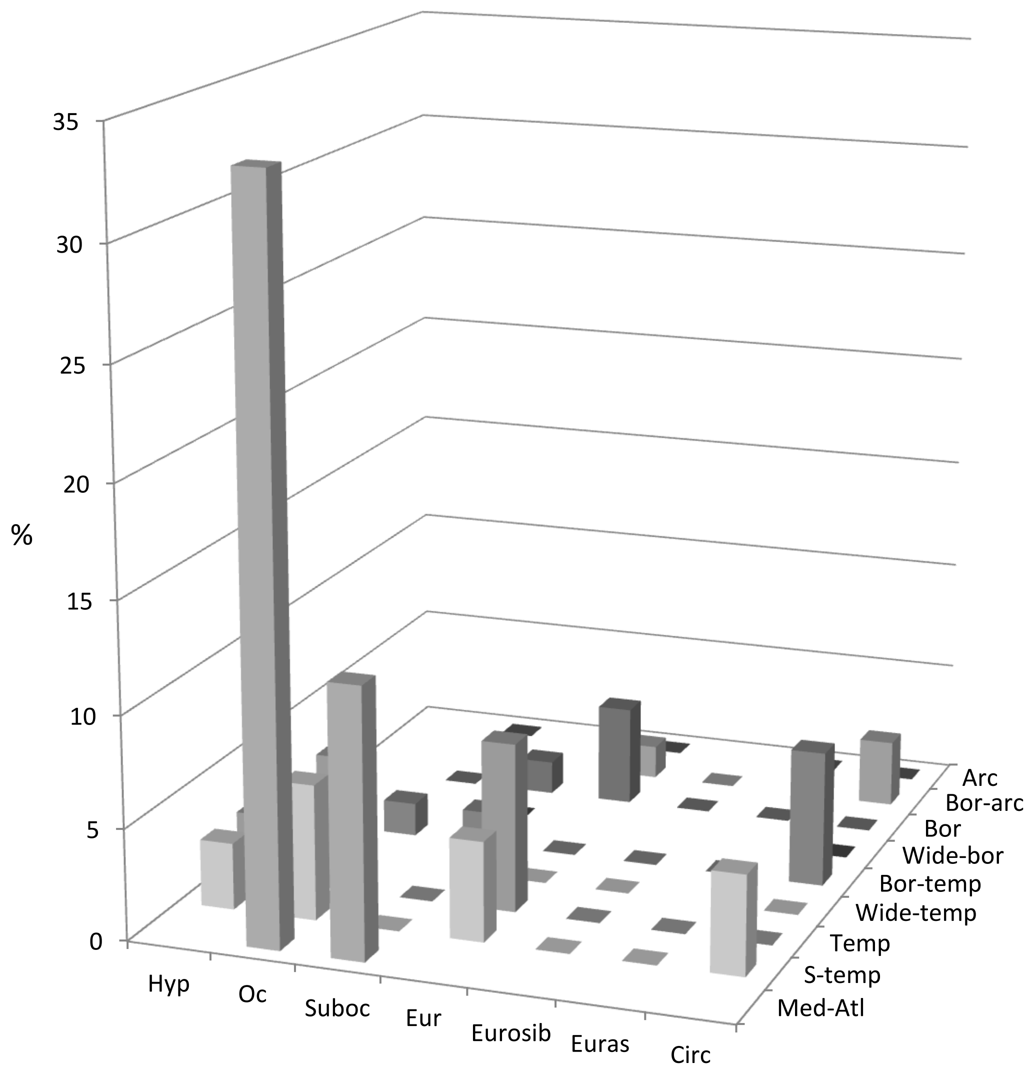

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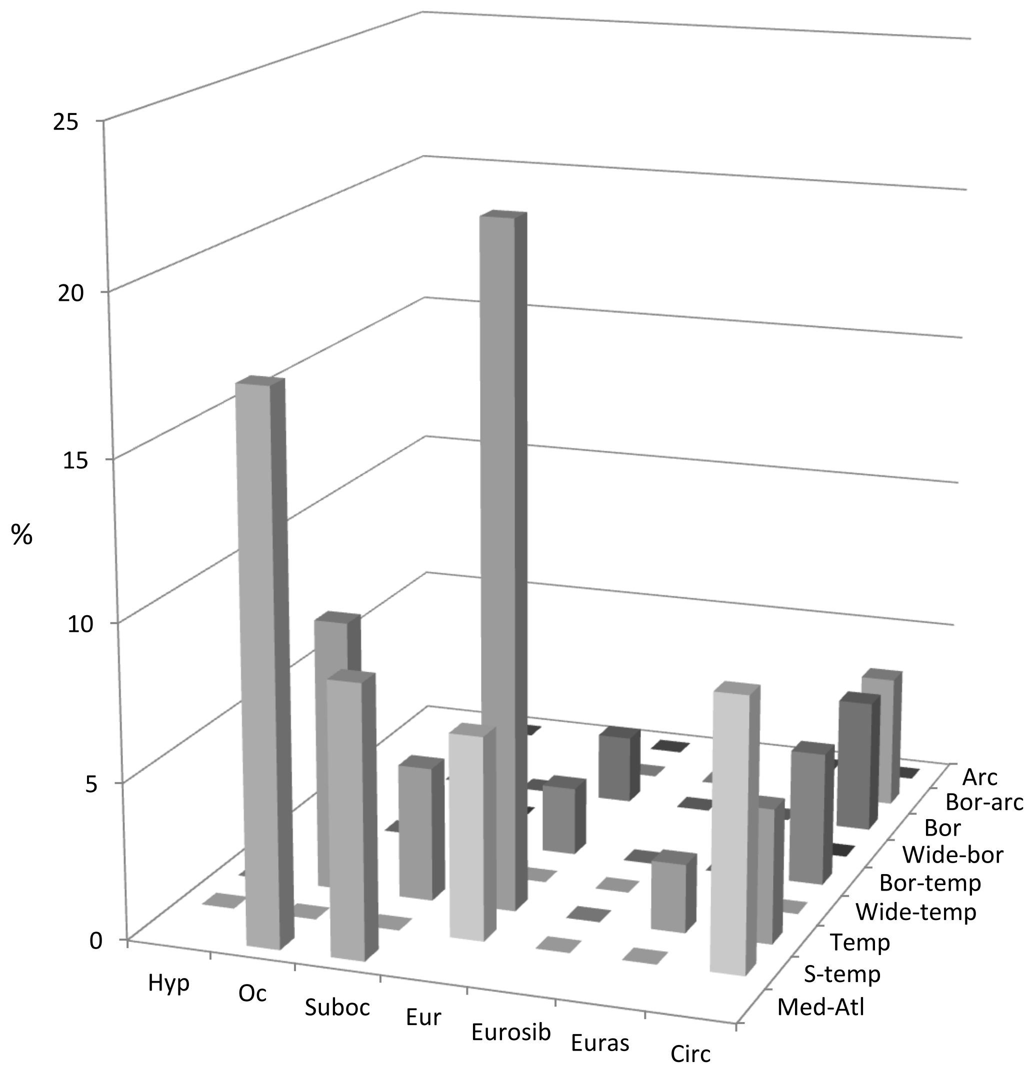
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