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Biogeographical patterns in the British and Irish flora

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The hectad (10 × 10 km square) distributions of the 1405 native British and Irish vascular plants were classified by the SPHERIKM cluster analysis program into 20 clusters, each of which is characterised by the key species used to initiate the cluster. The clusters reflect the influence of climate, altitude, geology and habitat on distribution patterns at this scale. Clusters with restricted distributions have high concentrations of threatened species, particularly the *Medicago sativa* cluster, centred on Breckland (55% of the species are threatened in Britain, although only 29% are regarded as priorities for conservation), and the *Carex atrata* cluster of montane species (45% threatened, and 49% conservation priority species). Some clusters are composed predominantly of species with similar European distributions whereas others are much more phytogeographically heterogeneous. A comparison with a similar analysis of the distribution of British and Irish mosses and liverworts reveals many similarities, especially between the vascular plants and the mosses, although there are many more common vascular plants than bryophytes and many more coastal species.

Keywords: Climate, Cluster analysis, Coast, Geology, Phytogeography, SPHERIKM, Threat

Introduction

The systematic collection of information on the distribution of British and Irish vascular plants has been a major preoccupation of botanists for over 150 years. Initially, records were summarised for groups of counties, called ‘provinces’ in Britain (Watson 1847–59) and ‘districts’ in Ireland (Moore & More 1866), then for sub-provinces (Watson 1872), vice-counties (Watson 1873–74; Praeger 1901) and latterly for 10-km grid squares (Perring & Walters 1962). However, there have been relatively few attempts to analyse patterns of distribution revealed by the data which have been compiled so meticulously. Watson (1847–59) did use the data he had collected on the occurrence of species in provinces to identify the ‘types of distribution’ shown by British species. His ‘types’ were widely used in the 19th century by the authors of county floras to analyse the phytogeographical make-up of the plants in their areas (Preston & Hill 1997), but they were replaced in the 20th century by classifications based on the wider distribution of species, following E.J. Salisbury (1932) and J.R. Matthews (1937, 1955). Praeger (1902) devised a similar classification of Irish plants into distributional types but these were never widely used.

The *Atlas of the British Flora* (Perring & Walters 1962) provided distribution maps which, because of their finer scale, revealed much closer correlations with ecological factors such as altitude, climate and geology than had been apparent from previous maps. At the same time methods of numerical classification were being devised which provided more objective ways of classifying distribution patterns than earlier classifications by eye and expert judgement. Proctor (1967), for example, analysed the vice-comital distribution of British liverworts by Association Analysis. However, for decades it was not possible to apply numerical methods to the large datasets generated by grid-square recording, which for British and Irish vascular plants involves presence/absence records of over 1400 native species in over 3500 10-km grid squares. Some studies were based on a sample of species: Hill (1991), for example, analysed the British distribution of 20 species of vascular plants and 20 species of birds, and Hill & Dominguez Lozano (1994) selected one in eight British liverworts (37 species) for their study in order ‘to restrict the problem to a manageable size’.

The BSBI’s resurvey of the British and Irish flora in 1987–99 resulted in an updated atlas and accompanying database at the 10-km square scale. Patterns of occurrence of species in Britain and Ireland were analysed by Preston & Hill (1997) and Preston *et al*. (2002) in relation to a revised classification of the wider European and extra-European distribution of the species, and to their history as natives, archaeophytes and neophytes. However, these studies examined the distribution of species with particular characteristics, rather than classified all the species’ distributions into groups based solely on geographical occurrence.

It has now become possible to analyse the large datasets generated by European or national atlas projects, and this has stimulated a new interest in ‘biogeographical regionalizations’ (Kreft & Jetz 2010). Typically, such studies seek to recognise biogeographical elements (groups of species with a similar distribution) or biogeographical regions (areas with a similar biota). We have recently been attempting to develop methods to identify floristic elements by the detection of recurrent patterns in the distribution maps produced by atlas projects. We started with a study of European vascular plants, and then analysed British and Irish mosses and liverworts (Finnie *et al*. 2007; Preston *et al*. 2011, 2013). The bryophyte studies have thrown light on the ecological factors controlling the distribution of mosses and liverworts at the 10-km square scale, and have revealed significant differences in the reproductive strategies, conservation statuses and wider ranges of the species comprising different biogeographical elements. In the current paper, we use a method set out by Hill *et al*. (2013) to divide the native British and Irish vascular plants into 20 floristic elements, and examine similar attributes of their component species.

Methods

Data

The dataset we analysed was that used for the *New Atlas of the British & Irish Flora* (Preston *et al*. 2002), which outlines the source of the records. The occurrence of taxa was summarised in 10 × 10-km squares ('hectads'). We restricted our analysis to native or doubtfully native ('native or alien') species, excluding hybrids, archaeophytes and neophytes. Records of infraspecific taxa were included with those of the appropriate species; alien records of native species were excluded from the dataset. All records were included, irrespective of date. Data for 1405 species and 3857 hectads were included in the analysis, giving a total of 1,510,290 species/hectad records. Nomenclature is that of the *New Atlas*, which follows Stace (1997). Ecological and phytogeographical data on species were taken from the PLANTATT spreadsheet, updated from Hill *et al*. (2004) and downloadable from www.brc.ac.uk. In the text below, initial capitals are used to distinguish the Broad Habitats for which species are listed in PLANTATT (e.g. Calcareous Grassland) from less formally defined habitats.

Classification methods

Species were clustered by the SPHERIKM program (Hill *et al*. 2013), which minimizes the within-group dispersion of *k* clusters on the surface of a sphere. In SPHERIKM, unlike most programs for spherical k-means clustering, each species is weighted by a fixed power *p* of its frequency, so that the commoner species get greater weight. If species *j* has n_j occurrences, then it has weight $(n_j)^{0.5*p}$. This set of weights is called W*p*. For the native vascular plants, we applied only the three weighting schemes W0, which is unweighted, W0.5 and W1. For the analysis presented here, we used the perpendicular spherical k-means option (PSKM) with weights W0.5. SPHERIKM first identifies 'key species' and then uses these as 'seeds' to initiate clusters. Each cluster was named after its key species. The fit of each species to its cluster was measured by *S*, the cosine of the angle between the species and its cluster centroid (note that this terminology follows Preston *et al*. 2011, 2013, whereas *S* is used in a different sense by Hill *et al*. 2013). Having derived *k* clusters, SPHERIKM goes on to arrange them in a hierarchy. The hierarchy was calculated by Ward's method, which amalgamates clusters in pairs, at each stage selecting the amalgamation that minimally increases the average within-group dispersion (see Hill *et al*. 2013). The hierarchy from Ward's method was represented as a tree by means of Dendroscope (Huson *et al*. 2007).

Distribution clusters

The number of species in each cluster is given in Table 1, with data on their average range size, the percentage of species at their northern limit in our area and the proportion of extinct and threatened species and of conservation priority species in Britain. Details of height and life-form are provided in Table 2, the preference of the species for Broad Habitats is summarised in Table 3, and further information on their ecological attributes is given in Table 4. The distribution of the species in each cluster in Britain and Ireland is summarised as a coincidence map and their phytogeographical affinities are illustrated in Figures 1–7. The phytogeographical classification is that of Preston & Hill (1997). 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 Oceanic 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, and a small category for Mediterranean-montane species. The clusters are described individually below, and their most characteristic species are listed in the Appendix. To avoid undue repetition, 'group' is often used as a synonym of cluster.

Romulea columnae *cluster (57 species)*

This has the most restricted distribution of the 20 clusters (Figure 1A). It includes all the plants which are confined as natives to the Channel Islands in the British Isles (e.g. *Orchis laxiflora*, *Ranunculus paludosus*) and the sole species confined to the Lizard peninsula (*Juncus pygmaeus*). It also includes those which occur in the Channel Islands and also have very restricted ranges in Britain, on the Lizard peninsula (e.g. *Herniaria ciliolata*, *Isoetes histrix*), the Isles of Scilly (e.g. *Ornithopus pinnatus*, *Viola kitaibeliana*), the New Forest (e.g. *Galium constrictum*, *Ludwigia palustris*) or at other sites (e.g. *Bupleurum baldense* and *Romulea columnae* itself). Some more widespread species link this group to the south-westerly *Crithmum maritimum* cluster (e.g. *Rumex maritimus*, *Trifolium occidentale*). The geographical range of these species is characterised by notably high summer and winter temperatures. Although the species grow in a range of habitats, they are particularly frequent in two coastal Broad Habitats (Supralittoral Rock and Supralittoral Sediment) and in open, dry and nutrient-poor microhabitats. A high proportion of species are annuals, and the species have a lower average height than do those in any other cluster except the *Carex atrata* group at the other end of the phytogeographical spectrum. There are many species with Mediterranean-Atlantic ranges in Europe (Figure 1B), and 65% reach their northern European limit in our area. The proportion of threatened species in Great Britain is higher than that in any cluster other than the eastern *Medicago sativa* group, although the proportion of priority species is much lower.

Crithmum maritimum *cluster (72 species)*

These species have more widespread south-westerly ranges than those in the *Romulea columnae* cluster (Figure 1C). Almost half have strongly coastal distributions, including all the most characteristic species in the cluster (*Beta vulgaris*, *Catapodium marinum*, *Lavatera arborea*), but the group also includes species which occur inland in S.W. England and S. Wales (e.g. *Agrostis curtisii*, *Sibthorpia europaea*). The hotspots for the group are in Cornwall (Lizard peninsula, West Penwith, north Cornish coast) and Devon (Braunton Burrows). Not surprisingly, the species are concentrated in coastal Broad Habitats. Their ranges have a higher mean January temperature than those of any of the clusters other than *R. columnae*, but the mean July temperature is lower than that of several other southern clusters (*Clematis vitalba*, *Hippocrepis comosa*, *Limonium vulgare*, *Medicago sativa*, *Tamus communis*) and the mean precipitation is higher than these southern groups although still lower than the average for the British Isles as a whole. The wider ranges of these species are broadly similar to those in the *Romulea columnae* cluster, but Mediterranean-Atlantic species are less predominant and the Oceanic Temperate and Oceanic and Suboceanic Southern-temperate elements are very well represented (Figure 1D). Over half the species reach their northern limit in our area.

Clematis vitalba *cluster (73 species)*

These are species of southern England, extending westwards along the coast of Wales (Figure 1E). The cluster includes species of many lowland habitats but those of Broad-leaved Woodland and (especially) Boundary & Linear Features are particularly well represented. Despite the relatively wide range of these species, some 27% are threatened. Many species have European Temperate ranges but there are also numerous species from the Southern-temperate and Mediterranean-Atlantic elements (Figure 1F); half the species are at their northern limit in our area.

Hippocrepis comosa *cluster (68 species)*

It is immediately apparent from the distribution map (Figure 2A) that these are species of the English chalk and oolitic limestone. The hotspots for the species in this element are the Cotswolds, Chiltern Hills and North Downs. The species are almost confined to three Broad Habitats, Calcareous Grassland (48%), Broad-leaved Woodland (28%) and Boundary & Linear Features (10%). They grow in drier and more base-rich sites than the plants in any other cluster; they are also found in less fertile sites than the species in the more widespread *Clematis vitalba* cluster. A notable feature of the life-form spectrum is the high proportion of geophytes in the cluster, which reflects the large number of orchids in this group. Many of the species have Temperate (especially European Temperate) ranges but there is also an interesting minority with Submediterranean-Subatlantic ranges (Figure 2B). Many of the species are threatened (45%) and regarded as conservation priorities (34%).

Medicago sativa *cluster (38 species)*

This is the smallest group and one of the most restricted in range (Figure 2C). The most characteristic species, including *Medicago sativa* itself (which here refers to the native subsp. *falcata*), are rarities found in the sandy soils of Breckland. There are concentrations of species of Acidic Grassland and Fen, Marsh & Swamp, the latter reflecting the presence in the cluster of some wetland species from Fenland and Broadland (e.g. *Carex appropinquata*, *Lathyrus palustris*, *Peucedanum palustre*). There is therefore a wide variation in Ellenberg F values in the cluster, and to a lesser extent in Ellenberg R, but mean Ellenberg N values are significantly lower than those for the flora as a whole. The eastern distribution of the species in Britain is reflected in the greater predominance in this cluster, compared to the *Clematis vitalba* and *Hippocrepis comosa* clusters, of Eurosiberian, rather than European, Temperate and Southern-temperate species (Figure 2D). Few species reach their northern limit in our area, most extending further north in mainland Europe. Over half the species (55%) are threatened in Britain, the highest concentration in any cluster. although only 29% are treated as conservation priorities.

Limonium vulgare *cluster (59 species)*

This is, with the more widespread *Glaux maritima* cluster, one of the two predominantly coastal clusters; these species are concentrated on the soft coasts of south and south-east England (Figure 2E). Many are salt-marsh plants but there are also species of dry coastal grassland (e.g. *Hordeum marinum*), coastal shingle (e.g. *Lathyrus japonicus*) and brackish waters (e.g. *Ruppia cirrhosa*). The proportion of annuals is higher than in any cluster other than the *Romulea columnae* group. Most of the species have Southern-temperate or Mediterranean-Atlantic ranges. Unlike the *Medicago sativa* group their eastern range in England is not a reflection of easterly wider ranges; most have Oceanic, Suboceanic or European ranges (Figure 2F).

Oenanthe crocata *cluster (55 species)*

In Britain these species are concentrated in south-west England and Wales, with extensions eastward to the Weald and northwards along the coast to south-west Scotland; in Ireland they are concentrated in the south, and otherwise show a centrifugal distribution, avoiding the calcareous central plain (Figure 3A). They are rather thinly dispersed, and few 10-km squares support >50% of the species. They are found in a wide range of habitats, and Inland Rock is the only lowland Broad Habitat which is markedly over-represented. The most distinctive ecological feature of the species in the group is that they are strongly calcifuge; only the montane *Alchemilla alpina* cluster has a lower mean Ellenberg R value. Half the species on our flora which are native to Ireland but not Britain (8 out of 16) are allocated to this element. The species are drawn primarily from the Oceanic and European Temperate elements (Figure 3B), and 53% are at their northern limit in our area. The proportion of threatened and priority species in Britain is not high.

Tamus communis *element (80 species)*

These species are more widespread than those in the *Clematis vitalba* element, being frequent in much of southern and central England though they fade out in south-west England and Wales and are poorly represented in Ireland (Figure 3C). The *Tamus communis* and *Stachys sylvatica* clusters have the highest proportion of trees and shrubs (although there are as many tree and shrub species in the larger *Urtica dioica* cluster), and the mean maximum height of plants in these two clusters exceeds three metres. Like the *Clematis vitalba* cluster, there are many species of Boundary & Linear Features in this cluster, and a moderately high proportion Broad-leaved Woodland species, but there are also concentrations of plants of Neutral Grassland and Calcareous Grassland. The ecological parameters show that the species tend to occur in relatively dry, calcareous habitats. Phytogeographically, the cluster is drawn to a remarkable extent from species with European and Eurosiberian distributions (Figure 3D). Very few species in this cluster are threatened.

Lemna trisulca *element (70 species)*

Although the plants in this cluster have a similar overall range to those of the *Tamus communis* element in England and Wales (Figure 3E) they are very different ecologically. Over half the species in the cluster are hydrophytes, and almost all are wetland and waterside species found in three Broad Habitats, Fen, Marsh & Swamp, Standing Waters & Canals and Rivers & Streams. This is reflected in the concentrations in Fenland and Broadland, as well as the good representation of species in central Ireland, and especially in the vicinity of Lough Erne and Lough Neagh. The high Ellenberg F, R and N values indicate that they are plants of calcareous, eutrophic waters. Despite the ecological coherence of the cluster, the species are drawn from a wide range of phytogeographical elements. The proportion of Circumpolar species is the highest for any lowland cluster (Figure 3F), a reflection of the broad distributions of many aquatic plants.

Epilobium hirsutum *cluster (85 species)*

These species are not only widespread but also frequent throughout much of lowland Britain and Ireland; they become less frequent in western Ireland, the uplands of mid Wales, the Pennines and the Southern Uplands of Scotland and are largely absent from the Highlands and Islands (Figure 4A). They grow in a wide range of lowland habitats, although the Hydrophyte life-form and the Fen, Marsh & Swamp and Rivers & Streams Broad Habitats are particularly well represented. Ecologically, the species grow in rather more calcareous and nutrient-rich habitats than average. Most have Temperate or Southern-temperate wider ranges (Figure 4B), and none is threatened in Britain.

Chaerophyllum temulum *cluster (93 species)*

In eastern Britain the species in this cluster have similar ranges to those of the *Epilobium hirsutum* cluster (although they are notably less frequent in the species-poor areas of reclaimed land around The Wash). However, they become increasingly less frequent in western Britain and they are rare in Ireland, where the only appreciable concentrations are in the north and east (Figure 4C). The main differences in the Broad Habitats of these two clusters are the much greater concentration of Broad-leaved Woodland species and the much poorer representation of wetland species in the *C. temulum* cluster. The clusters also differ in the wider distribution of their species; whereas the *E. hirsutum* cluster is composed almost equally of Temperate and Southern-temperate species, the *C. temulum* group consists primarily of Temperate species but also includes a substantial minority with Boreo-temperate affinities (Figure 4D).