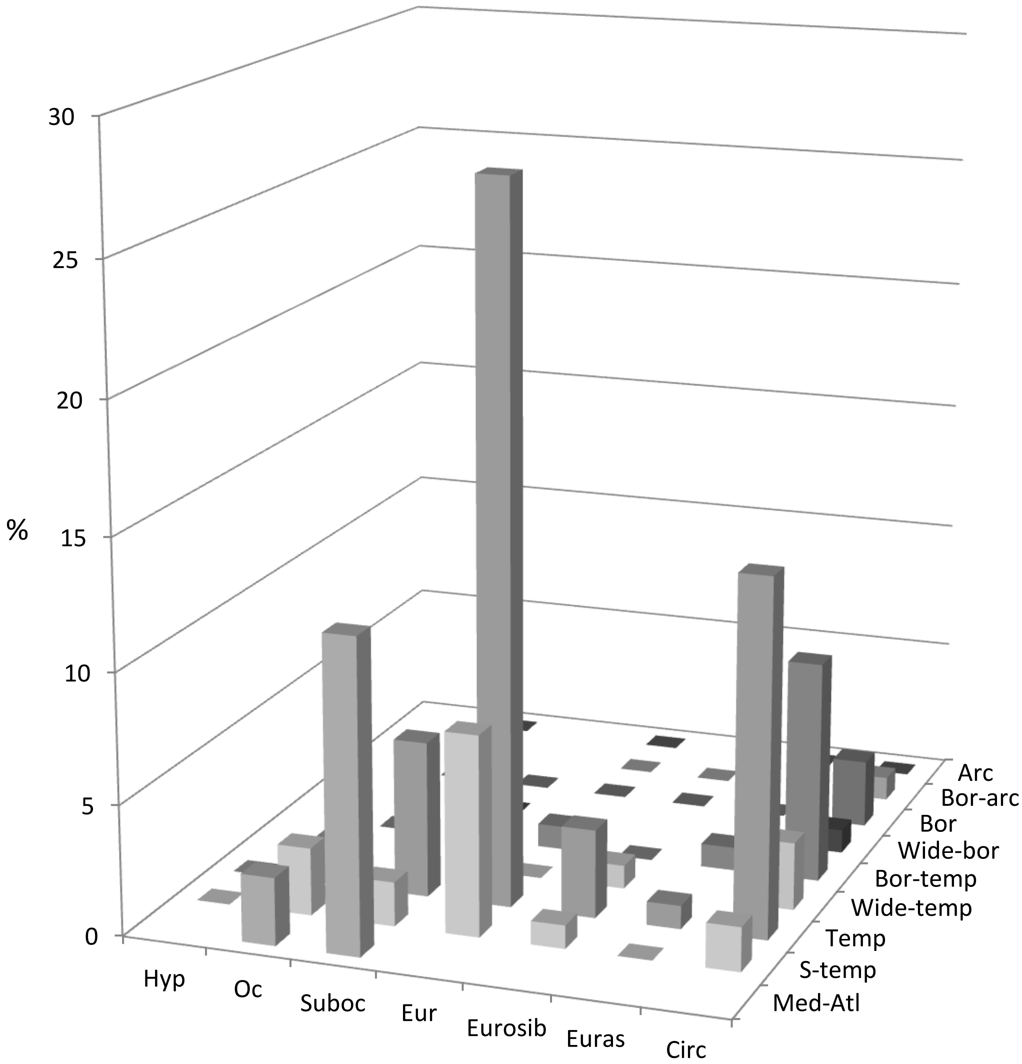

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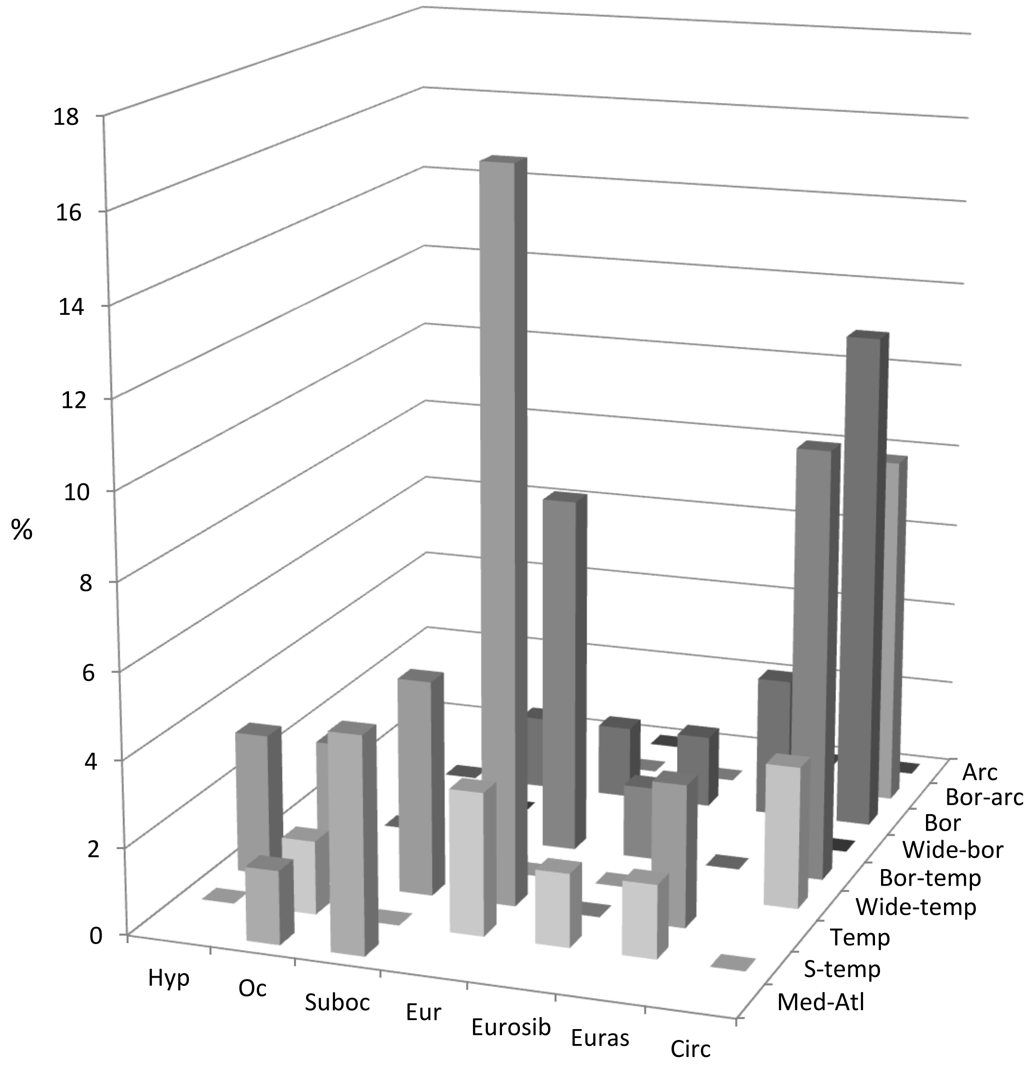
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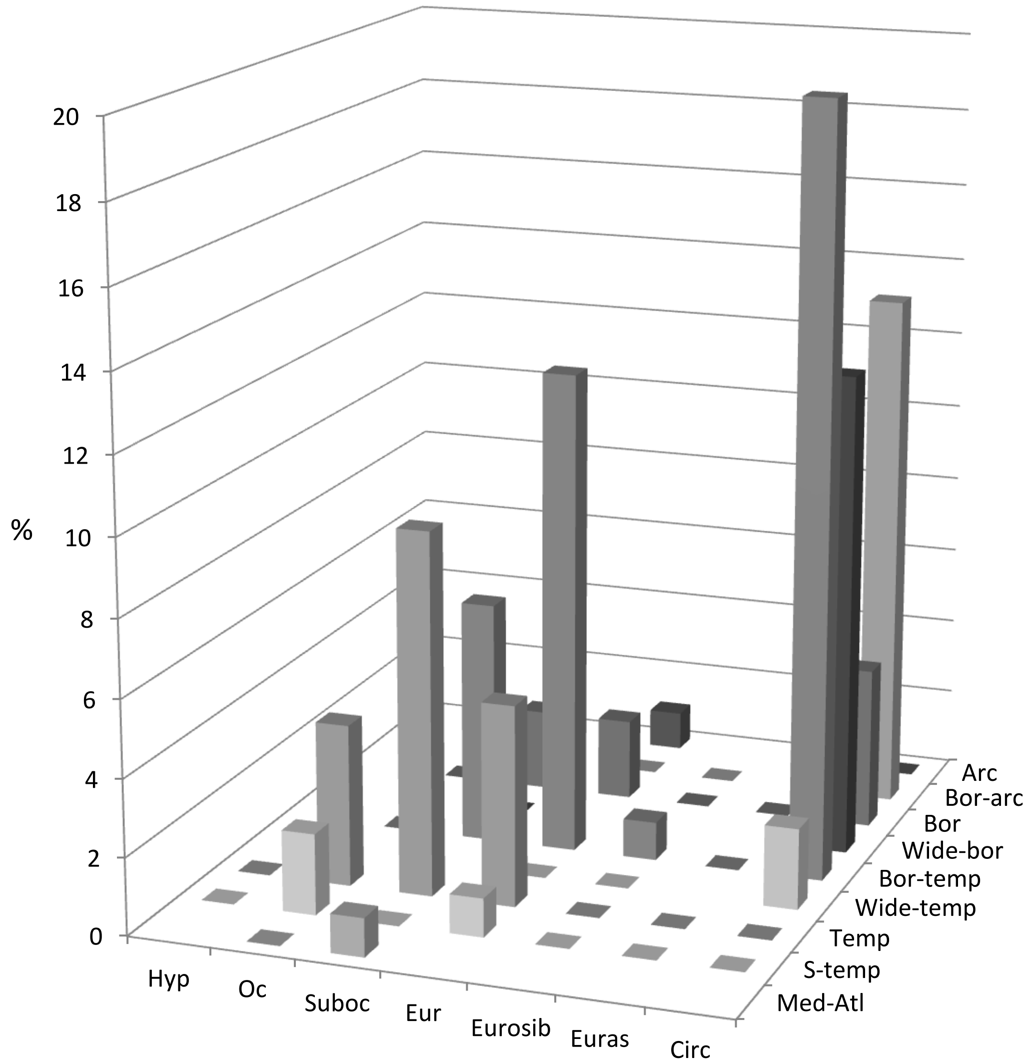

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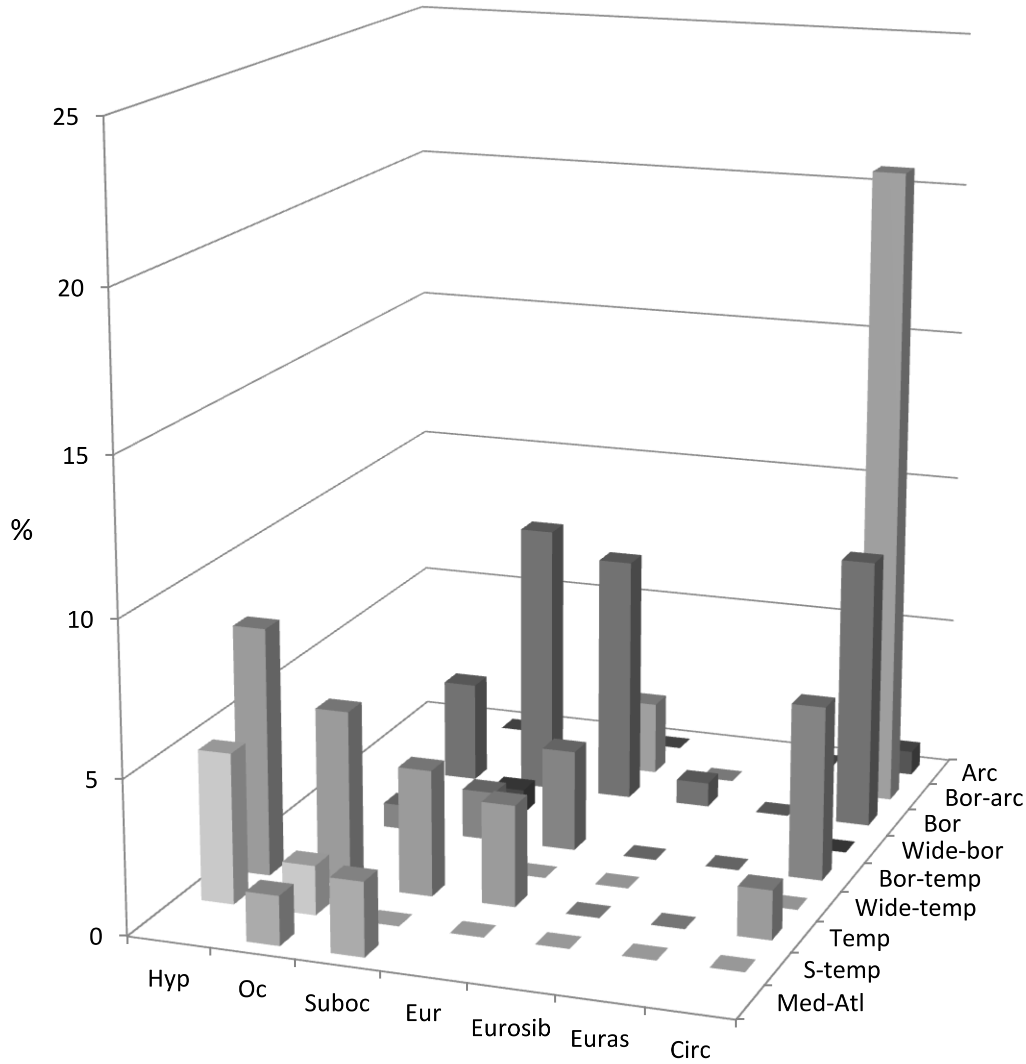