Stachys sylvatica *cluster (86 species)*

The *Epilobium hirsutum*, *Stachys sylvatica* and *Urtica dioica* clusters form a sequence characterised by species with increasingly ubiquitous ranges. Plants in the *S. sylvatica* cluster are infrequent only in western Ireland, around The Wash, in the highest and most northerly parts of Scotland and in the Outer Hebrides and Northern Isles (Figure 4E). As mentioned above, the highest proportion of trees and shrubs is found in this and the *Tamus communis* cluster. There is a higher percentage of Broad-leaved Woodland species in this than in any other cluster, and this is reflected in the low Ellenberg Light value. The other species occur in a broad range of habitats. They have broad, Temperate or Boreo-temperate wider ranges (Figure 4F) and none is threatened in Britain.

Urtica dioica *cluster (151 species)*

This is much the largest cluster and it is comprised of species which occur throughout Britain and Ireland; the most characteristic species are not only ubiquitous at the 10-km square scale (Figure 5A) but in many areas they are amongst the most frequent species at finer scales. The members of the cluster have a wide range of broader distributions, excluding only the most extreme elements (Arctic, Boreo-arctic and Mediterranean-Atlantic). The highest proportions of species with extremely wide world distributions (Wide-boreal and Wide-temperate) are found in this and the following cluster (Figure 5B). The only threatened species in Britain in this cluster, *Coeloglossum viride*, has the least good fit of any of its component species.

Glaux maritima *cluster (57 species)*

This is the coastal equivalent to the *Urtica dioica* cluster, and comprises species which are found all round the coasts of Britain, Ireland and the Channel Islands (Figure 5C). All three coastal Broad Habitats are well-represented, and the Ellenberg values confirm that the species grow in open, saline habitats. Many are strictly coastal but some extend inland, most obviously onto the sandy soils of Breckland. The species have a very wide range of wider distributions, and the proportion of Circumpolar species is higher than that in any lowland cluster except for that characterised by *Lemna trisulca* (Figure 5D). Few (5%) are threatened in Britain, although 9% are regarded as conservation priorities.

Calluna vulgaris *cluster (60 species)*

The characteristic species of this cluster are extremely common calcifuges of nutrient-poor, often moist, habitats, absent only from those areas of Britain and Ireland with uniformly base-rich soils (Figure 5E). In areas of acidic geology, especially in the north and west, they are amongst the most frequent species. The major Broad habitats of the species are Acid Grassland, Dwarf Shrub Heath, Fen, Marsh & Swamp and Bog. Most of the species have Boreo-temperate or Temperate ranges (Figure 5F), and, like the members of the other very widespread clusters, few are threatened.

Minuartia verna *cluster (44 species)*

This has fewer species than any other cluster and a more restricted distribution than most, centred on the Carboniferous Limestone in northern England with outliers on the same rock, especially in Somerset, Wales and the Burren (Figure 6A). The 10-km squares with the highest proportion of species are both in the Craven Pennines, in the vicinity of Malham and Upper Wharfedale; interestingly, these are not the squares which include the botanically famous mountains of Ingleborough and Pen-y-ghent although they border these squares. Most of the species grow in the Calcareous Grassland and Inland Rock Broad Habitats, and the Ellenberg values, as expected, indicate that they favour dry, base-rich habitats. The cluster includes both Circumpolar Arctic-montane (*Gentiana verna*, *Minuartia stricta*) and Mediterranean-Atlantic (*Neotinea maculata*) species, but most members have Boreal-montane, Boreo-temperate and Temperate ranges;

Southern-temperate species are completely absent (Figure 6B). One-third of the species are threatened in Britain, and one-fifth are treated as conservation priority species.

Alchemilla glabra *cluster (66 species)*

In Britain these species are often frequent in the uplands; they have a distinctly easterly bias to their Scottish range, and they extend southwards into England along the Pennine chain (Figure 6C). In Ireland they are northern, with few marked concentrations in the mountains of the west and south. They are essentially upland rather than montane; none is confined to high altitudes but many ascend to high altitudes in the mountains. They occur in a range of habitats, especially Broad-leaved Woodland, Coniferous Woodland, Fen, Marsh & Swamp and Inland Rock; the Ellenberg values indicate that they grow in more shaded sites than the other northern and western clusters. Their wider ranges are centred on the Boreal zone; 46% have Boreal-montane ranges and a further 39% have wider, Boreo-arctic to Boreo-temperate distributions. Oceanic and Suboceanic species are virtually absent, and almost half (47%) have Circumpolar ranges (Figure 6D).

Selaginella selaginoides *cluster (70 species)*

This is a westerly counterpart of the *Alchemilla glabra* cluster, found in the uplands of western Ireland and Scotland, the Lake District and North Wales with a southerly outlier in the Dorset heaths and the New Forest (Figure 6E). The habitats of the species differ in the virtual absence of woodland plants and the reduced proportion of Inland Rock species; plants of wetland Broad habitats (Fen, Marsh & Swamp; Bog; Standing Water & Canals) are more richly represented and account for over half the species in the cluster, and 31% of the species are hydrophytes. There is a small percentage of coastal species. The mean Ellenberg values suggest that the species grow in more open and wetter habitats than those of the *A. glabra* cluster and in very nutrient-poor sites. Whereas the *A. glabra* cluster is unique in including no annual species, the proportion of annuals in the *S. selaginoides* cluster is similar to that in the flora as a whole. The cluster includes three members of the Ericaceae, *Daboecia cantabrica*, *Erica erigena* and *E. mackaiana*, which are usually regarded as native to Ireland but not Britain (but see Foss & Doyle 1988). Although Boreal species are particularly well represented in this cluster, it is phytogeographically heterogeneous. There is a good representation of Circumpolar species (as in the *A. glabra* cluster) but many more Oceanic species than in that cluster (Figure 6F). A similar proportion of species in both these clusters is threatened, but the proportion of conservation priority species in the *S. selaginoides* cluster is much higher.

Alchemilla alpina *cluster (54 species)*

The most characteristic members of this cluster are our commoner montane plants. Their distribution matches that of the highest ground in Britain and Ireland (Figure 7A), although less convincingly in Ireland than in Britain as the species are so much rarer there. Their main Broad habitats are Montane habitats and Inland Rock, with some species from other habitats, especially Calcareous Grassland, Fen, Marsh & Swamp and Bog. Predictably, they grow in areas with low January and July temperatures and high rainfall. Although the group includes a few calcicoles, many species are calcifuge and the mean Ellenberg R value is lower than that of the *Alchemilla glabra*, *Selaginella selaginoides* or *Carex atrata* clusters. The proportion of chamaephytes, generally high in the northern groups, is higher in this cluster than in any other. Over half the species have Arctic-montane distributions, and most of the rest are Boreo-arctic or Boreal-montane (Figure 7B).

Carex atrata *cluster (67 species)*

The very restricted range of the *Carex atrata* cluster is nested within that of the *Alchemilla alpina* cluster (Figure 7C). It includes many of the montane species which are rare in Scotland and very rare or absent from England and Wales. Only five of the 67 species are recorded from Ireland, the most frequent and notable of these being *Dryas octopetala*. The members of the *Carex atrata* cluster grow in areas with much colder temperatures than those which characterise the *A. alpina* cluster. Many of the species are calcicoles and the major concentrations of species are in the Breadalbane Mountains, the Caenlochan-Clova region and in the vicinity of Ben Alder, all three areas described as Grade 1 upland sites by Ratcliffe (1977). Two-thirds of the species have Arctic-montane ranges and the remainder are mostly Boreo-arctic or Boreo-montane (Figure 7D). The cluster includes a high proportion of threatened species, matched or exceeded only by two clusters with very restricted ranges in southern England, and the highest proportion of conservation priority species in any group.

Ecological separation of the clusters

Figure 8 illustrates the results of a Principal Coordinates Analysis of the ecological characteristics of the clusters summarised in Table 4. The first three axes account for 46%, 21% and 15% of the variance. The first axis separates species of base-rich, nutrient-rich and warmer habitats with low rainfall from those with the opposite characteristics. The second axis separates those clusters found in open, saline habitats from the rest. The third axis separates some of those clusters which are close together on the first two axes on the basis of mean winter temperature and nutrient requirements. However, the two widespread, primarily English clusters (*Clematis vitalba*, *Tamus communis*) and the two montane clusters (*Alchemilla alpina*, *Carex atrata*) are scarcely separated on these axes. In each of these cases the cluster with the more restricted range is nested within the range of the more widespread cluster. Two of the most widespread clusters (*Epilobium hirsutum*, *Urtica dioica*) are also close although, surprisingly, the *Stachys sylvatica* cluster, which has a distribution which is intermediate between the two, is separated on the basis of greater shade tolerance.

The cluster hierarchy is presented in Figure 9. The major division is between 13 clusters which are widespread or restricted to the north and west and seven with ranges which are concentrated in England. The group of 13 is initially subdivided into four coastal and nine inland clusters, and the two montane clusters in the latter are then separated from the seven lowland or upland clusters. The most surprising feature of the diagram is the inclusion of the *Epilobium hirsutum* cluster with the smaller, predominantly English clusters, despite its similarity to the *Stachys sylvatica* and *Urtica dioica* clusters.

Comparison with bryophytes

Analogous classifications of the distribution of 300 liverworts and hornworts and of 747 mosses in Britain and Ireland have been published by Preston *et al*. (2011, 2013). The liverworts were classified into 10 clusters and the mosses into 10, 15 and 20 clusters. The similarity of the vascular clusters to the 10 liverwort clusters and the 15 moss clusters, measured by the metric *S*, is shown in Table 5. A different program was used to classify the data, and the coverage of bryophytes in hectads is less complete than that of vascular plants, so some caution is needed when comparing the three classifications.

The vascular plant classification includes three clusters of species which are widespread throughout much of the British Isles (*Epilobium hirsutum*, *Stachys sylvatica* and *Urtica dioica*), together with the *Chaerophyllum temulum* cluster which is widespread in Britain but not Ireland. By contrast, there is one cluster of widespread mosses (*Bryum capillare*) and one of liverworts (*Pellia epiphylla*). Although different clustering programs differ in the extent to which they recognise widespread as opposed to restricted clusters, the occurrence of 30% of vascular plants in these widespread clusters compared to 11% of mosses and 10% of liverworts reveals a very real difference between the vascular plants and bryophytes in the proportion of widespread species. The *Bryum capillare* cluster is closest to the *Stachys sylvatica* (*S*=0.91) and *Urtica dioica* (*S*=0.89) clusters. However, the *Pellia epiphylla* cluster, though not dissimilar to these vascular plant clusters (both *S*=0.84), is actually closest to the *Calluna vulgaris* cluster (*S*=0.86), indicating the rather calcifuge tendency of even the most widespread liverwort group. There is a close moss equivalent to the *Calluna vulgaris* cluster in the *Pleurozium schreberi* cluster (*S*=0.87) of widespread, calcifuge mosses. The predominantly English *Tamus communis* cluster has an equivalent in both mosses (*Rhynchostegium confertum*, *S*=0.88) and liverworts (*Lophocolea heterophylla*, *S*=0.81); the *S* metric indicates that these bryophyte clusters are even more similar to the *Chaerophyllum temulum* cluster (*S*=0.90 and 0.88 respectively) but this may in part reflect the under-recording of bryophytes in Ireland.

South-western groups of species occur in all three taxonomic groups, the *Crithmum maritimum*, *Phaeoceros laevis* and *Scleropodium touretii* clusters. Both mosses and liverworts have three groups which fall along the *Calluna vulgaris*-*Alchemilla glabra*-*Selaginella selaginoides* series of increasing restriction to the north and west in Britain: these are the *Scapania undulata*, *Anastrepta orcadensis* and *Harpalejeunea molleri* clusters of liverworts and the *Pleurozium schreberi*, *Blindia acuta* and *Hylocomiastrum umbratum* moss clusters. The *Harpalejeunea molleri* and *Hylocomiastrum umbratum* clusters are hyperoceanic groups with more restricted ranges than that of the *Selaginella selaginoides* cluster. There are more mosses than liverworts associated with calcareous rock and soil and the *Weissia longifolia* and *Mnium stellare* clusters are broadly equivalent to the *Hippocrepis comosa* (*S*=0.86) and *Minuartia verna* (*S*=0.63) clusters. However, the *Mnium stellare* cluster, though centred on the Carboniferous Limestone of northern England, has its main outliers in different areas to the *Minuartia verna* cluster (e.g. Sligo rather than the Burren in Ireland). The classification of both moss and liverwort distributions subdivides the montane species more than the vascular plant classification, which may be a feature of the different clustering procedure, but general groups of montane species broadly similar to the *Carex atrata* cluster are recognised both for liverworts (*Moerckia blyttii*, *S*=0.84) and mosses (*Kiaeria falcata*, *S*=0.83).

There are inevitably clusters of the vascular plants which are not matched in the bryophytes, as there are 20 clusters rather than 10 for liverworts and 15 for mosses. However, the presence of 116 species (8%) in two coastal clusters indicates that there are many more coastal vascular plants than bryophytes. The *Syntrichia ruraliformis* cluster of mosses is coastal but it includes only 26 species (3%) and they have a very patchy distribution on soft coasts whereas the *Glaux* cluster (*S*=0.53) includes many frequent coastal species. Other vascular plant clusters with no close equivalents amongst either mosses or liverworts are the *Limonium vulgare*, *Romulea columnae* and *Medicago sativa* clusters. The last, which is found drier areas than any other cluster, is particularly distant from any of the bryophyte clusters. The most distant bryophyte cluster to any of the vascular pkant cluster is the *Cladopodiella fluitans* group of liverworts of bogs and other acidic habitats.

Discussion

Number and composition of clusters

The choice of 20 clusters is an arbitrary one. We chose it for convenience after examining a number of possibilities, as it displayed the range of variation in distribution patterns but the number of clusters was not too large to assimilate. Mardia (1979) suggested a rule for selecting the number of clusters, $k=\sqrt{(n/2)}$, which would mean 26 or 27 clusters for vascular plants, but this is just as arbitrary as our choice. Methods for selecting the statistically optimum number of clusters are also available, but the results sometimes conflict with the needs of the user (Hill *et al*. 2013). Thus

Rueda *et al*. (2010) considered that the optimum number of clusters for the distribution of 342 species of European non-marine birds was just three, which we regard as too few to be very informative. By contrast, Hill *et al*. (2013) developed a method based on the Akaike information criterion ('quasi-AIC') which suggested that 164 arable bryophytes were best divided into 24 clusters, too many to represent a succinct overview. In these circumstances there are strong arguments for choosing the number of clusters which is appropriate for the purposes of potential users, rather than accepting a potentially less appropriate but statistically optimum number.

The other factor which clearly influences the result of the classification is the W0.5 weighing of the SPHERIKM program. A number of groups tend to appear repeatedly in classifications whatever the weighting but the equivalent analysis with W1 weights produced several additional clusters of widespread species, whereas the unweighted analysis (W0) produced very uneven-sized clusters ranging from 15 species centred on Bristol to 203 species in the ubiquitous group. Our weighting is an attempt to avoid both these extremes. Hill *et al*. (2013) present in outline a W1 classification of the same data. Both the choice of cluster number and of the clustering program emphasises the fact that clustering techniques are very useful ways of examining pattern in datasets but there are numerous ways of dividing up large datasets and there is no single, 'correct' classification. There is perhaps a parallel between the classification of these datasets and the classification of quadrats into types of vegetation, whereas in classifying individual organisms into species we tend to work on the assumption that there is a single, optimum classification.

Any allocation of species into a fixed number of clusters must include in each cluster a range of species from those that fit the cluster pattern well to those that are included simply because they provide the least bad solution. The Cosine measure *S* provides a measure of the goodness of fit. Our analyses have included data on all members assigned to the cluster, but it would be possible to eliminate species with low *S* values if a classification was needed which did not necessarily have to include each species.

Factors governing the distribution of species; the effects of scale

The clusters recognised in this analysis reflect a number of environmental factors, including climate, geology and soils and the presence of specific habitats, particularly coastal and aquatic habitats. The extent to which different rocks, soil types or plant habitats contribute to the observed patterns must depend on their distribution and the number of specialist species associated with them; habitats are most likely to feature if they are not represented in every hectad (and so themselves display a pattern at the hectad scale) and if they support numerous specialist species.