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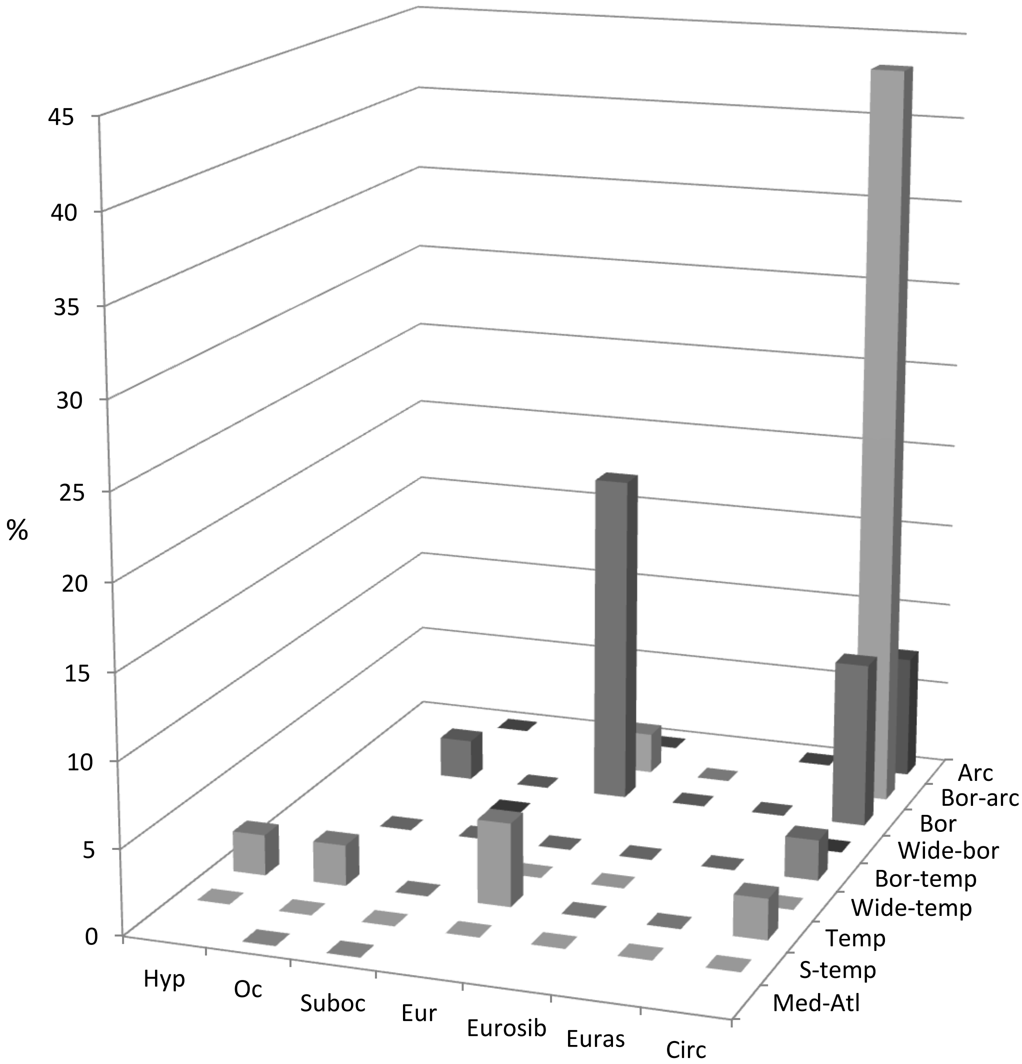
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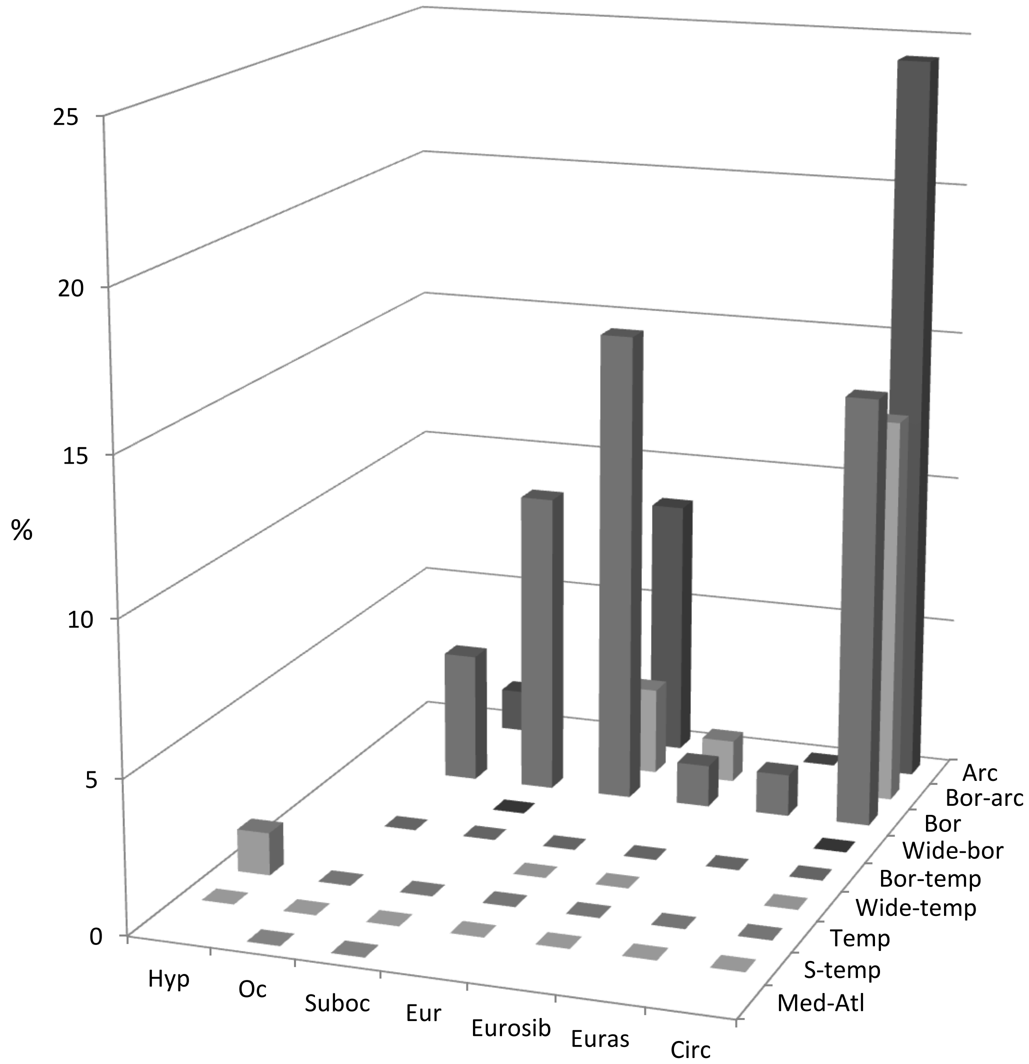

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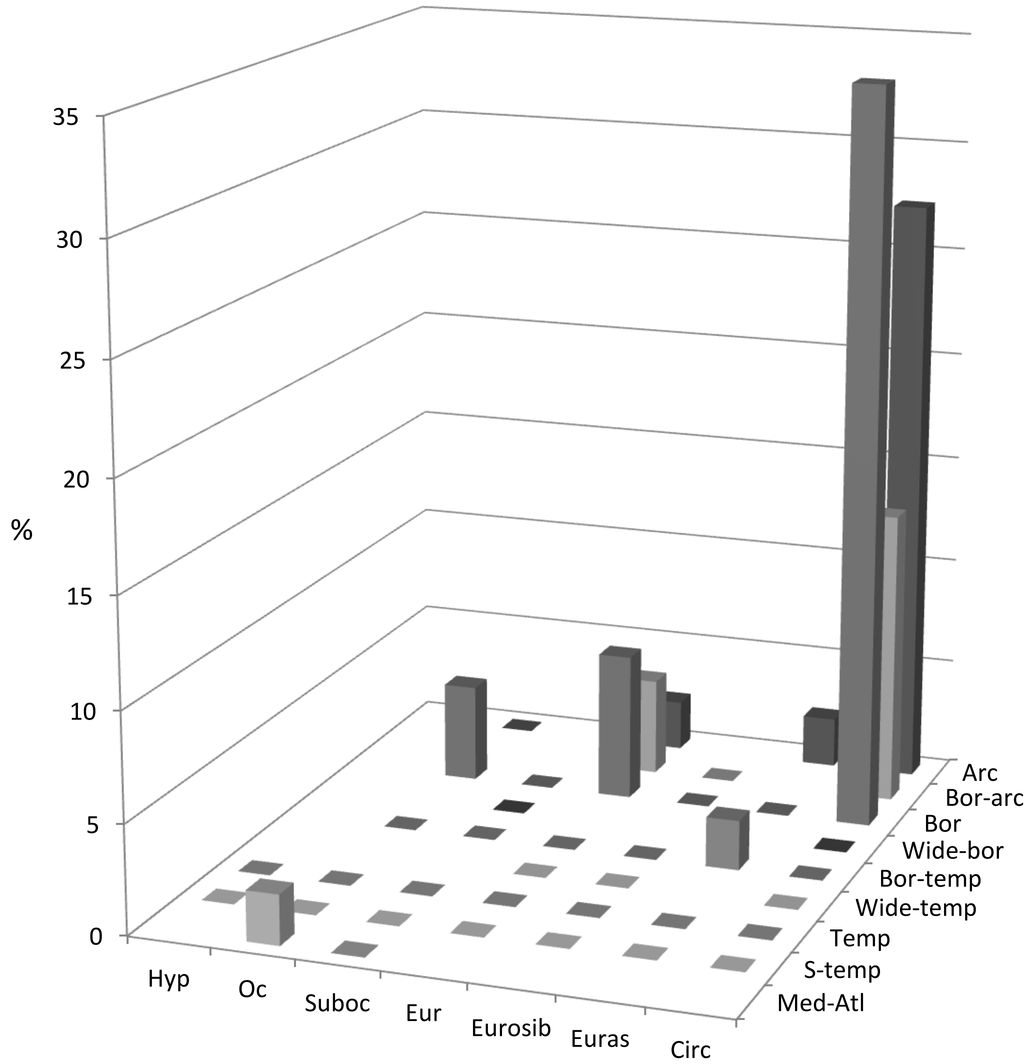
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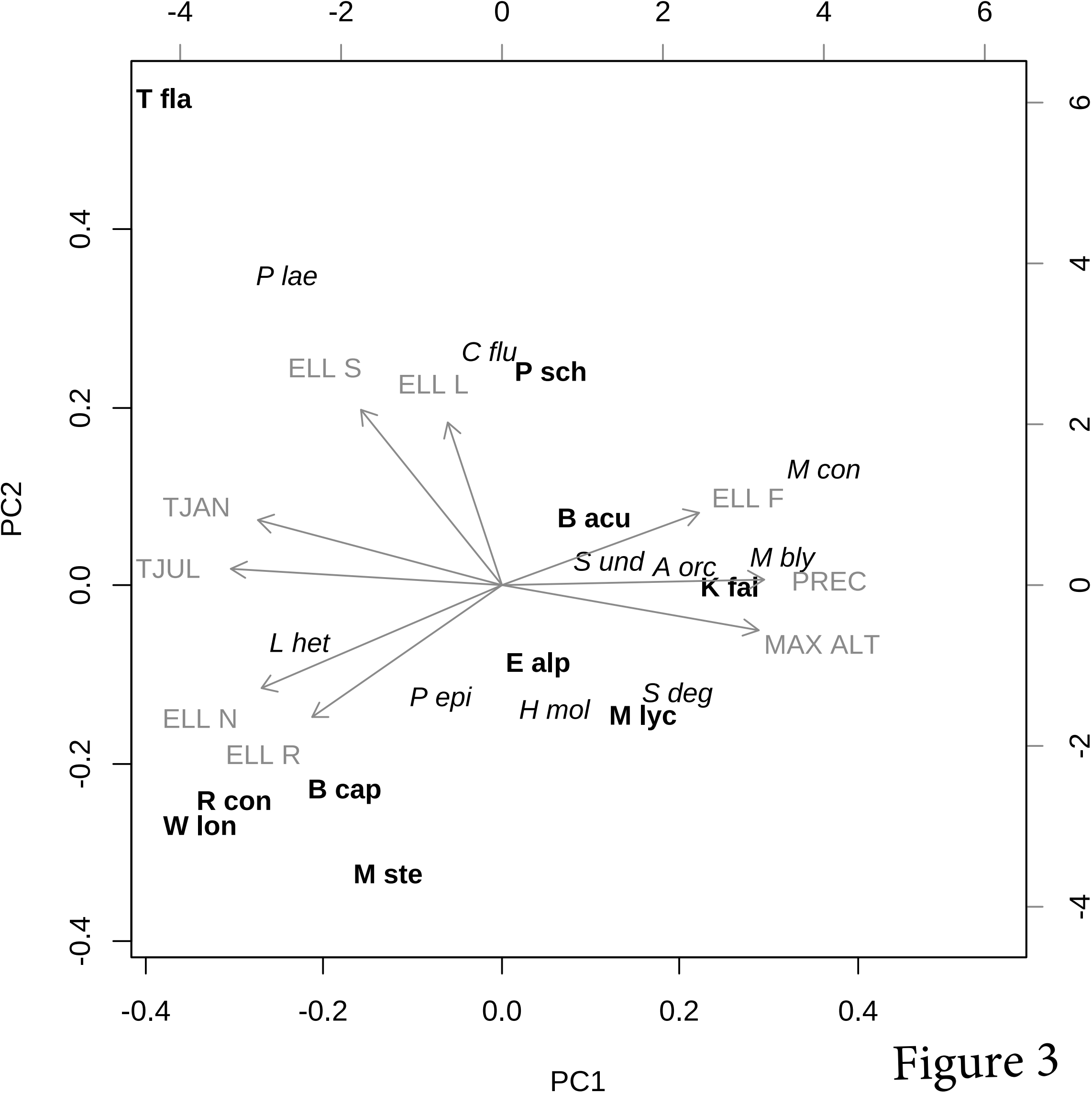