Whether or not the patterns are affected by barriers to dispersal requires further investigation, but an initial inspection suggests that they are not. The frequency of species in Ireland mirrors that in western Britain, and the frequency of species in Shetland is similar to that in northern mainland Scotland. It might at first sight appear that the *Chaerophyllum temulum* cluster of species which are frequent in southern Britain but uncommon or rare in Ireland includes many species which have been prevented from reaching Ireland by a sea barrier. However, at least 58 of the 93 species in this group are mapped as natives in Ireland by Preston *et al*. (2002), and some of the remainder are doubtfully native in Britain. The Irish natives include species such as *Astragalus danicus, Helianthemum nummularium, Mercurialis perennis, Ranunculus fluitans, Sanguisorba officinalis* and *Stachys officinalis*, all species which have much more restricted ranges in Ireland than one would expect from their British distributions. It is clear from Figure 4C that the species in this cluster are very much less frequent in Cornwall, Wales and S.W. Scotland than they are further east. This suggests that they may be ill-adapted to the environment of both western Britain and Ireland, although one could argue that the barrier preventing some of them reaching Ireland might have been the unsuitable terrain in western Britain rather than just the Irish Sea. A more detailed study of the presence of species in Ireland in relation to the floristic elements we have defined might throw further light on the ‘Irish problem’, which has been discussed in detail by Perring (1996) and Webb (1983).

It has been recognised for many years that distributions are controlled by different factors at different scales; Good (1974) describes distributions as controlled primarily by climate and secondarily by edaphic factors. Maps of the European distribution of species in 50 × 50-km squares usually show the influence of climate, mediated by altitude; they may also show major regional floristic differences which reflect the vagaries of migration histories (Heikinheimo *et al*. 2012). In the British Isles there is sufficient climatic variation for the influence of climate to be apparent as a controlling factor, but the grain-size of the 10-km squares is sufficiently fine to show geological and other influences as well; indeed, this is one of the reasons why 10-km square distribution mapping was adopted by the BSBI in 1950 (Preston 2013). At the county scale Good (1948) reached the similar conclusion that distributions were often the product of climate interacting with other factors such as geology, topography and habitat availability. It is interesting that, at the 10-km square scale in Britain and Ireland, similar factors control the distributions of vascular plants and mosses despite their very different life-forms, leading to similar clusters for the two groups. For liverworts there are even fewer coastal species than in the mosses, and few lowland calcicoles, so that climate and montane geology tend to be the predominant controlling features.

Many British county floras summarise data as tetrad (2 × 2-km square) maps (see Preston 2013), but there have been few analyses of the patterns of tetrad occurrence. Tetrads in Montgomeryshire were classified by Trueman *et al*. (1995) using the records of only the species mapped in their flora, which were primarily native plants and archaeophytes which were neither very common nor rare. They showed that much the strongest gradient in the distribution of these species in the county was from the upland, moorland areas in the west to the more fertile lowlands in the east; other important variables included the presence of wetland and woodland habitats, of base-rich substrates and, in the uplands, the degree of exposure. These are not dissimilar to the factors which determine the clusters recognised for Britain and Ireland in this paper, although coastal habitats, important determinants of pattern at the national scale, are absent from inland Montgomeryshire. In a study of the tetrad distribution of bryophytes in Lancashire, Callaghan & Ashton (2008) also concluded that the strongest gradient was an altitudinal one, although again altitude is correlated with several factors which more directly affect the distribution of species. In northern Belgium, where the topography is less varied, distribution patterns are primarily related to soil factors (Van Landuyt *et al*. 2011). A recent classification of tetrads on the basis of all vascular plant species recorded in Staffordshire, including many aliens, is particularly interesting in that Hawksford & Hopkins (2011) interpret the main axis of variation as reflecting the degree of human influence. Urban tetrads with a high proportion of neophytes were at one end of this axis and tetrads with a much more semi-natural flora at the other. However, the degree of human influence is strongly correlated with climate, topography, geology and land-use. Subsidiary factors included geology, the presence of wetland habitats and the degree of agricultural intensity.

British and Irish ranges in relation to wider ranges and threat

To what extent do the ranges of species in Britain and Ireland reflect their wider distribution? In all cases the British and Irish clusters are formed from species from more than one major biome, but they vary in their phytogeographical heterogeneity. The climatically extreme, *Romulea columnae*, *Crithmum maritimum*, *Alchemilla alpina* and *Carex atrata* clusters are relatively homogeneous, but so are some more widespread clusters, including those characterised by *Oenanthe crocata*, *Stachys sylvatica* and, especially, *Tamus communis*. By contrast, the *Glaux maritima*, *Minuartia verna* and *Selaginella selaginoides* clusters are particularly heterogeneous. The *Glaux maritima* cluster includes at least four species from every major biome category from Boreo-arctic to Southern-temperate.

The proportion of threatened species in Britain in the clusters is closely related to the mean number of British hectads in which the species occur, showing the clear relationship between rarity and threat. Threatened species are concentrated in the predominantly Arctic-montane *Carex atrata* and Mediterranean-Atlantic *Romulea columnae* clusters, and the *Hippocrepis comosa*, *Medicago sativa* and *Minuartia verna* clusters, which are less extreme phytogeographically but nevertheless very limited in range in Britain (Figure 10). The very high proportion of threatened species in the *Medicago sativa* cluster confirms earlier observations of the highly threatened nature of the 'continental' element in the British flora (Preston 2007). By contrast more widespread clusters, such as the *Clematis vitalba*, *Crithmum maritimum* and *Oenanthe crocata* clusters, may contain a high proportion of species at their northern limit in Britain but have a smaller proportion of threatened species. The bryophytes also show a similar propensity for threatened species to be concentrated in the clusters which have limited distributions in Britain and Ireland and are dominated by species of Arctic, Boreal or Mediterranean-Atlantic affinities (Preston *et al*. 2011, 2013).

Implications for species and habitat conservation

Does the identification of the clusters allow us to draw any conclusions for the conservation of species and habitats? In general, the proportion of priority species that are identified for conservation action within each cluster (Table 1) broadly matches the proportion of threatened species. The low numbers in clusters with a high proportion of common and widespread species, such as the *Urtica dioica*, *Oenanthe crocata* and *Chaerophyllum temulum* clusters, are to be expected, but the relationship also hold true for some clusters with limited ranges and a high proportion of threatened species, such as the *Alchemilla alpina* and *Carex atrata* clusters (the latter having the highest proportion of its species identified as priority species for conservation, 49%).

There are several important exceptions, however. Although 49% of species in the *Romulea columnae* cluster are threatened, just 11% (i.e. 5 species) have priority conservation status**.** Similarly, whilst 55% of the *Medicago sativa* cluster are threatened, only 29% (i.e. 11 species) are priorities. In the case of the ecologically homogenous *Romulea columnae* cluster, dominated as it is by annuals of open, dry and nutrient-poor microhabitats, it could be argued that this disproportionately low selection of species for conservation action is acceptable as key species have been selected as "flagship species" to represent the wider group; conservation action for these key species is likely to benefit the entire suite of species present at sites where they occur. Conversely, species of the *Medicago sativa* cluster, while also highly restricted in area, are ecologically heterogenous, including both typical Breckland rarities as well as Fenland and Broadland species. In this case it would seem appropriate that a revision of priorities would be beneficial to improve the conservation of species within this cluster. In only one cluster does the opposite, an over-representation of priority species, appear to be true. In the *Selaginella selaginoides* cluster, 18% of species are threatened but 32% (21 species) are identified as conservation priorities. This relatively widespread cluster nevertheless includes many species of highly restricted range which have low *S* values in this group. These include *Carex buxbaumii, Crassula aquatica*, *Potamogeton epihydrus* and rare *Euphrasia* species, such as *E. campbelliae, E. rivularis* and *E. rotundifolia*, which have been identified for conservation action.

There appears to be a close match between the protected area network, including directly protected areas such as National Nature Reserves (NNRs), sites protected by legislation such as Sites of Special Scientific Interest (SSSIs) and areas designated for their international importance such as Special Areas of Conservation (SACs), and the distribution of clusters with threatened species. The five clusters with very high proportions of threatened species *Medicago sativa* (55%), *Romulea columnae* (49%), *Carex atrata* (45%), *Hippocrepis comosa* (45%) and *Minuartia verna* (33%) all represent very characteristic, well defined and highly localised assemblages that are well represented through the protected area network. These clusters can be broadly matched to specific landscape areas with high levels of protection and conservation action, such as Breckland SAC for the *Medicago sativa* cluster, The Lizard SAC for the *Romulea columnae* cluster, many chalk and limestone grasslands designated as SSSIs and SACs for species in the *Hippocrepis comosa* cluster, and the Ben Lawers SAC (amongst others) for the *Carex atrata cluster*. The SAC network, designated under the EC Habitats Directive (see http://jncc.defra.gov.uk/page-23), is especially significant in this respect, as internationally important vegetation communities which include these species are specifically identified for conservation (such as “hydrophilous tall herb fringe communities” which include, for example, *Carex atrata* amongst their species). Mechanisms are therefore in place to protect and conserve these clusters of threatened species, although whether such mechanisms are actually effective in the field is another question entirely.

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Appendix

The 25 most characteristic plants assigned to each of the 20 moss clusters are listed here in order of decreasing similarity to the cluster pattern, as measured by the cosine measure of similarity (S).

***Romulea columnae* cluster**: Romulea columnae (0.82); Orchis laxiflora (0.81); Spergula arvensis (0.77); Juncus capitatus (0.74); Polycarpon tetraphyllum (0.74); Viola kitaibeliana (0.73); Herniaria ciliolata (0.68); Pilosella peleteriana (0.67); Bupleurum baldense (0.66); Festuca huonii (0.66); Trifolium occidentale (0.65); Mibora minima (0.65); Poa infirma (0.64); Rumex rupestris (0.64); Scilla autumnalis (0.64); Cyperus longus (0.61); Ranunculus paludosus (0.61); Armeria arenaria (0.60); Trifolium incarnatum (0.59); Lotus angustissimus (0.59); Geranium purpureum (0.55); Hypericum linariifolium (0.55); Gnaphalium luteoalbum (0.55); Ornithopus pinnatus (0.55); Orobanche purpurea (0.54).

***Crithmum maritimum* cluster**: Crithmum maritimum (0.81); Beta vulgaris (0.78); Catapodium marinum (0.77); Lavatera arborea (0.75); Calystegia soldanella (0.73); Erodium maritimum (0.72); Eryngium maritimum (0.72); Glaucium flavum (0.72); Spergularia rupicola (0.72); Euphorbia paralias (0.72); Euphorbia portlandica (0.71); Raphanus raphanistrum (0.71); Carduus tenuiflorus (0.71); Rubia peregrina (0.68); Trifolium ornithopodioides (0.67); Crambe maritima (0.67); Linum bienne (0.65); Euphrasia tetraquetra (0.65); Trifolium scabrum (0.64); Lotus subbiflorus (0.61); Isolepis cernua (0.60); Vulpia fasciculata (0.57); Phleum arenarium (0.57); Asplenium obovatum (0.56); Parentucellia viscosa (0.56).

***Clematis vitalba* cluster**: Clematis vitalba (0.89); Medicago arabica (0.88); Iris foetidissima (0.86); Sison amomum (0.86); Euphorbia amygdaloides (0.85); Orobanche minor (0.84); Trifolium micranthum (0.80); Lathyrus nissolia (0.79); Rumex pulcher (0.79); Viburnum lantana (0.77); Bromus commutatus (0.77); Trifolium fragiferum (0.76); Carex divulsa (0.75); Clinopodium ascendens (0.74); Spiranthes spiralis (0.73); Verbascum nigrum (0.73); Petroselinum segetum (0.72); Geranium columbinum (0.72); Geranium rotundifolium (0.72); Trifolium striatum (0.71); Ulmus minor sensu Stace (0.70); Sorbus torminalis (0.69); Centaurium pulchellum (0.69); Salvia verbenaca (0.69); Cuscuta epithymum (0.67).

***Hippocrepis comosa* cluster**: Hippocrepis comosa (0.81); Cephalanthera damasonium (0.81); Asperula cynanchica (0.77); Onobrychis viciifolia (0.77); Polygala calcarea (0.76); Thymus pulegioides (0.76); Sorbus aria (0.74); Clinopodium acinos (0.73); Campanula glomerata (0.72); Orobanche elatior (0.70); Thesium humifusum (0.69); Ophrys insectifera (0.67); Atropa belladonna (0.66); Crepis biennis (0.65); Euphrasia pseudokerneri (0.65); Herminium monorchis (0.64); Monotropa hypopitys (0.63); Orchis ustulata (0.63); Minuartia hybrida (0.63); Polygonatum multiflorum (0.62); Gentianella amarella (0.62); Tephroseris integrifolia (0.60); Helleborus viridis (0.60); Epipactis purpurata (0.58); Gentianella anglica (0.55).

***Medicago sativa* cluster**: Medicago sativa (0.76); Silene otites (0.72); Phleum phleoides (0.65); Medicago minima (0.65); Verbascum pulverulentum (0.63); Crassula tillaea (0.63); Silene conica (0.60); Herniaria glabra (0.59); Thymus serpyllum (0.58); Vulpia ciliata (0.57); Muscari neglectum (0.53); Veronica verna (0.52); Hypochaeris glabra (0.51); Peucedanum palustre (0.50); Galium parisiense (0.50); Artemisia campestris (0.50); Carex appropinquata (0.45); Carex ericetorum (0.44); Filago lutescens (0.44); Stratiotes aloides (0.43); Tephroseris palustris (0.42); Liparis loeselii (0.39); Corynephorus canescens (0.37); Scleranthus perennis (0.36); Lathyrus palustris (0.35).

***Limonium vulgare* cluster**: Limonium vulgare (0.79); Parapholis strigosa (0.78); Elytrigia atherica (0.78); Salicornia ramosissima (0.77); Atriplex portulacoides (0.77); Spartina anglica (0.76); Hordeum marinum (0.75); Seriphidium maritimum (0.75); Bupleurum tenuissimum (0.72); Puccinellia fasciculata (0.72); Atriplex littoralis (0.72); Sarcocornia perennis (0.71); Cochlearia anglica (0.70); Carex divisa (0.70); Salicornia dolichostachya (0.70); Parapholis incurva (0.69); Puccinellia rupestris (0.69); Puccinellia distans (0.67); Trifolium squamosum (0.67); Ranunculus baudotii (0.67); Salicornia pusilla (0.66); Apium graveolens (0.66); Salicornia europaea (0.64); Spartina maritima (0.63); Ruppia cirrhosa (0.62).

***Oenanthe crocata* cluster**: Oenanthe crocata (0.85); Hypericum androsaemum (0.83); Jasione montana (0.81); Umbilicus rupestris (0.80); Potentilla anglica (0.80); Anagallis tenella (0.79); Ulex gallii (0.78); Lythrum portula (0.78); Polypodium interjectum (0.76); Sedum anglicum (0.75); Carex laevigata (0.74); Fumaria muralis (0.74); Hypericum elodes (0.74); Scutellaria minor (0.73); Lepidium heterophyllum (0.72); Ranunculus omiophyllus (0.72); Osmunda regalis (0.71); Dryopteris aemula (0.62); Fumaria bastardii (0.60); Wahlenbergia hederacea (0.55); Anagallis minima (0.54); Radiola linoides (0.53); Euphrasia anglica (0.53); Fumaria capreolata (0.52); Juncus foliosus (0.46).

***Tamus communis* cluster**: Tamus communis (0.92); Acer campestre (0.92); Ligustrum vulgare (0.91); Ulmus procera (0.91); Humulus lupulus (0.91); Senecio erucifolius (0.91); Cornus sanguinea (0.91); Solanum nigrum (0.90); Viola odorata (0.90); Bryonia dioica (0.90); Vicia tetrasperma (0.89); Plantago media (0.88); Carduus nutans (0.88); Malva moschata (0.88); Pastinaca sativa (0.88); Epilobium tetragonum (0.88); Myosoton aquaticum (0.86); Reseda lutea (0.86); Chenopodium rubrum (0.86); Lamiastrum galeobdolon (0.86); Hordeum secalinum (0.85); Rubus caesius (0.85); Silaum silaus (0.85); Centaurea scabiosa (0.85); Erigeron acer (0.85).

***Lemna trisulca* cluster**: Lemna trisulca (0.85); Rumex hydrolapathum (0.82); Glyceria maxima (0.82); Zannichellia palustris (0.81); Potamogeton pectinatus (0.81); Ceratophyllum demersum (0.81); Myriophyllum spicatum (0.81); Berula erecta (0.80); Veronica catenata (0.80); Oenanthe fistulosa (0.79); Sagittaria sagittifolia (0.79); Nuphar lutea (0.78); Butomus umbellatus (0.78); Bidens tripartita (0.76); Lemna gibba (0.76); Carex pseudocyperus (0.75); Typha angustifolia (0.75); Thalictrum flavum (0.75); Rorippa amphibia (0.75); Bidens cernua (0.74); Schoenoplectus lacustris

(0.73); Ranunculus circinatus (0.73); Ranunculus trichophyllus (0.73); Spirodela polyrhiza (0.73); Callitriche obtusangula (0.69).