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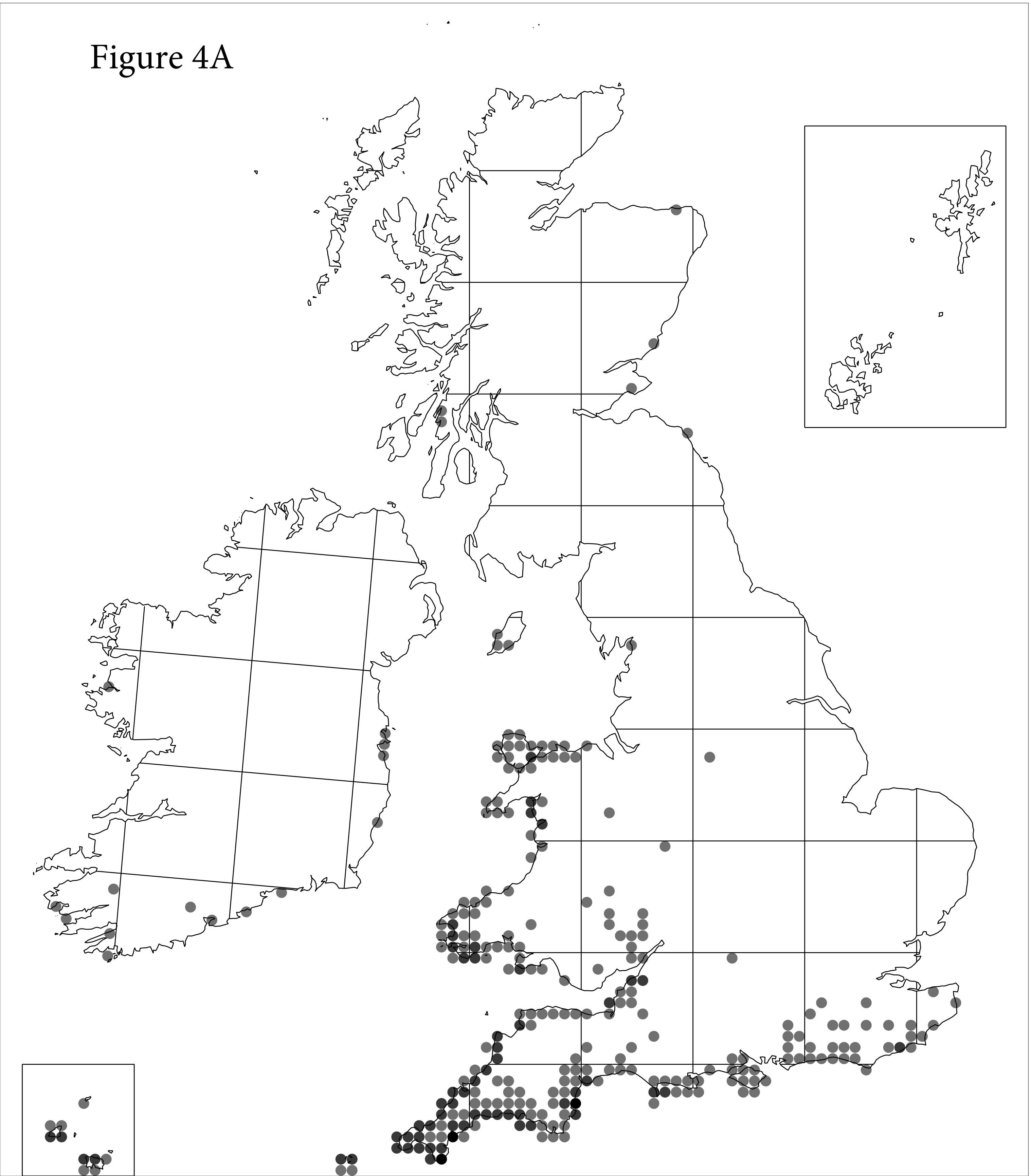
Figure 3

Figure 4A



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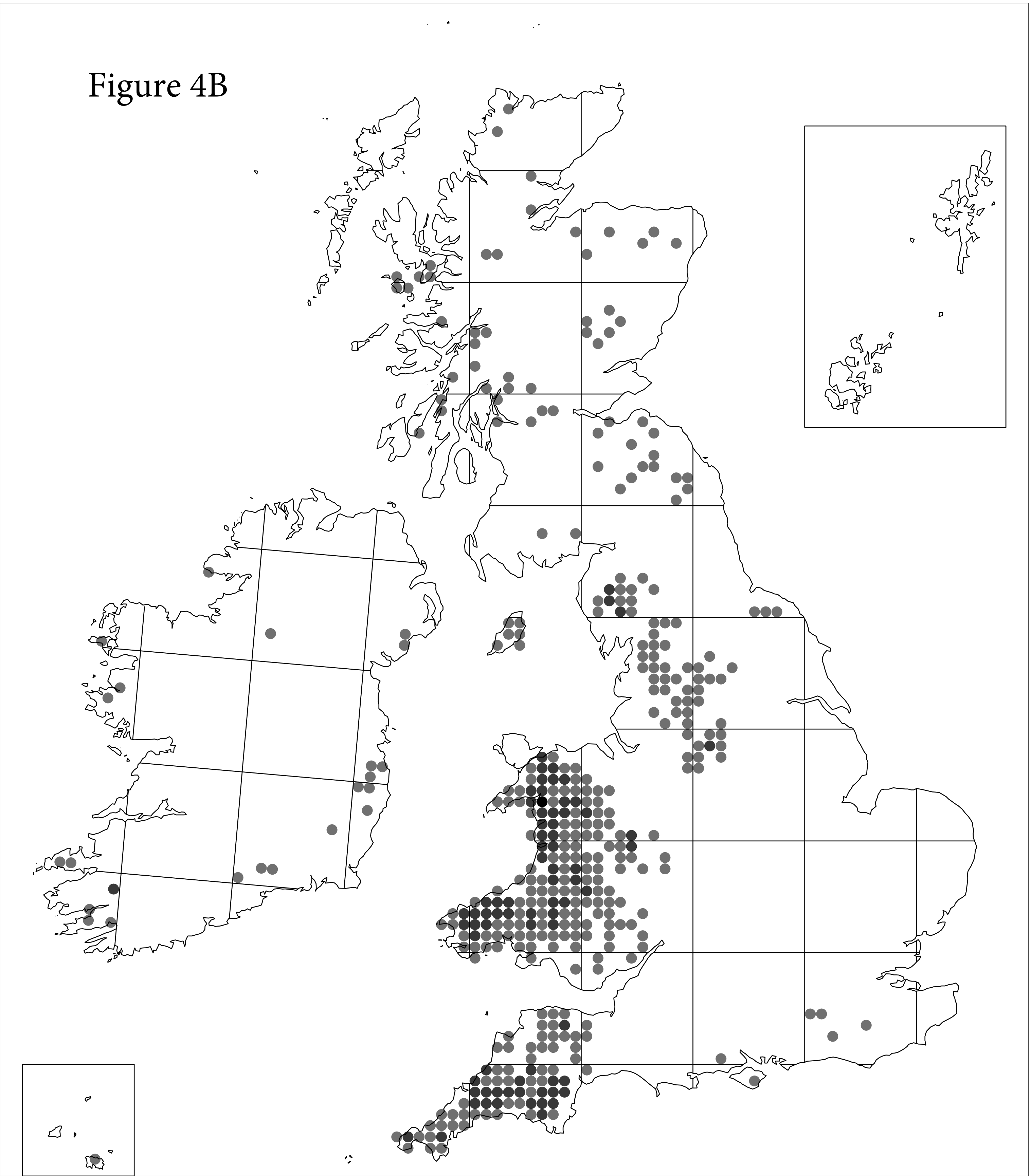

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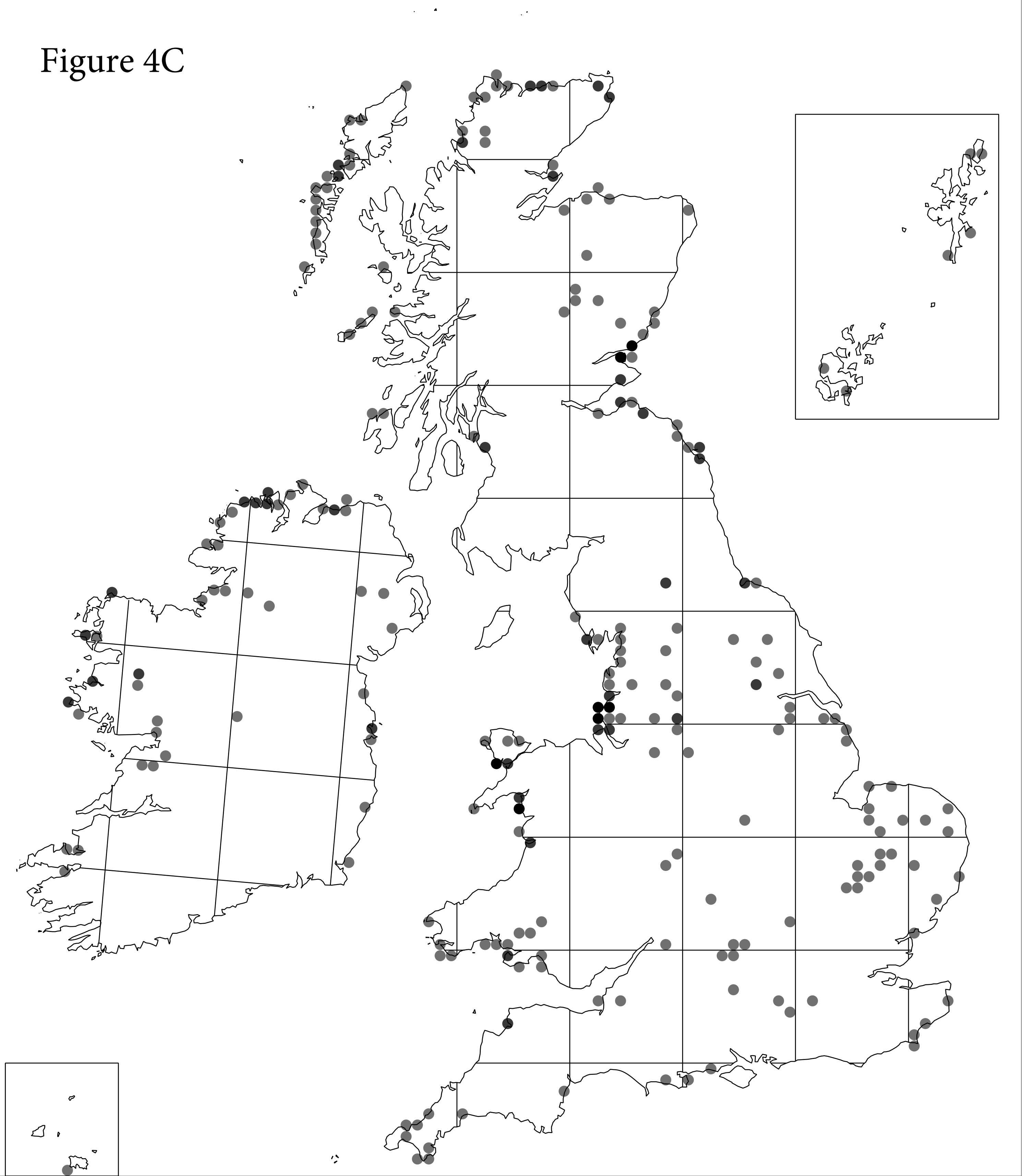