***Epilobium hirsutum* cluster**: Epilobium hirsutum (0.94); Rumex sanguineus (0.94); Potentilla reptans (0.94); Medicago lupulina (0.93); Lemna minor (0.93); Epilobium parviflorum (0.93); Solanum dulcamara (0.93); Malus sylvestris s.l. (0.93); Juncus inflexus (0.92); Rumex conglomeratus (0.92); Anagallis arvensis (0.92); Carex hirta (0.92); Typha latifolia (0.92); Agrimonia eupatoria (0.92); Festuca arundinacea (0.92); Arum maculatum (0.91); Alisma plantago-aquatica (0.91); Apium nodiflorum (0.91); Barbarea vulgaris (0.91); Alliaria petiolata (0.91); Ranunculus bulbosus (0.91); Convolvulus arvensis (0.91); Hypericum perforatum (0.91); Trifolium campestre (0.90); Arenaria serpyllifolia (0.90).

***Chaerophyllum temulum* cluster**: Chaerophyllum temulum (0.93); Aethusa cynapium (0.91); Ribes rubrum (0.91); Mercurialis perennis (0.91); Linaria vulgaris (0.91); Tragopogon pratensis (0.91); Moehringia trinervia (0.90); Myosotis sylvatica (0.89); Phleum bertolonii (0.89); Poa nemoralis (0.89); Taxus baccata (0.89); Galium mollugo (0.89); Stachys officinalis (0.88); Dipsacus fullonum s.l. (0.88); Carduus crispus (0.88); Cruciata laevipes (0.88); Tanacetum vulgare (0.88); Adoxa moschatellina (0.88); Carpinus betulus (0.87); Leontodon hispidus (0.87); Trifolium medium (0.87); Ononis repens (0.86); Clinopodium vulgare (0.86); Elymus caninus (0.85); Hypericum hirsutum (0.84).

***Stachys sylvatica* cluster**: Stachys sylvatica (0.97); Geum urbanum (0.96); Lapsana communis (0.96); Fagus sylvatica (0.96); Scrophularia nodosa (0.96); Stellaria graminea (0.96); Prunus spinosa (0.96); Fragaria vesca (0.95); Stellaria holostea (0.95); Ilex aquifolium (0.95); Anthriscus sylvestris (0.95); Veronica beccabunga (0.95); Quercus robur (0.95); Ajuga reptans (0.95); Phalaris arundinacea (0.95); Hyacinthoides non-scripta (0.95); Alopecurus pratensis (0.95); Chamerion angustifolium (0.94); Glechoma hederacea (0.94); Torilis japonica (0.94); Lotus pedunculatus (0.94); Rubus idaeus (0.94); Salix caprea (0.94); Brachypodium sylvaticum (0.94); Ulmus glabra (0.94).

***Urtica dioica* cluster**: Urtica dioica (0.99); Ranunculus repens (0.99); Achillea millefolium (0.99); Anthoxanthum odoratum (0.99); Cirsium vulgare (0.99); Trifolium repens (0.99); Cynosurus cristatus (0.99); Plantago major (0.99); Trifolium pratense (0.99); Bellis perennis (0.99); Ranunculus acris (0.99); Prunella vulgaris (0.99); Holcus lanatus (0.99); Plantago lanceolata (0.99); Rumex acetosa (0.99); Cerastium fontanum (0.99); Juncus effusus (0.99); Lotus corniculatus (0.99); Lolium perenne (0.99); Poa annua (0.99); Rumex obtusifolius (0.99); Agrostis stolonifera (0.99); Hypochaeris radicata (0.99); Festuca rubra agg. (0.99); Cirsium arvense (0.99).

***Glaux maritima* cluster**: Glaux maritima (0.92); Juncus gerardii (0.90); Triglochin maritimum (0.89); Honckenya peploides (0.88); Armeria maritima (0.88); Puccinellia maritima (0.87); Atriplex glabriuscula (0.86); Plantago maritima (0.84); Silene uniflora (0.83); Spergularia marina (0.83); Plantago coronopus (0.83); Elytrigia juncea (0.83); Spergularia media (0.83); Aster tripolium (0.83); Tripleurospermum maritimum (0.82); Carex arenaria (0.82); Cakile maritima (0.82); Ammophila arenaria (0.81); Sagina maritima (0.80); Cochlearia officinalis s.l. (0.80); Cerastium diffusum (0.79); Bolboschoenus maritimus (0.78); Suaeda maritima (0.77); Cochlearia danica (0.77); Carex extensa (0.76).

***Calluna vulgaris* cluster**: Calluna vulgaris (0.95); Molinia caerulea (0.95); Luzula multiflora (0.95); Blechnum spicant (0.95); Galium saxatile (0.95); Juncus bulbosus (0.95); Carex echinata (0.95); Carex viridula (0.94); Eriophorum angustifolium (0.94); Erica tetralix (0.94); Pedicularis sylvatica (0.93); Polygala serpyllifolia (0.93); Danthonia decumbens (0.93); Salix aurita (0.93); Vaccinium myrtillus (0.93); Nardus stricta (0.93); Carex binervis (0.92); Viola palustris (0.92); Dactylorhiza maculata (0.92); Aira praecox (0.92); Erica cinerea (0.92); Montia fontana (0.91); Deschampsia flexuosa (0.91); Luzula sylvatica (0.91); Drosera rotundifolia (0.91).

***Minuartia verna* cluster**: Minuartia verna (0.69); Primula farinosa (0.65); Dryopteris submontana (0.62); Sesleria caerulea (0.59); Gymnocarpium robertianum (0.59); Galium sterneri (0.59); Ribes alpinum (0.57); Draba muralis (0.56); Epipactis atrorubens (0.55); Thlaspi caerulescens (0.53); Polygonatum odoratum (0.52); Alchemilla glaucescens (0.52); Myosotis stolonifera (0.52); Actaea spicata (0.46); Hornungia petraea (0.45); Potentilla neumanniana (0.45); Polemonium caeruleum (0.45); Cypripedium calceolus (0.45); Viola rupestris (0.42); Allium scorodoprasum (0.41); Carex ornithopoda (0.40); Sorbus rupicola (0.40); Crepis mollis (0.36); Helianthemum oelandicum (0.31); Polygala amarella (0.31).

***Alchemilla glabra* cluster**: Alchemilla glabra (0.88); Crepis paludosa (0.85); Equisetum sylvaticum (0.83); Empetrum nigrum (0.83); Geum rivale (0.82); Gymnocarpium dryopteris (0.82); Oreopteris limbosperma (0.82); Cystopteris fragilis (0.81); Vaccinium vitis-idaea (0.81); Phegopteris connectilis (0.81); Carex curta (0.81); Trollius europaeus (0.80); Prunus padus (0.79); Cirsium heterophyllum (0.79); Geranium sylvaticum (0.78); Alchemilla xanthochlora (0.77); Lycopodium clavatum (0.75); Dactylorhiza purpurella (0.75); Rubus saxatilis (0.74); Alchemilla filicaulis (0.74); Listera cordata (0.74); Parnassia palustris (0.70); Botrychium lunaria (0.68); Viola lutea (0.65); Salix phylicifolia (0.65).

***Selaginella selaginoides* cluster**: Selaginella selaginoides (0.83); Pinguicula vulgaris (0.83); Littorella uniflora (0.81); Carex dioica (0.80); Festuca vivipara (0.80); Sparganium angustifolium (0.80); Lobelia dortmanna (0.79); Huperzia selago (0.79); Eleocharis quinqueflora (0.79); Myrica gale (0.79); Antennaria dioica (0.78); Euphrasia micrantha (0.75); Isoetes lacustris (0.75); Eleocharis multicaulis (0.74); Drosera anglica (0.74); Juniperus communis (0.73); Schoenus nigricans (0.72); Hymenophyllum wilsonii (0.71); Utricularia minor (0.70); Utricularia intermedia s.l. (0.70); Sedum rosea (0.69); Rhynchospora alba (0.69); Pinguicula lusitanica (0.68); Gentianella campestris (0.68); Euphrasia scottica (0.68).

***Alchemilla alpina* cluster**: Alchemilla alpina (0.85); Oxyria digyna (0.82); Thalictrum alpinum (0.82); Gnaphalium supinum (0.82); Epilobium anagallidifolium (0.82); Juncus trifidus (0.82); Luzula spicata (0.81); Saxifraga aizoides

(0.81); Saxifraga stellaris (0.81); Carex bigelowii (0.81); Saussurea alpina (0.80); Vaccinium uliginosum (0.80); Cornus suecica (0.80); Loiseleuria procumbens (0.80); Saxifraga oppositifolia (0.79); Juncus triglumis (0.79); Salix herbacea (0.78); Diphasiastrum alpinum (0.76); Carex pauciflora (0.76); Sibbaldia procumbens (0.76); Persicaria vivipara (0.76); Tofieldia pusilla (0.74); Arctostaphylos uva-ursi (0.73); Silene acaulis (0.71); Rubus chamaemorus (0.71).

***Carex atrata* cluster**: Carex atrata (0.81); Cerastium alpinum (0.76); Sagina saginoides (0.75); Poa alpina (0.74); Saxifraga nivalis (0.74); Carex vaginata (0.74); Salix lapponum (0.73); Cystopteris montana (0.73); Salix myrsinites (0.73); Salix reticulata (0.72); Athyrium distentifolium (0.72); Juncus castaneus (0.71); Carex saxatilis (0.71); Veronica alpina (0.70); Salix arbuscula (0.68); Veronica fruticans (0.68); Phleum alpinum (0.67); Juncus biglumis (0.66); Potentilla crantzii (0.63); Minuartia sedoides (0.63); Carex capillaris (0.61); Woodsia alpina (0.59); Athyrium flexile (0.58); Poa glauca (0.58); Cerastium cerastoides (0.57).

Legends for figures

Figure 1 The distribution of species (A, C, E) and their phytogeographical affinities (B, D, F) in the following clusters: *Romulea columnae* (A, B), *Crithmum maritimum* (C, D), *Clematis vitalba* (E, F). The mapping symbols indicate hectads in which 10–25% (yellow), 25–50% (orange) and >50% (red) of the species in the cluster are recorded. The bars on the phytogeography diagrams 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 Oceanic (Oc), Suboceanic (Suboc), European (Eur), Eurosiberian (Eurosib), Eurasian (Euras) and Circumpolar (Circ) Eastern Limit Categories.

Figure 2 The distribution of species (A, C, E) and their phytogeographical affinities (B, D, F) in the following clusters: *Hippocrepis comosa* (A, B), *Medicago sativa* (C, D), *Limonium vulgare* (E, F). For an explanation of the maps and diagrams, see Figure 1.

Figure 3 The distribution of species (A, C, E) and their phytogeographical affinities (B, D, F) in the following clusters: *Oenanthe crocata* (A, B), *Tamus communis* (C, D), *Lemna trisulca* (E, F). For an explanation of the maps and diagrams, see Figure 1.

Figure 4 The distribution of species (A, C, E) and their phytogeographical affinities (B, D, F) in the following clusters: *Epilobium hirsutum* (A, B), *Chaerophyllum temulum* (C, D), *Stachys sylvatica* (E, F). For an explanation of the maps and diagrams, see Figure 1.

Figure 5 The distribution of species (A, C, E) and their phytogeographical affinities (B, D, F) in the following clusters: *Urtica dioica* (A, B), *Glaux maritima* (C, D), *Calluna vulgaris* (E, F). For an explanation of the maps and diagrams, see Figure 1.

Figure 6 The distribution of species (A, C, E) and their phytogeographical affinities (B, D, F) in the following clusters: *Minuartia verna* (A, B), *Alchemilla glabra* (C, D), *Selaginella selaginoides* (E, F). For an explanation of the maps and diagrams, see Figure 1.

Figure 7 The distribution of species (A, C) and their phytogeographical affinities (B, D) in the following clusters: *Alchemilla alpina* (A, B), *Carex atrata* (C, D). For an explanation of the maps and diagrams, see Figure 1.

Figure 8 Principal Components Analysis biplots showing environmental characteristics of the clusters: (A) Axis 2 (PC2) plotted against Axis 1 (PC1); (B) Axis 3 (PC3) plotted against Axis 2 (PC2). For the unabbreviated cluster names, see Table 1.

Figure 9 Hierarchical classification of vascular plant clusters.

Figure 10. The number of British species with the IUCN conservation status Extinct (EX, EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Data Deficient (DD) and Least Concern (LC) in each cluster. Species which occur as natives only in Ireland or the Channel Islands are excluded.

Table 1 The vascular plant clusters, with the number of species in the cluster and their mean number of hectads (with standard error) in Britain (GB), Ireland (IR) and the Channel Islands (CI), the percentage of species at their northern European limit in our area and the percentage of British species which are extinct or threatened, or are listed as conservation priority species under Section 41 of the Natural Resources and Rural Communities Act 2006.

Cluster name	No. spp	GB hectads	IR hectads	CI hectads	% N limit	% British species extinct or threatened	% British conservation priority species
Romulea columnae	57	13 (2)	1 (1)	6 (1)	65	49	11
Crithmum maritimum	72	183 (47)	51 (15)	5 (1)	57	22	21
Clematis vitalba	73	365 (32)	17 (5)	5 (1)	49	27	18
Hippocrepis comosa	68	137 (20)	5 (2)	0 (0)	29	45	34
Medicago sativa	38	42 (8)	3 (1)	1 (1)	16	55	29
Limonium vulgare	59	129 (16)	15 (3)	3 (0)	37	25	16
Oenanthe crocata	55	417 (63)	184 (29)	4 (1)	53	13	9
Tamus communis	80	869 (43)	38 (7)	4 (0)	24	4	4
Lemna trisulca	70	515 (48)	118 (15)	1 (0)	4	22	14
Epilobium hirsutum	85	1591 (46)	482 (19)	8 (0)	21	0	0
Chaerophyllum temulum	93	1102 (58)	67 (8)	3 (0)	8	8	5
Stachys sylvatica	86	2037 (46)	571 (24)	7 (1)	9	0	0
Urtica dioica	151	2514 (26)	854 (12)	10 (0)	3	1	1
Glaux maritima	57	550 (46)	145 (14)	6 (1)	7	5	9
Calluna vulgaris	60	1778 (70)	560 (30)	4 (1)	2	3	2
Minuartia verna	44	45 (9)	7 (2)	0 (0)	9	33	21
Alchemilla glabra	66	564 (59)	78 (13)	0 (0)	5	15	12
Selaginella selaginoides	70	422 (48)	140 (17)	1 (0)	10	18	32
Alchemilla alpina	54	218 (22)	13 (3)	0 (0)	2	21	19
Carex atrata	67	35 (4)	1 (0)	0 (0)	7	45	49
Total	1405	854 (24)	221 (8)	4 (0)	20	19	14

Table 2 Mean plant height of terrestrial species (with standard error) and percentage of different life forms in each vascular plant cluster

Cluster name	No. spp	Mean ht (cm)	% Geophyte	% Chamaephyte	% Hemicryptophyte	% Hydrophyte	% Nanophanerophyte	% Phanerophyte	% Therophyte
Romulea columnae	57	34 (4)	14	5	32	2	0	0	47
Crithmum maritimum	72	74 (17)	4	14	47	1	4	4	25
Clematis vitalba	73	197 (64)	5	3	38	4	7	7	36
Hippocrepis comosa	68	78 (23)	35	7	41	1	3	3	9
Medicago sativa	38	56 (9)	5	8	58	8	0	0	21
Limonium vulgare	59	95 (22)	2	7	32	8	5	5	41
Oenanthe crocata	55	95 (30)	5	9	47	5	7	5	20
Tamus communis	80	308 (77)	10	5	51	1	4	13	16
Lemna trisulca	70	92 (9)	1	0	28	61	0	0	10
Epilobium hirsutum	85	103 (16)	7	1	48	16	4	4	20
Chaerophyllum temulum	93	120 (39)	15	9	48	4	3	2	18
Stachys sylvatica	86	335 (83)	12	3	44	9	3	13	15
Urtica dioica	151	166 (34)	9	5	60	3	1	7	15
Glaux maritima	57	46 (5)	9	7	54	7	0	0	23
Calluna vulgaris	60	51 (5)	8	12	57	7	5	0	12
Minuartia verna	44	63 (14)	18	16	43	0	11	2	9
Alchemilla glabra	66	98 (26)	18	11	56	5	6	5	0
Selaginella selaginoides	70	44 (10)	4	10	34	31	3	1	16
Alchemilla alpina	54	108 (60)	0	35	48	4	2	6	6
Carex atrata	67	28 (3)	1	27	66	0	4	0	1
Total	1405	123 (10)	9	9	47	9	3	4	18

Table 3 Preferential Broad Habitats for species in each cluster.