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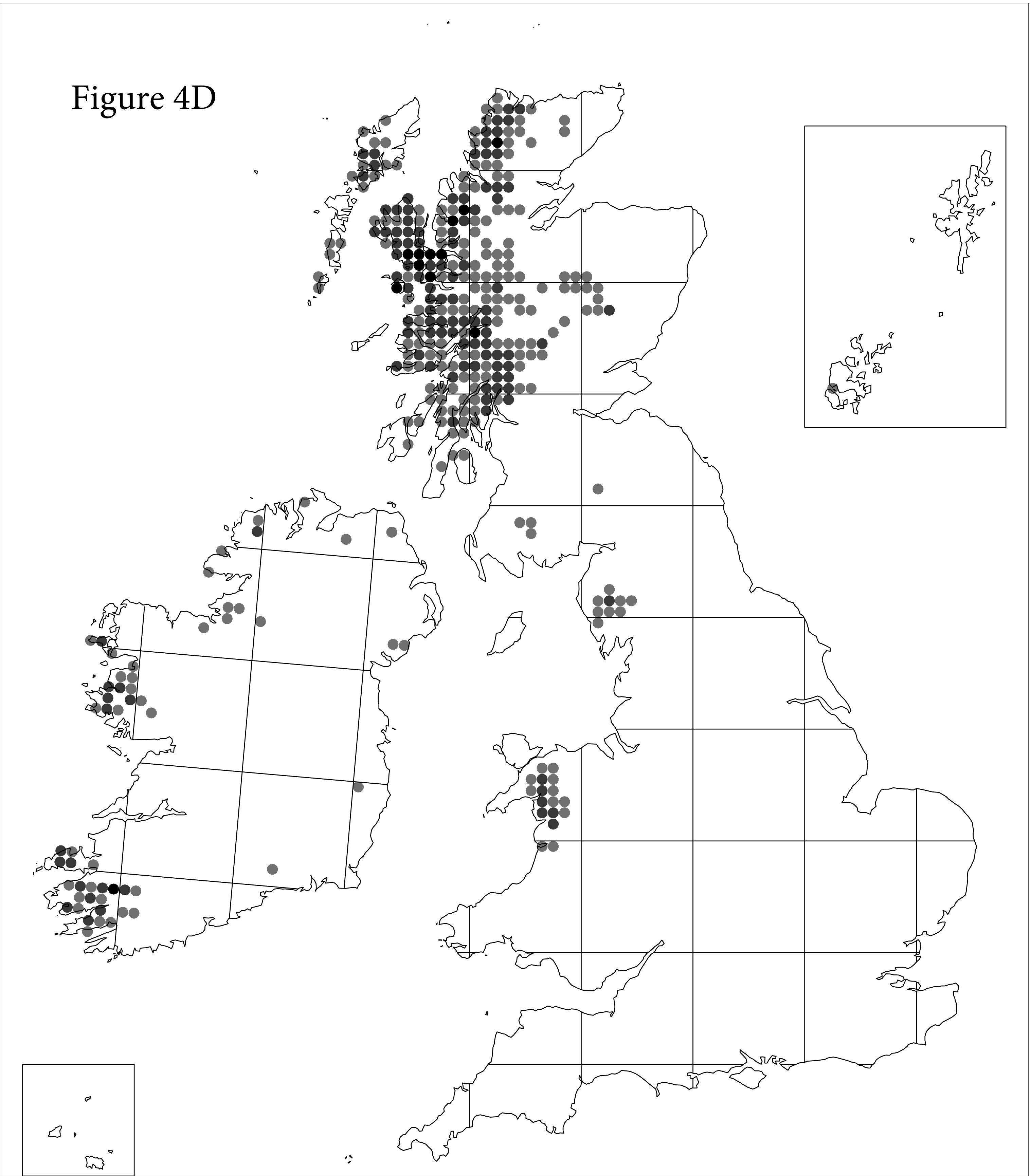

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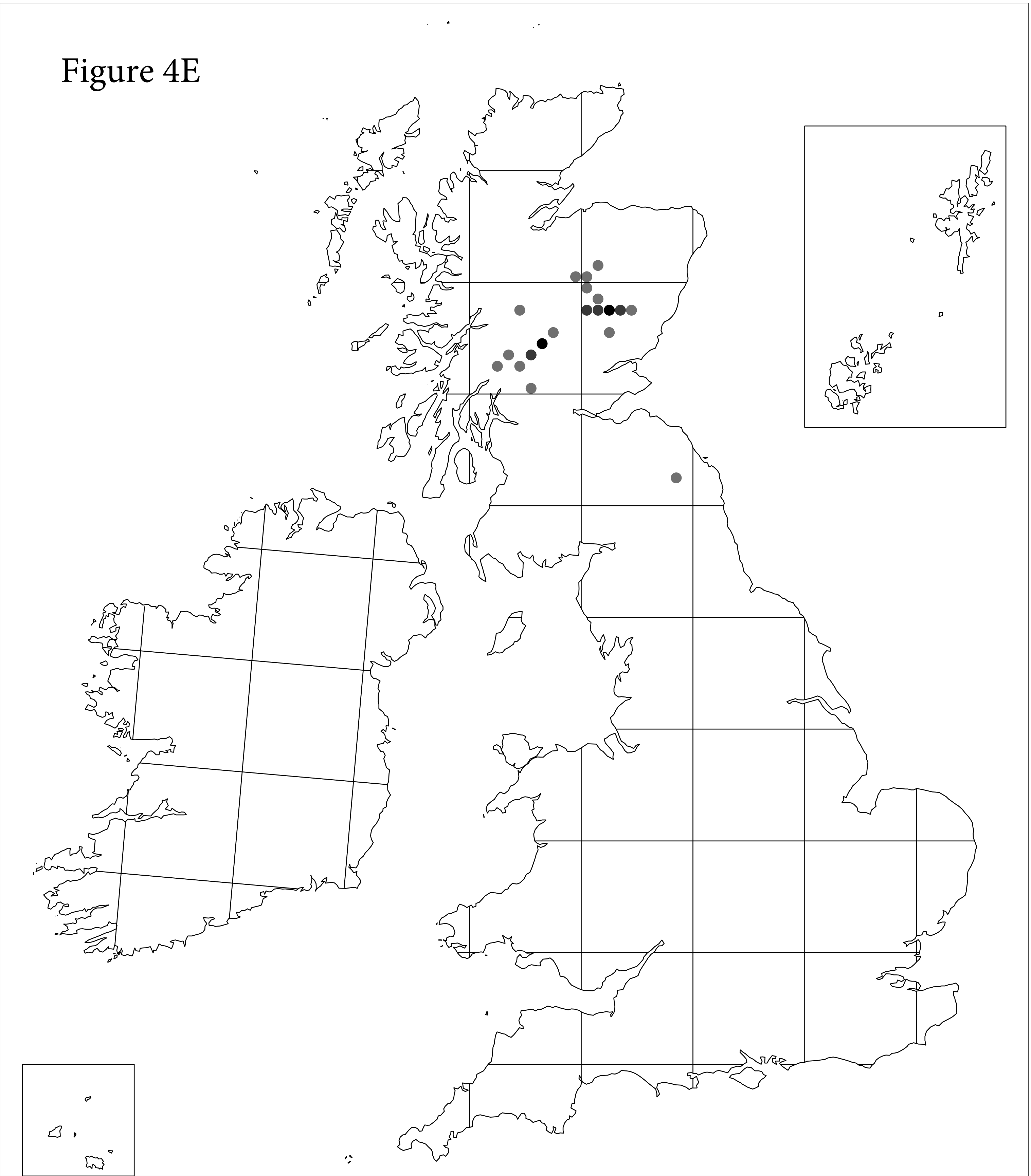

Figure 4F