	Rom col	*Cri mar*	*Cle vit*	*Hip com*	*Med sat*	*Lim vul*	*Oen cro*	*Tam com*	*Lem tri*	*Epi hir*	*Cha tem*	*Sta syl*	*Urt dio*	*Gla mar*	*Cal vul*	*Min ver*	*Alc gla*	*Sel sel*	*Alc alp*	*Car atr*	All spp.
1 Broad-leaved Woodland	1	5	18	28	5	2	12	17	3	9	23	35	10	0	7	8	18	1	2	1	11
2 Coniferous Woodland	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	8	0	2	1	1
3 Boundary & Linear Features	10	10	29	10	14	2	11	27	0	13	13	13	11	3	2	3	4	1	0	0	9
4 Arable & Horticultural	3	2	5	2	1	0	4	3	0	3	2	3	5	2	0	0	0	0	0	0	2
5 Improved Grassland	2	2	1	0	0	0	0	1	0	0	0	1	6	0	0	0	0	0	0	0	1
6 Neutral Grassland	7	3	8	2	1	15	5	14	1	11	11	5	18	2	1	8	4	0	0	0	7
7 Calcareous Grassland	1	5	7	48	9	2	0	22	0	13	17	4	9	1	1	26	5	4	9	9	10
8 Acid Grassland	1	5	9	0	26	5	2	2	2	0	6	2	3	3	14	0	1	2	0	1	4
9 Bracken	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0
10 Dwarf Shrub Heath	5	10	5	0	0	0	9	0	1	0	2	1	2	1	12	0	5	8	5	4	3
11 Fen, Marsh & Swamp	4	3	0	2	24	0	16	5	29	21	7	13	20	9	21	8	15	25	8	11	12
12 Bog	7	1	0	0	0	0	1	0	0	0	1	0	0	0	17	0	6	11	8	0	2
13 Standing Water & Canals	1	2	7	1	11	6	5	1	43	7	2	6	1	2	4	1	9	21	4	0	6
14 Rivers & Streams	0	1	4	1	0	0	4	3	20	10	4	6	4	0	7	2	4	4	0	0	4
15 Montane	0	0	0	0	0	0	4	0	0	0	0	0	0	1	0	0	3	4	37	49	4
16 Inland Rock	12	5	3	3	4	5	24	3	1	8	6	5	6	2	8	44	21	11	25	23	10
17 Built-up Areas & Gardens	2	1	3	0	0	0	0	1	0	3	3	3	2	1	0	0	0	0	0	0	1
18 Supralittoral Rock	18	23	0	1	0	2	1	0	0	0	0	0	0	12	0	0	0	4	0	0	3
19 Supralittoral Sediment	25	20	1	0	4	21	0	1	0	2	1	0	1	31	1	0	0	1	0	1	5
21 Littoral Sediment	0	3	1	0	0	41	2	0	0	0	0	0	0	30	0	0	0	3	0	0	3
23 Sublittoral Sediment	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Note: Species are recorded from up to four Broad Habitats by Hill *et al*. (2004). For this table, all species are each allocated a score of 1 which is divided between its Broad Habitats. The figures represent total score for the Broad Habitat in the cluster expressed as a percentage of the total score for that cluster.

Table 4 Mean values (with standard errors) for January temperature (T Jan), July temperature (T Jul), precipitation (Prec), Ellenberg L, F, R, N and S values and the percentage of coastal species for each cluster

Cluster name	No. spp	T Jan (°C)	T Jul (°C)	Prec (mm)	L	F	R	N	S	Coastal species (%)
Romulea columnae	57	**5.8 (0.1)**	**16.3 (0.1)**	**876 (12)**	**8.3 (0.1)**	**4.8 (0.3)**	5.8 (0.2)	**2.8 (0.2)**	0.6 (0.1)	28
Crithmum maritimum	72	**5.2 (0.1)**	**15.6 (0.0)**	1040 (14)	**7.9 (0.2)**	**5.0 (0.2)**	6.1 (0.2)	3.8 (0.2)	**1.3 (0.2)**	44
Clematis vitalba	73	**4.1 (0.0)**	**16.1 (0.0)**	**805 (8)**	6.8 (0.2)	**5.3 (0.2)**	6.3 (0.2)	4.8 (0.2)	**0.1 (0.1)**	1
Hippocrepis comosa	68	**3.7 (0.0)**	**16.1 (0.0)**	**773 (10)**	6.5 (0.2)	**4.3 (0.2)**	**7.9 (0.1)**	3.5 (0.2)	**0.0 (0.0)**	0
Medicago sativa	37	3.6 (0.1)	**16.0 (0.1)**	**682 (17)**	7.5 (0.2)	5.4 (0.5)	6.4 (0.3)	3.4 (0.3)	**0.1 (0.0)**	3
Limonium vulgare	59	**4.4 (0.0)**	**16.1 (0.1)**	**790 (15)**	**8.3 (0.1)**	6.7 (0.3)	**7.3 (0.1)**	**5.2 (0.2)**	**3.9 (0.4)**	63
Oenanthe crocata	55	**4.2 (0.1)**	14.7 (0.1)	**1250 (30)**	6.6 (0.2)	6.3 (0.3)	**5.1 (0.2)**	3.3 (0.2)	**0.1 (0.0)**	2
Tamus communis	80	**3.7 (0.0)**	**15.8 (0.0)**	**792 (7)**	6.8 (0.1)	**5.1 (0.2)**	**7.1 (0.1)**	**4.8 (0.2)**	**0.1 (0.0)**	0
Lemna trisulca	69	**3.7 (0.0)**	**15.6 (0.1)**	**807 (13)**	7.2 (0.1)	**9.9 (0.2)**	**6.8 (0.1)**	**5.8 (0.2)**	**0.2 (0.1)**	0
Epilobium hirsutum	85	**3.8 (0.0)**	**15.1 (0.0)**	**955 (5)**	7.0 (0.1)	6.3 (0.3)	**6.8 (0.1)**	**5.2 (0.2)**	**0.2 (0.1)**	0
Chaerophyllum temulum	93	3.4 (0.0)	**15.1 (0.0)**	**919 (8)**	**6.5 (0.2)**	5.4 (0.2)	6.3 (0.1)	4.6 (0.2)	**0.0 (0.0)**	0
Stachys sylvatica	86	3.5 (0.0)	14.7 (0.0)	1056 (4)	**6.1 (0.1)**	6.1 (0.2)	6.0 (0.1)	**5.1 (0.2)**	**0.1 (0.0)**	0
Urtica dioica	151	3.5 (0.0)	**14.5 (0.0)**	1099 (2)	**6.8 (0.1)**	6.1 (0.1)	**5.8 (0.1)**	**4.6 (0.1)**	**0.2 (0.0)**	0
Glaux maritima	57	**4.1 (0.0)**	**14.3 (0.1)**	1096 (14)	**8.3 (0.1)**	6.6 (0.3)	**6.8 (0.1)**	**4.8 (0.2)**	**2.8 (0.2)**	72
Calluna vulgaris	60	**3.3 (0.0)**	**14.1 (0.0)**	**1205 (7)**	7.1 (0.1)	**7.3 (0.2)**	**3.8 (0.2)**	**2.5 (0.1)**	**0.0 (0.0)**	0
Minuartia verna	44	**2.5 (0.1)**	**13.9 (0.1)**	**1279 (33)**	7.2 (0.2)	**5.0 (0.3)**	**7.4 (0.2)**	3.2 (0.3)	**0.0 (0.0)**	0
Alchemilla glabra	66	**2.4 (0.1)**	**13.4 (0.1)**	**1254 (26)**	**6.3 (0.2)**	6.5 (0.2)	**5.1 (0.2)**	3.5 (0.2)	**0.0 (0.0)**	0
Selaginella selaginoides	70	3.4 (0.1)	**13.4 (0.1)**	**1410 (27)**	**7.8 (0.1)**	**8.1 (0.3)**	**5.1 (0.2)**	**2.5 (0.2)**	0.3 (0.1)	9
Alchemilla alpina	54	**1.6 (0.1)**	**12.1 (0.1)**	**1835 (44)**	7.5 (0.2)	6.2 (0.3)	**4.4 (0.3)**	**2.2 (0.1)**	**0.0 (0.0)**	0
Carex atrata	67	**0.2 (0.1)**	**11.4 (0.1)**	**1873 (41)**	**7.6 (0.1)**	5.9 (0.2)	6.0 (0.2)	**2.4 (0.1)**	**0.0 (0.0)**	0
Total	1403	3.5 (0.0)	14.7 (0.0)	1081 (9)	7.1 (0.0)	6.1 (0.1)	6.1 (0.0)	4.0 (0.0)	0.5 (0.0)	10

Note: Temperature and precipitation values have been calculated for each species from the values for the hectads in which they occur (Hill *et al*. 2004). 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 vascular plants as a whole ($p<0.001$, t-test). Values are not available for two species.

Table 5 Comparison of vascular plant clusters with clusters for liverworts (k=10; Preston *et al*. 2011) and mosses (k=15; Preston *et al*. 2013). The similarity of the clusters is measured by the *S* metric (see Methods section of this paper for details). The most similar vascular plant cluster to each bryophyte cluster is shown in bold and the most similar moss cluster and liverwort cluster to each vascular plant cluster are underlined.

	Rom col	*Cri mar*	*Cle vit*	*Hip com*	*Med sat*	*Lim vul*	*Oen cro*	*Tam com*	*Lem tri*	*Epi hir*	*Cha tem*	*Sta syl*	*Urt dio*	*Gla mar*	*Cal vul*	*Min ver*	*Alc gla*	*Sel sel*	*Alc alp*	*Car atr*
Liverwort clusters																				
Pellia epiphylla	0.18	0.45	0.55	0.41	0.22	0.29	0.78	0.59	0.54	0.75	0.76	0.84	0.84	0.54	**0.86**	0.35	0.73	0.69	0.44	0.22
Phaeoceros laevis s.l.	0.44	**0.61**	0.34	0.12	0.09	0.21	0.49	0.24	0.19	0.33	0.29	0.33	0.33	0.36	0.33	0.10	0.15	0.24	0.06	0.03
Cladopodiella fluitans	0.07	0.19	0.27	0.18	0.15	0.12	0.38	0.23	0.25	0.30	0.31	0.34	0.34	0.22	0.40	0.14	0.32	**0.41**	0.24	0.13
Lophocolea heterophylla	0.19	0.44	0.75	0.58	0.37	0.36	0.68	0.81	0.73	0.84	**0.88**	0.81	0.74	0.42	0.66	0.31	0.50	0.38	0.15	0.08
Scapania undulata	0.08	0.25	0.23	0.16	0.10	0.13	0.63	0.27	0.27	0.46	0.49	0.63	0.67	0.43	**0.79**	0.37	0.78	0.77	0.63	0.34
Anastrepta orcadensis	0.02	0.06	0.03	0.03	0.02	0.03	0.30	0.05	0.07	0.16	0.18	0.33	0.40	0.25	0.51	0.25	0.60	0.65	**0.81**	0.59
Harpalejeunea molleri	0.06	0.17	0.07	0.04	0.03	0.07	0.45	0.06	0.10	0.21	0.16	0.34	0.41	0.39	0.49	0.14	0.43	**0.67**	0.50	0.18
Moerckia blyttii	0.01	0.03	0.02	0.02	0.02	0.01	0.12	0.03	0.04	0.08	0.10	0.17	0.23	0.11	0.30	0.16	0.38	0.38	0.67	**0.84**
Scapania degenii	0.00	0.01	0.01	0.02	0.01	0.01	0.07	0.02	0.02	0.06	0.09	0.13	0.15	0.06	0.20	0.20	0.30	0.24	0.44	**0.62**
Marsupella condensata	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.02	0.04	0.06	0.02	0.09	0.04	0.14	0.12	0.32	**0.55**
Moss clusters																				
Bryum capillare	0.16	0.44	0.64	0.50	0.30	0.34	0.76	0.73	0.68	0.85	0.87	**0.91**	0.89	0.55	0.85	0.36	0.71	0.63	0.37	0.19
Scleropodium tourettii	0.50	**0.81**	0.59	0.29	0.19	0.47	0.58	0.45	0.33	0.49	0.45	0.45	0.43	0.53	0.38	0.14	0.16	0.24	0.04	0.02
Fontinalis squamosa	0.11	0.31	0.28	0.12	0.06	0.12	**0.64**	0.29	0.21	0.44	0.46	0.51	0.49	0.26	0.55	0.24	0.47	0.39	0.25	0.12
Weissia longifolia	0.12	0.29	0.69	**0.86**	0.34	0.28	0.35	0.71	0.56	0.58	0.63	0.51	0.46	0.28	0.33	0.22	0.20	0.19	0.06	0.06
Rhynchostegium confertum	0.19	0.46	0.82	0.66	0.38	0.39	0.65	0.88	0.77	0.86	**0.90**	0.81	0.74	0.42	0.61	0.29	0.43	0.34	0.11	0.06
Syntrichia ruraliformis	0.16	0.41	0.30	0.23	0.30	0.34	0.38	0.33	0.39	0.42	0.39	0.41	0.43	**0.53**	0.40	0.20	0.29	0.38	0.13	0.11
Mnium stellare	0.07	0.20	0.30	0.34	0.10	0.13	0.46	0.39	0.32	0.49	0.55	0.55	0.53	0.29	0.56	**0.63**	0.62	0.44	0.37	0.27
Pleurozium schreberi	0.11	0.32	0.35	0.25	0.17	0.19	0.71	0.40	0.41	0.60	0.63	0.74	0.78	0.49	**0.87**	0.38	0.81	0.78	0.56	0.29
Amphidium mougeotii	0.04	0.15	0.09	0.07	0.04	0.07	0.48	0.13	0.15	0.30	0.32	0.48	0.55	0.35	0.67	0.32	0.73	**0.76**	0.75	0.47
Hylocomiastrum umbratum	0.01	0.08	0.03	0.03	0.02	0.04	0.31	0.03	0.07	0.14	0.12	0.29	0.36	0.30	0.45	0.13	0.46	0.66	**0.68**	0.39
Schistidium trichodon	0.01	0.04	0.05	0.06	0.07	0.03	0.13	0.08	0.09	0.14	0.18	0.22	0.25	0.12	0.30	0.33	0.42	0.33	0.50	**0.65**
Pseudoleskea incurvata	0.00	0.00	0.00	0.01	0.01	0.00	0.03	0.00	0.02	0.03	0.04	0.07	0.09	0.03	0.12	0.08	0.19	0.14	0.30	**0.57**
Kiaeria falcata	0.00	0.02	0.01	0.01	0.01	0.01	0.13	0.02	0.03	0.07	0.10	0.17	0.22	0.10	0.29	0.20	0.39	0.38	0.70	**0.83**
Polytrichastrum sexangulare	0.00	0.01	0.00	0.01	0.00	0.00	0.03	0.01	0.02	0.03	0.04	0.08	0.12	0.04	0.16	0.08	0.23	0.20	0.46	**0.73**
Mnium lycopodioides	0.01	0.01	0.01	0.01	0.01	0.01	0.04	0.01	0.02	0.04	0.06	0.08	0.11	0.04	0.13	0.11	0.21	0.17	0.35	**0.68**

Figure 1A

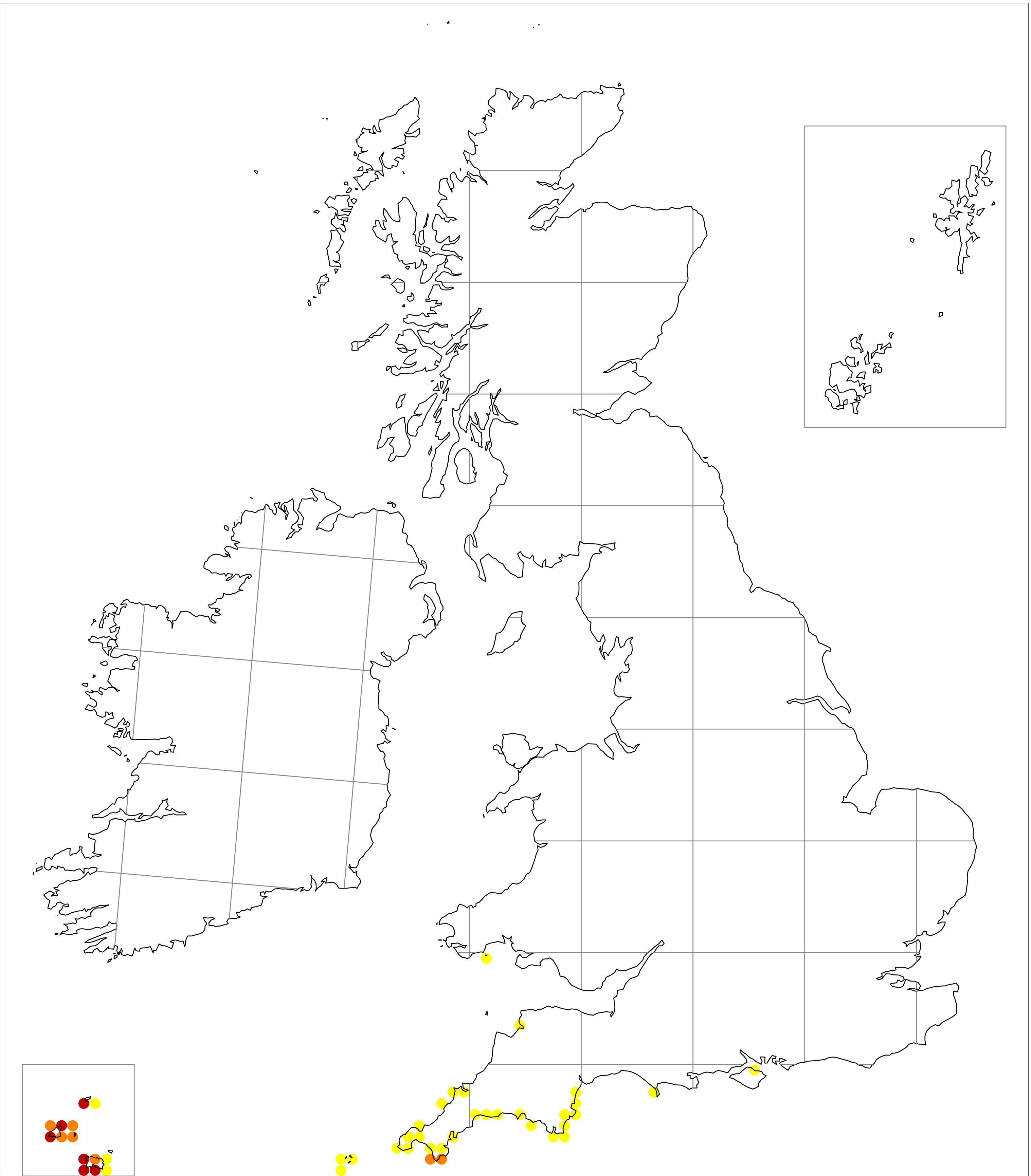

Figure 1B

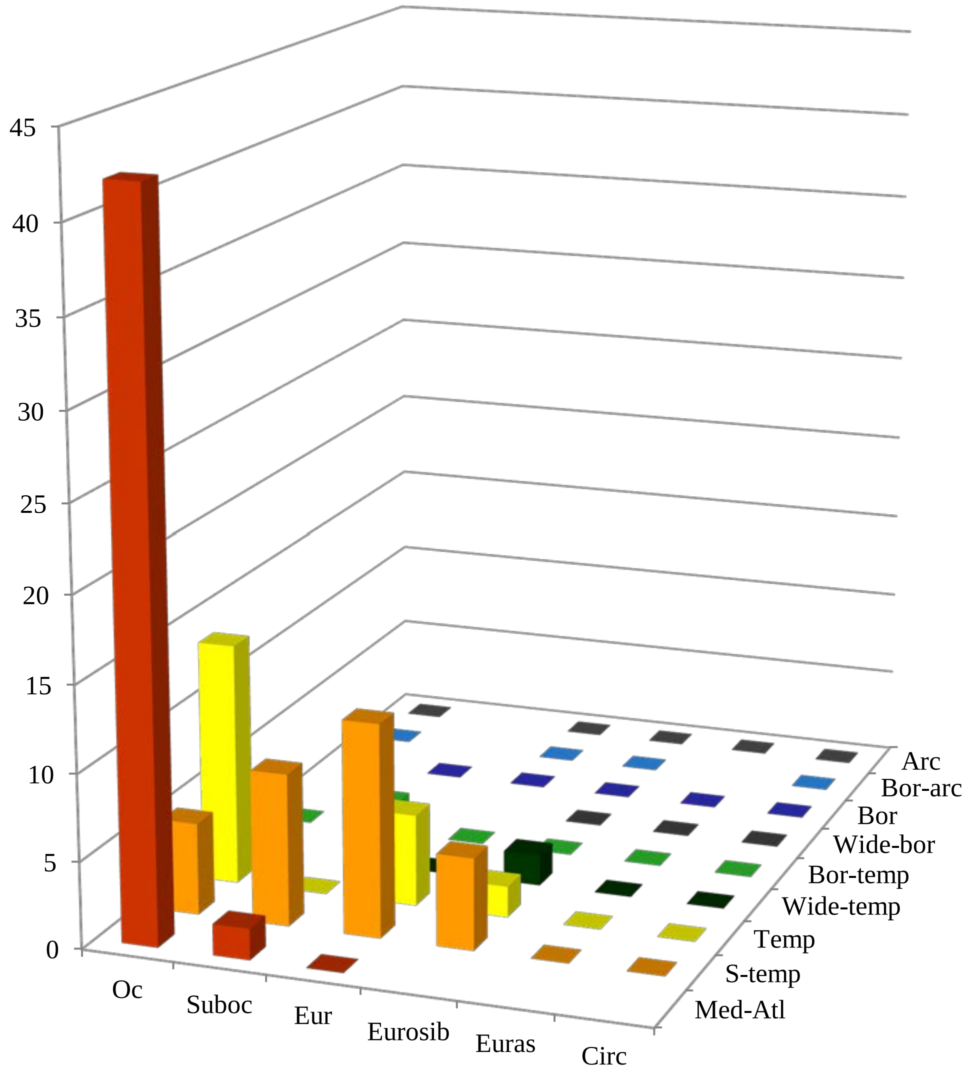

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Figure 1C

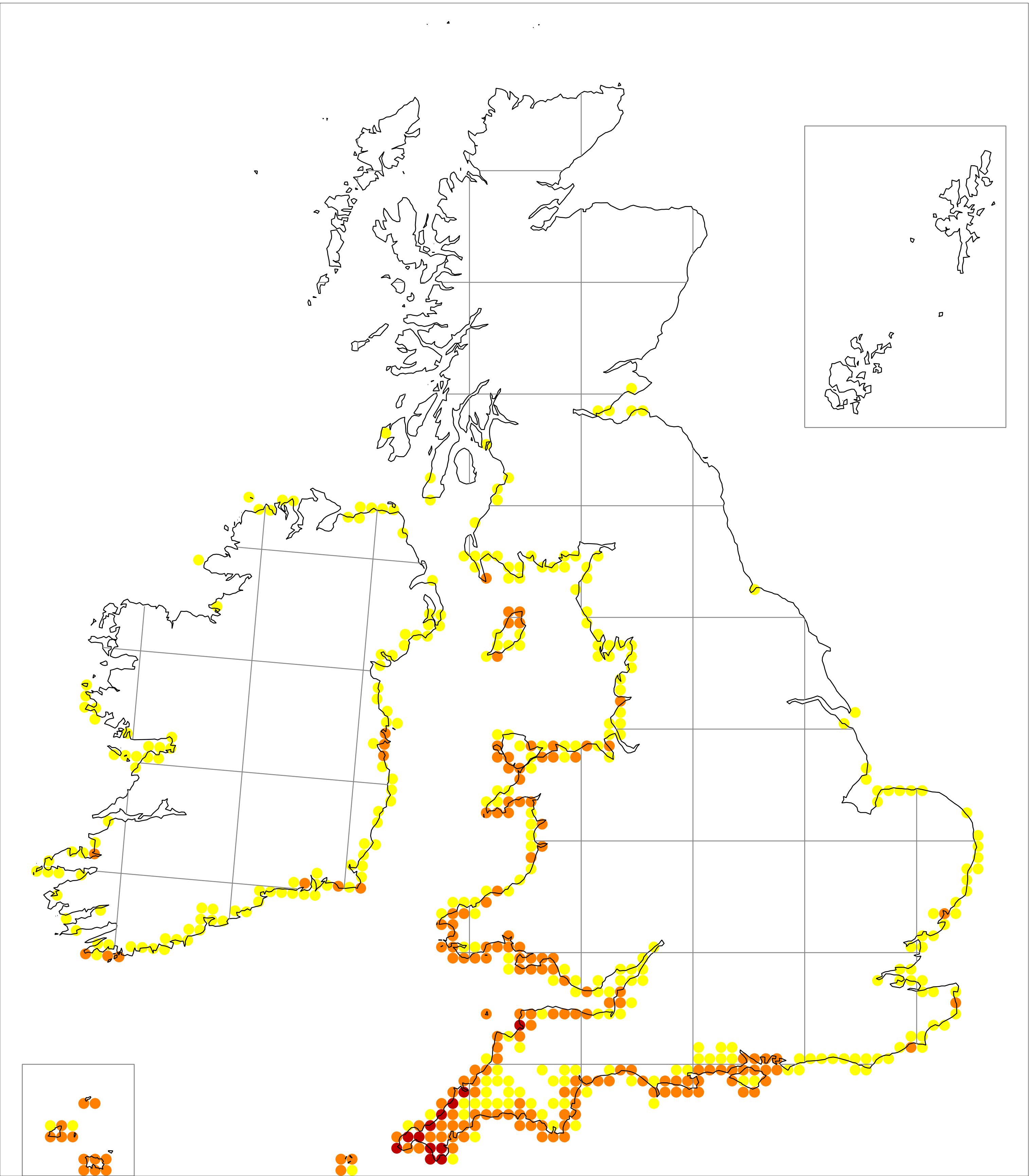

Figure 1D

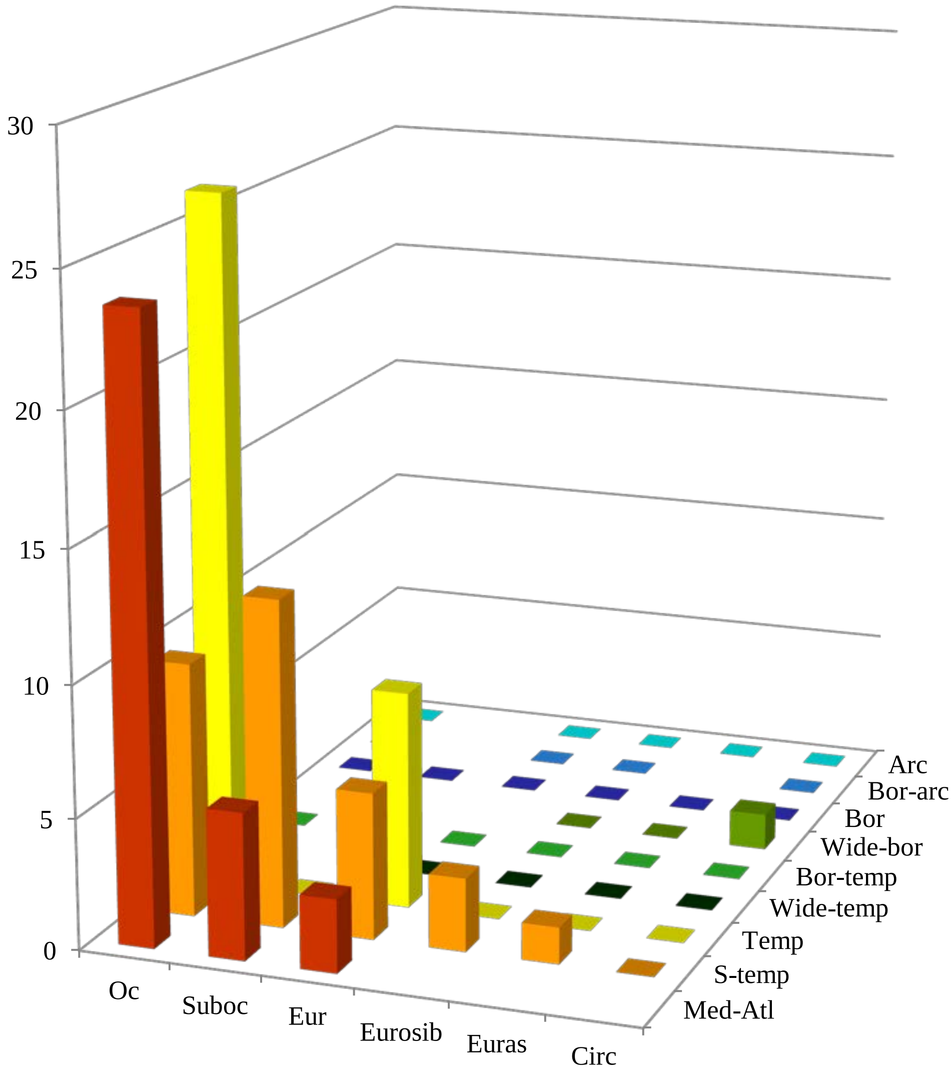

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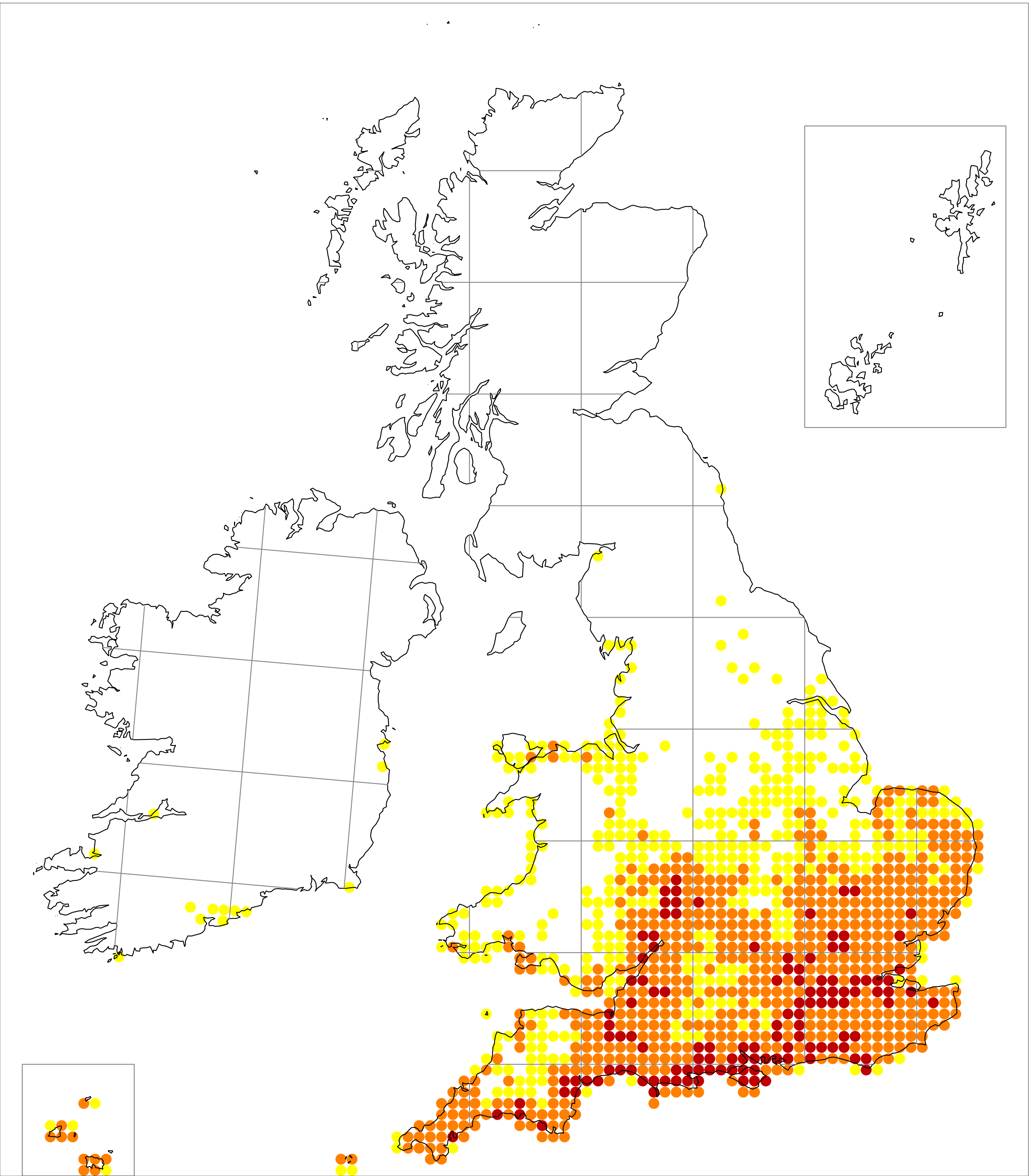
Figure 1E



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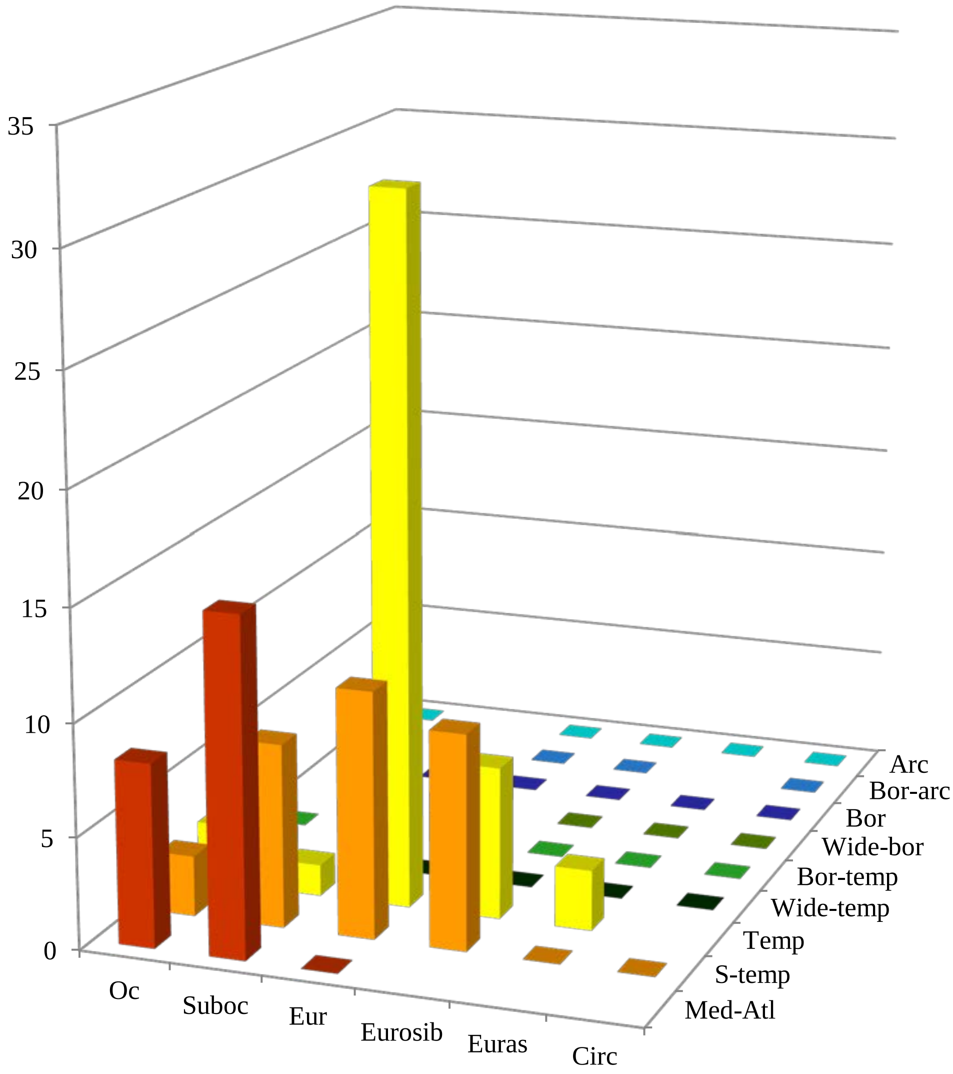

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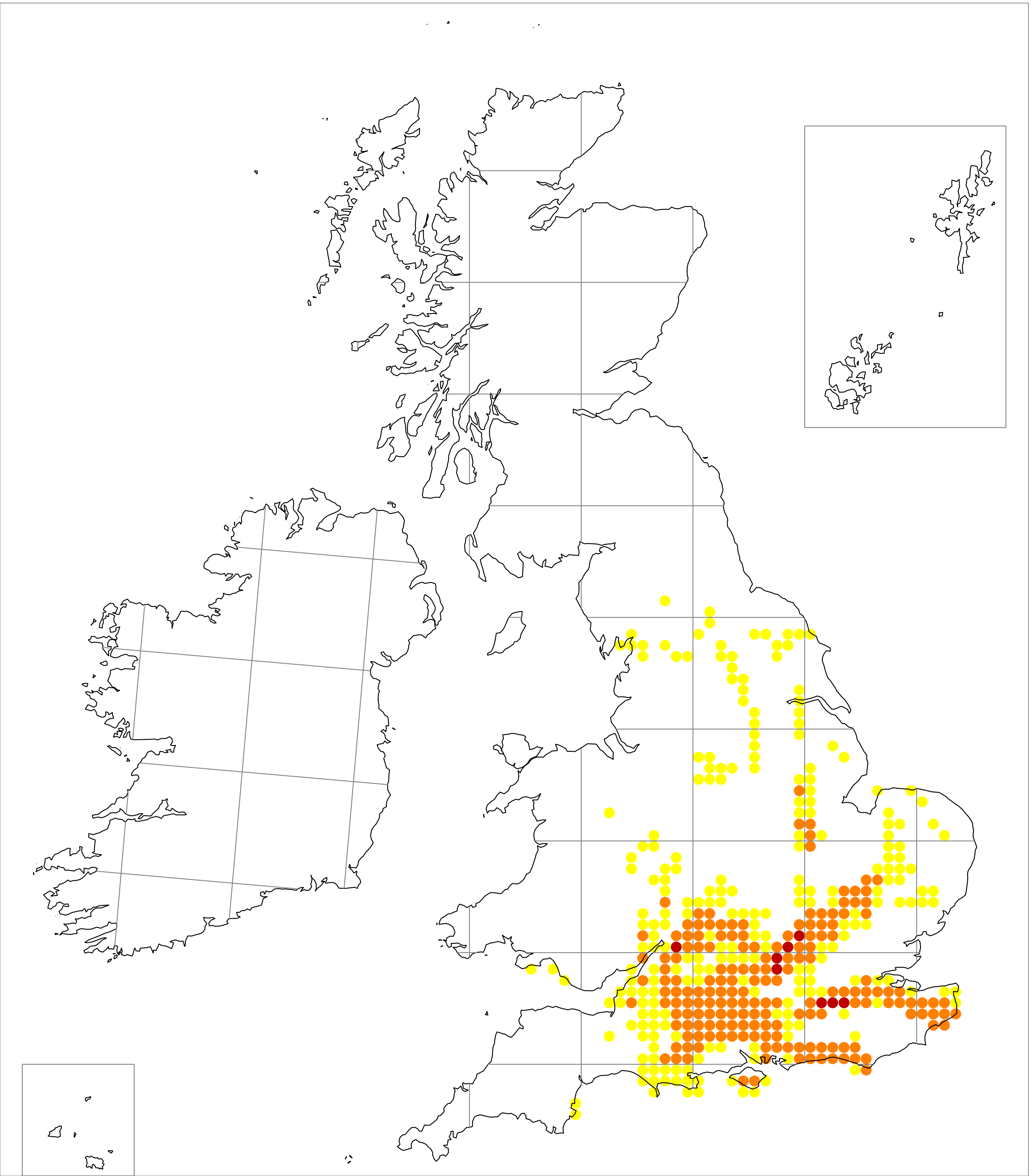
Figure 2A



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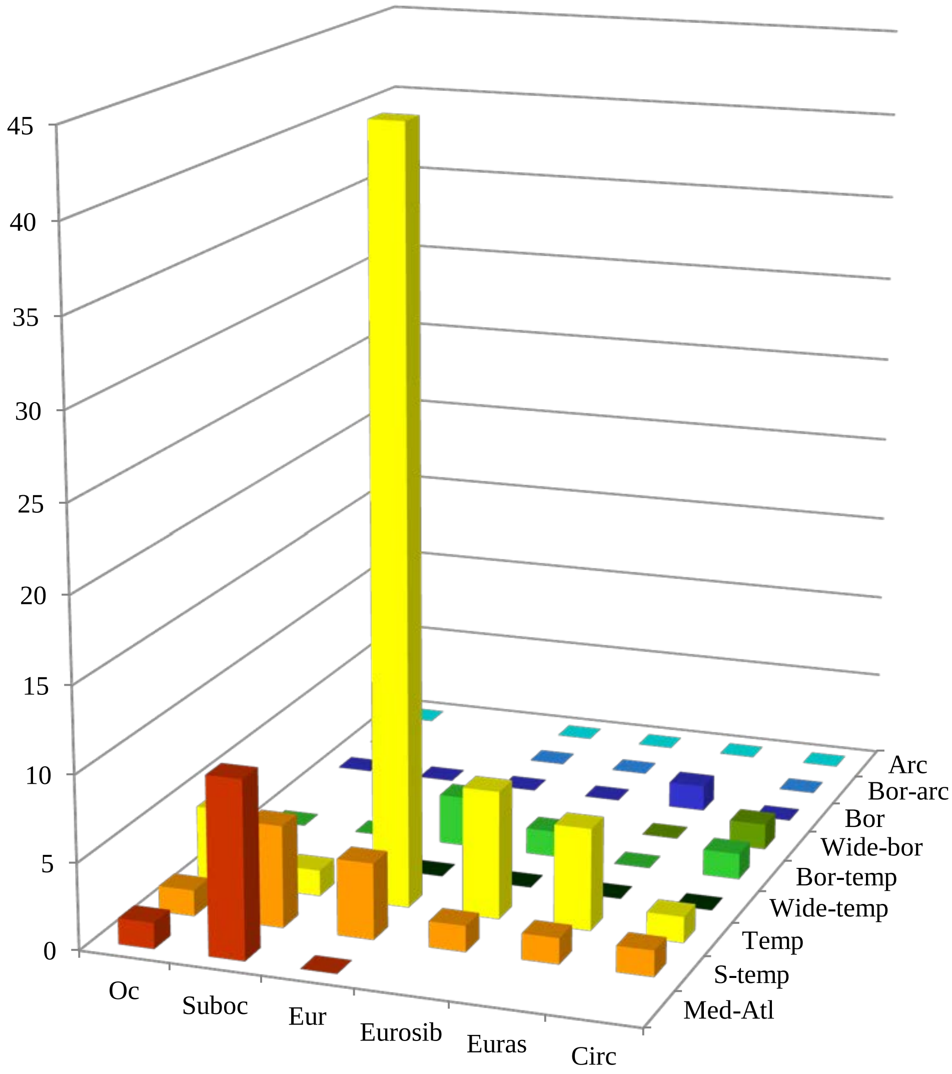
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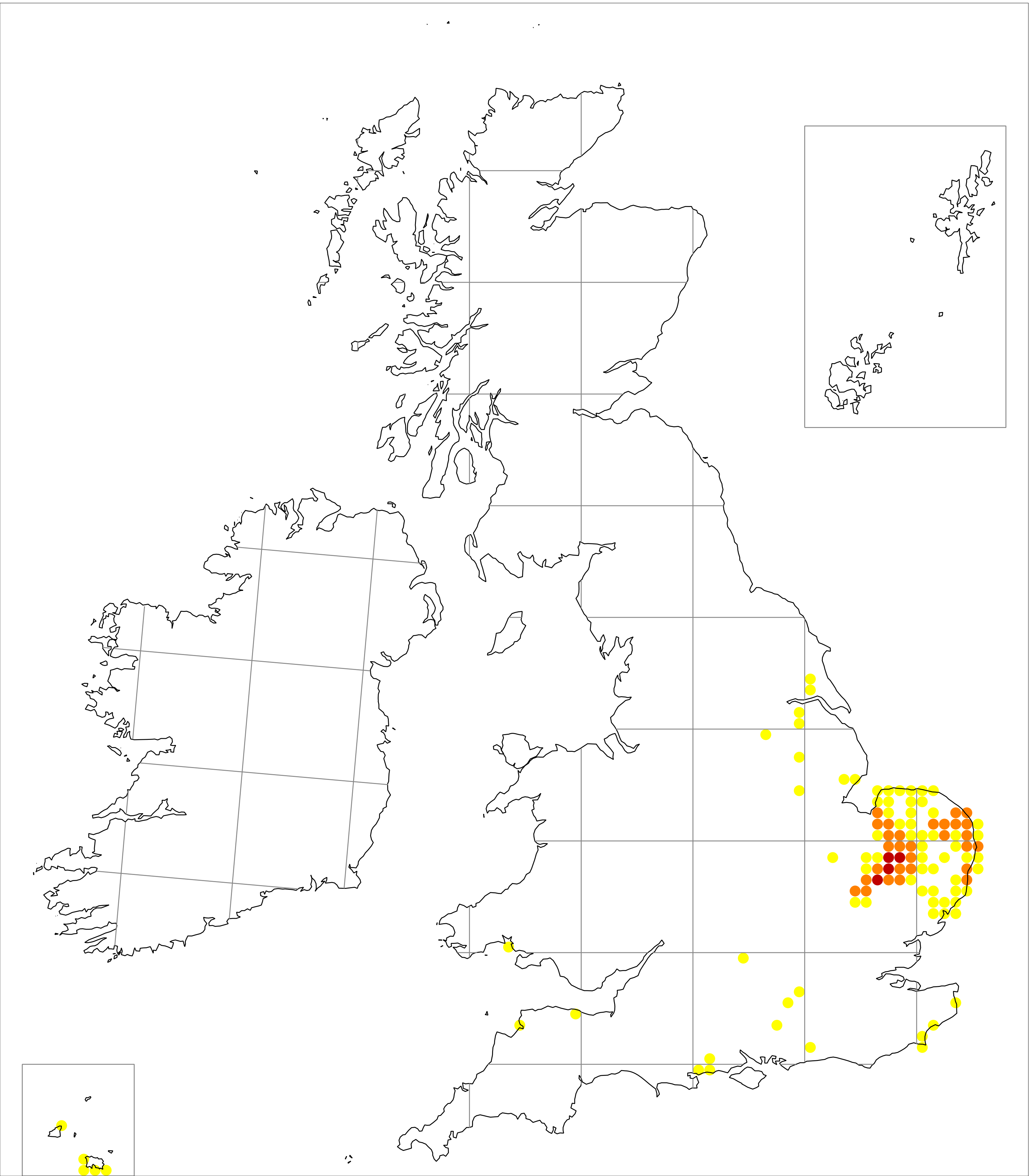
Figure 2C



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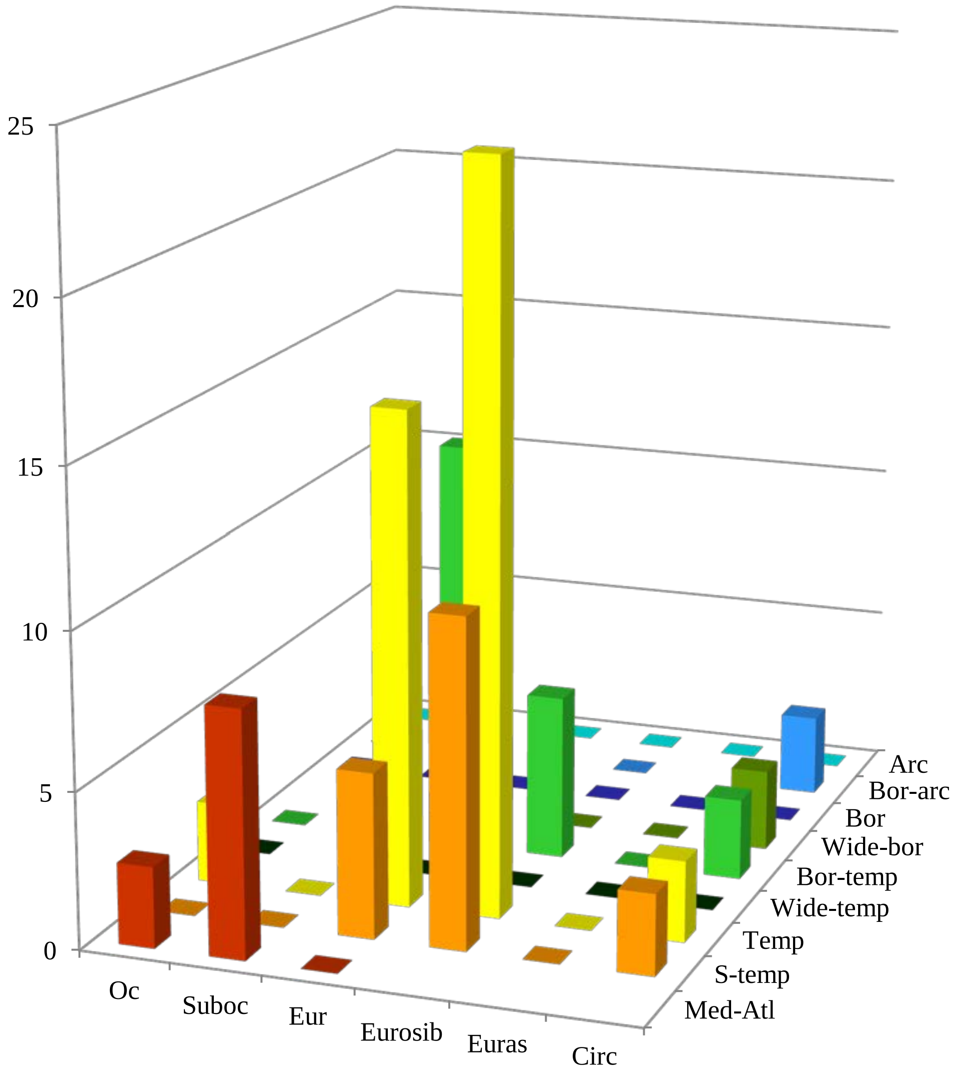
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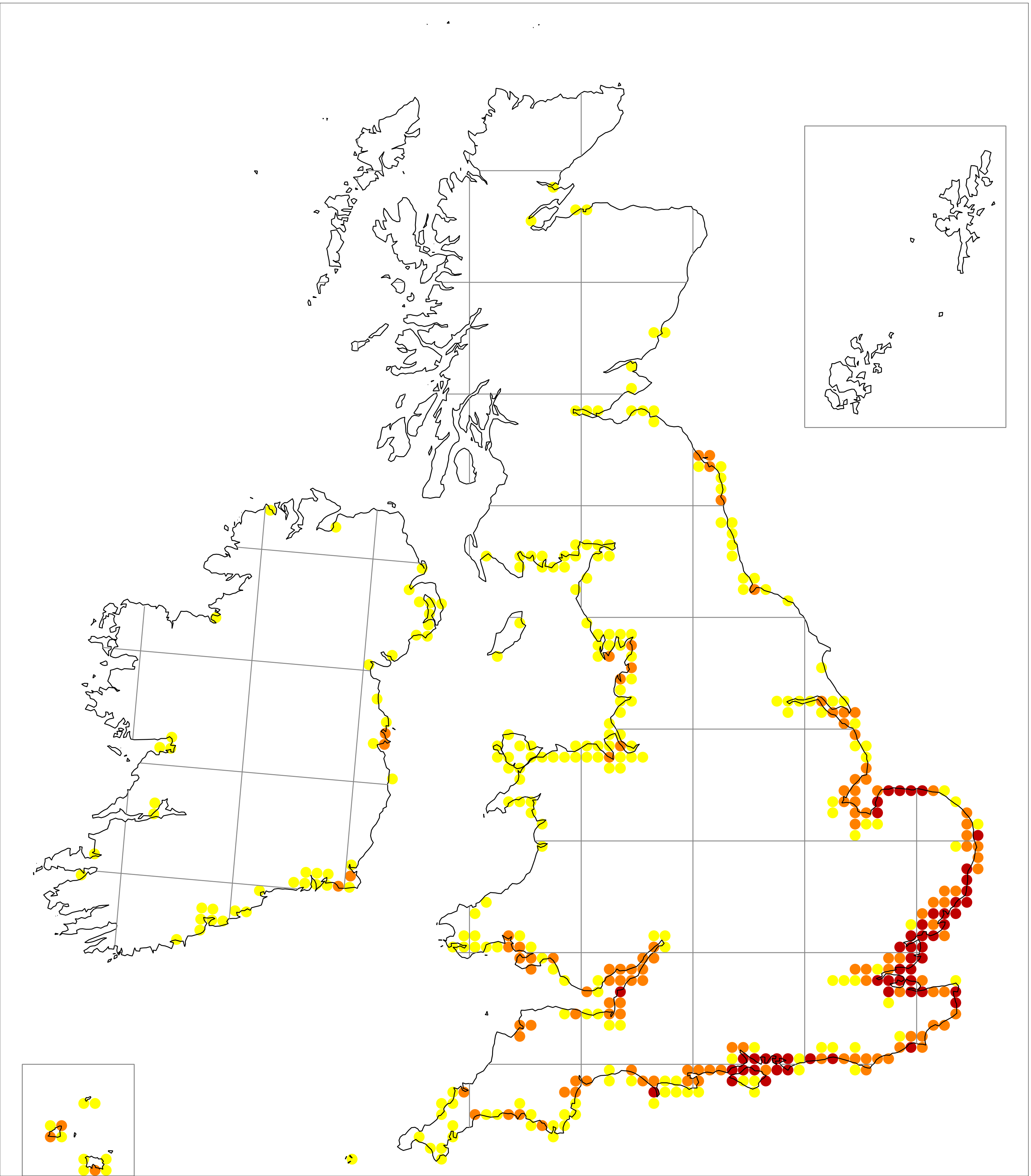
Figure 2E



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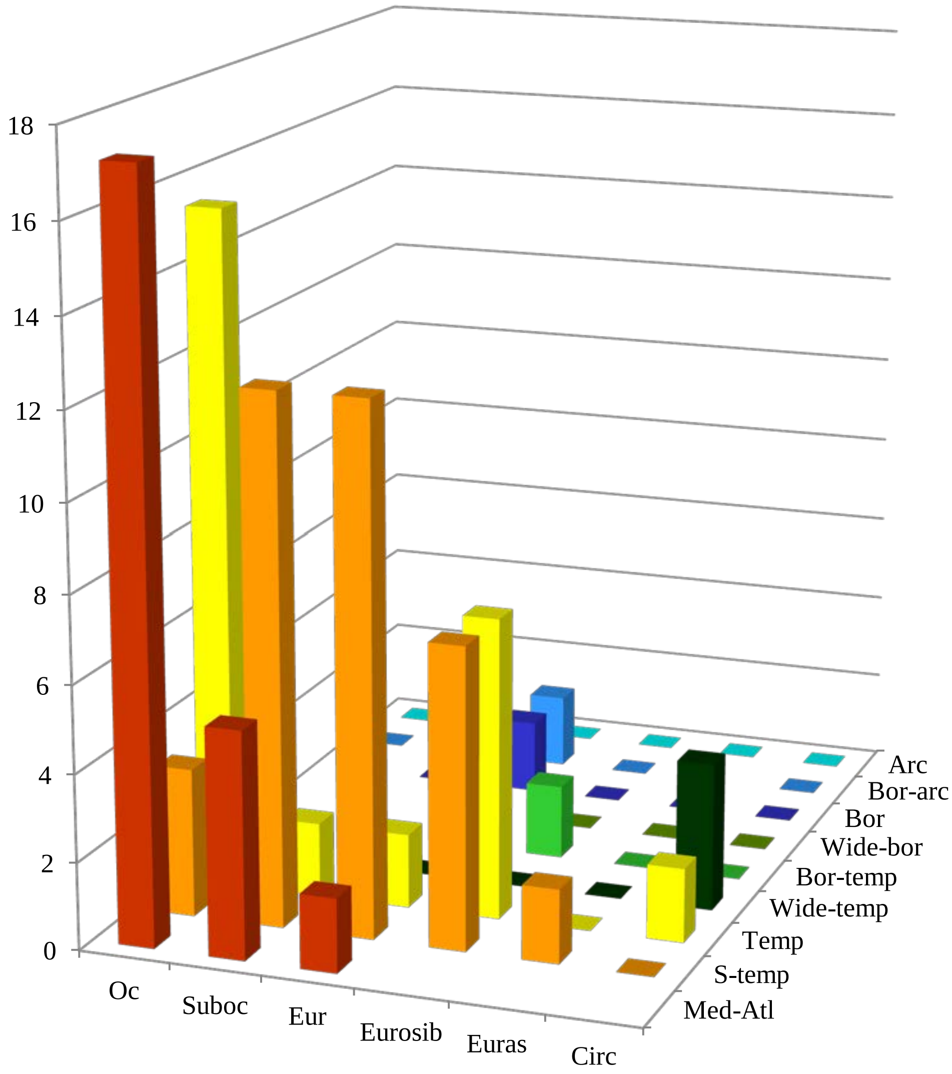

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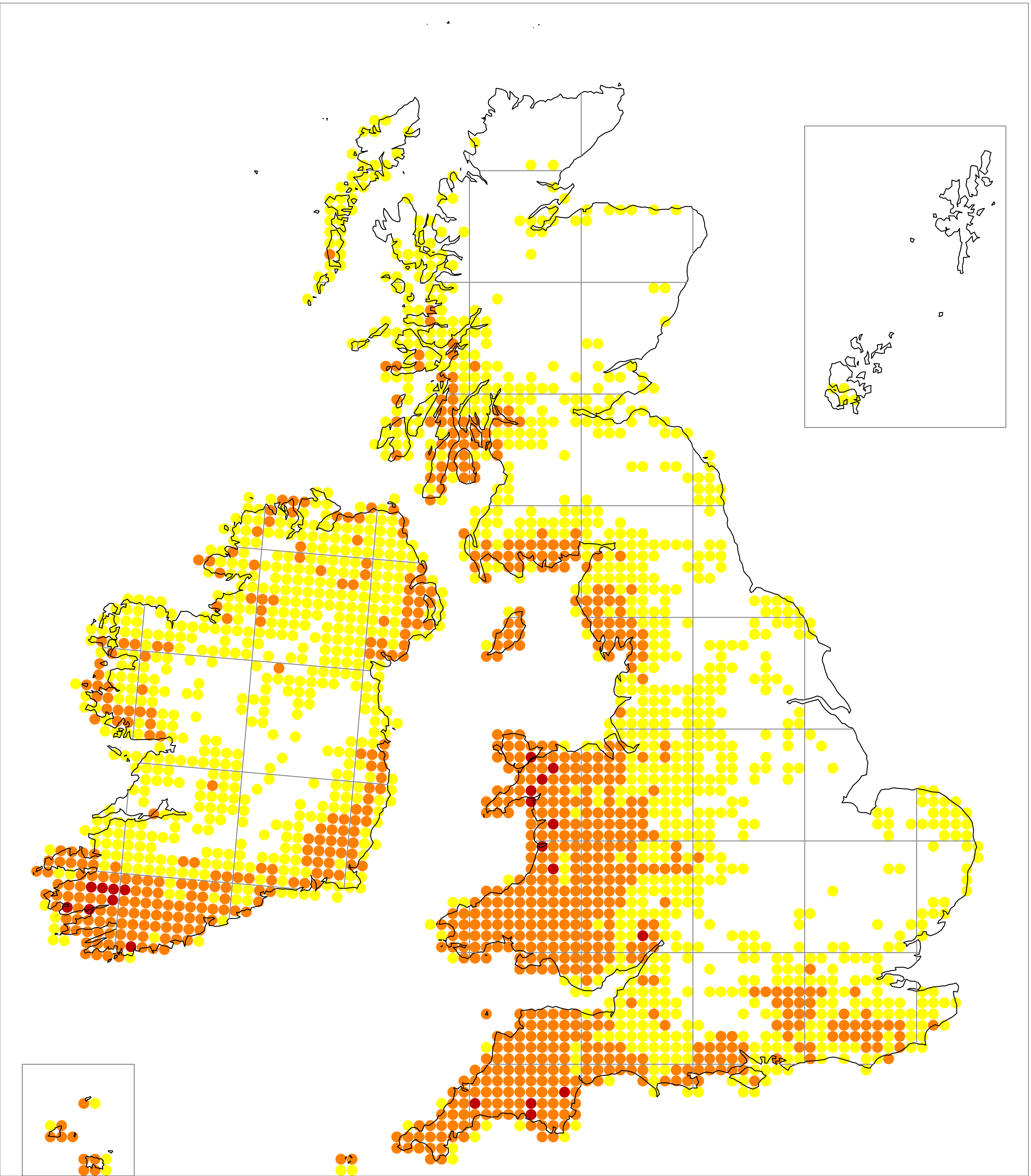
Figure 3A



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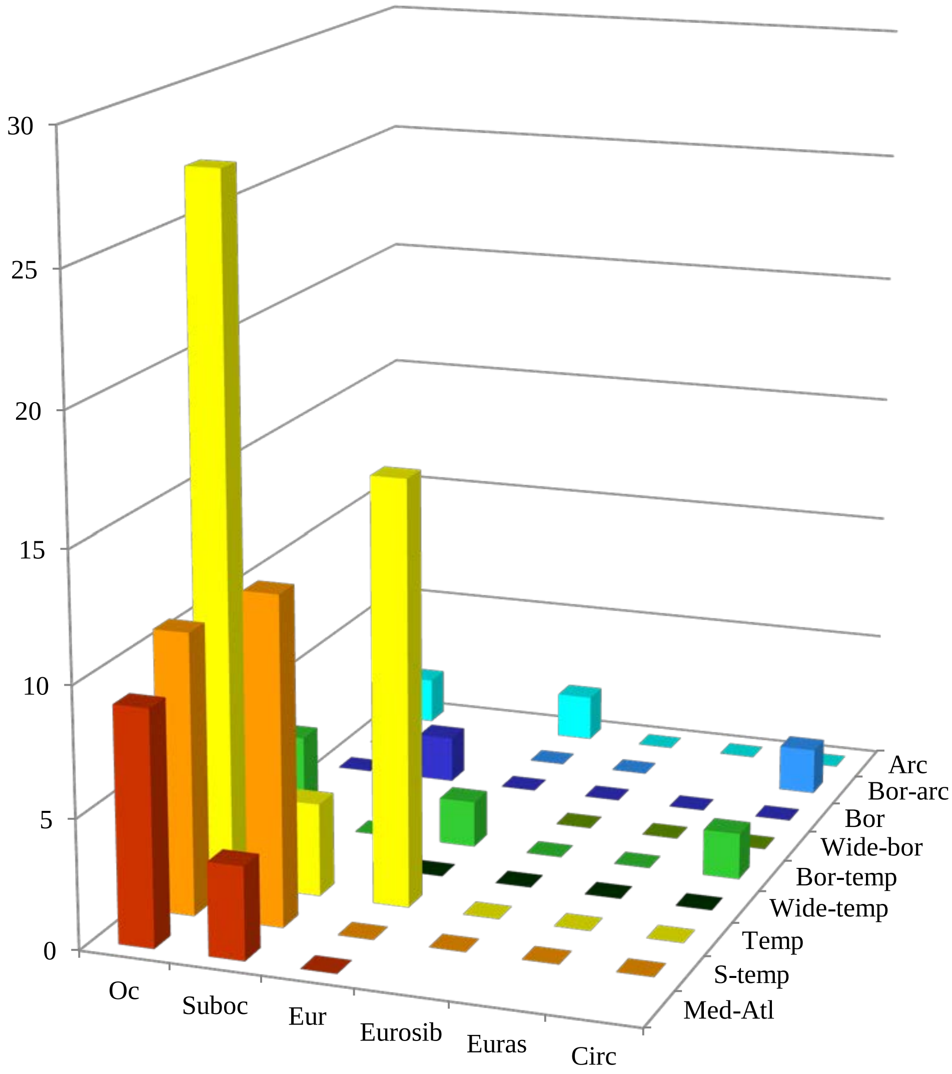

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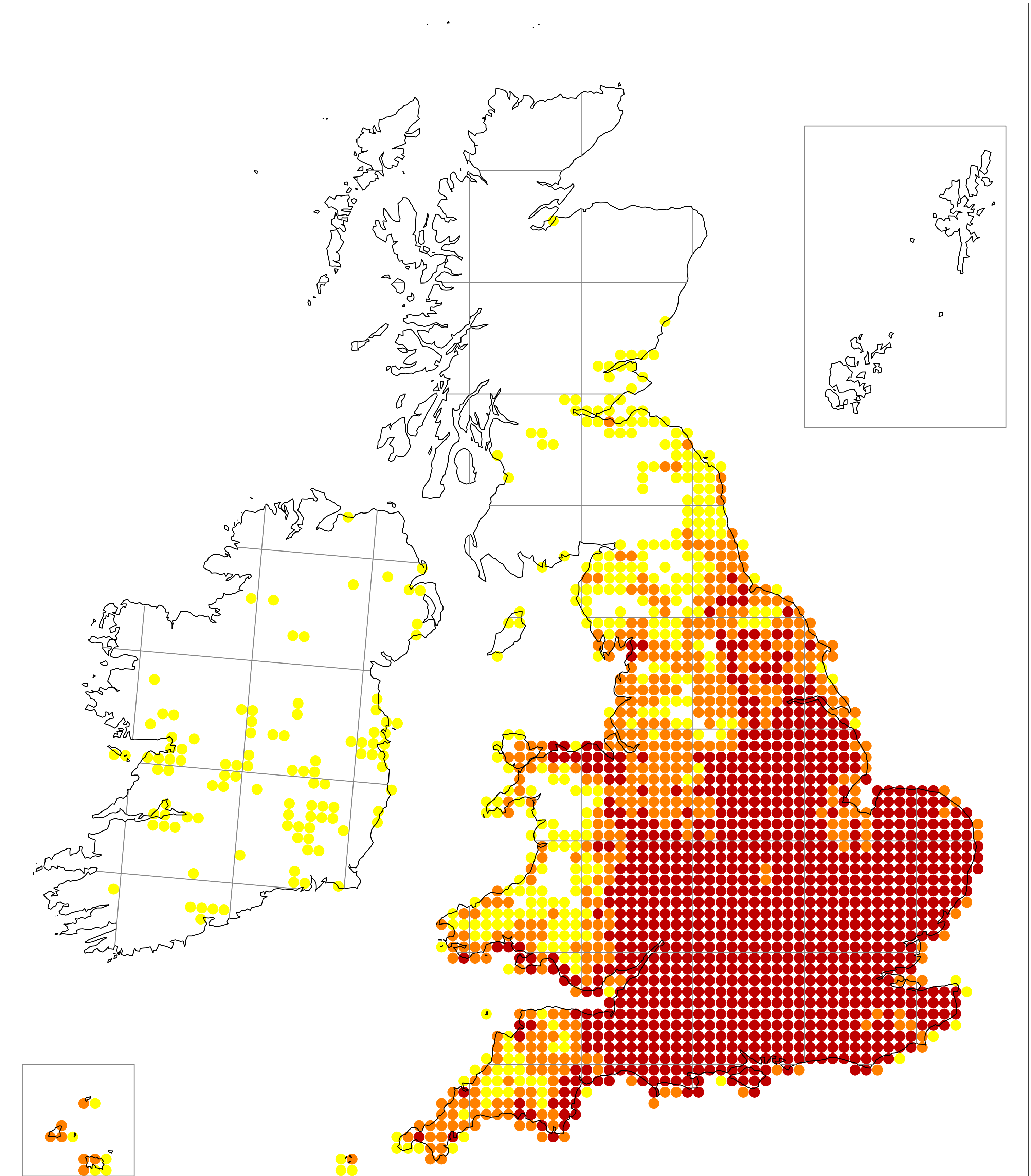
Figure 3C



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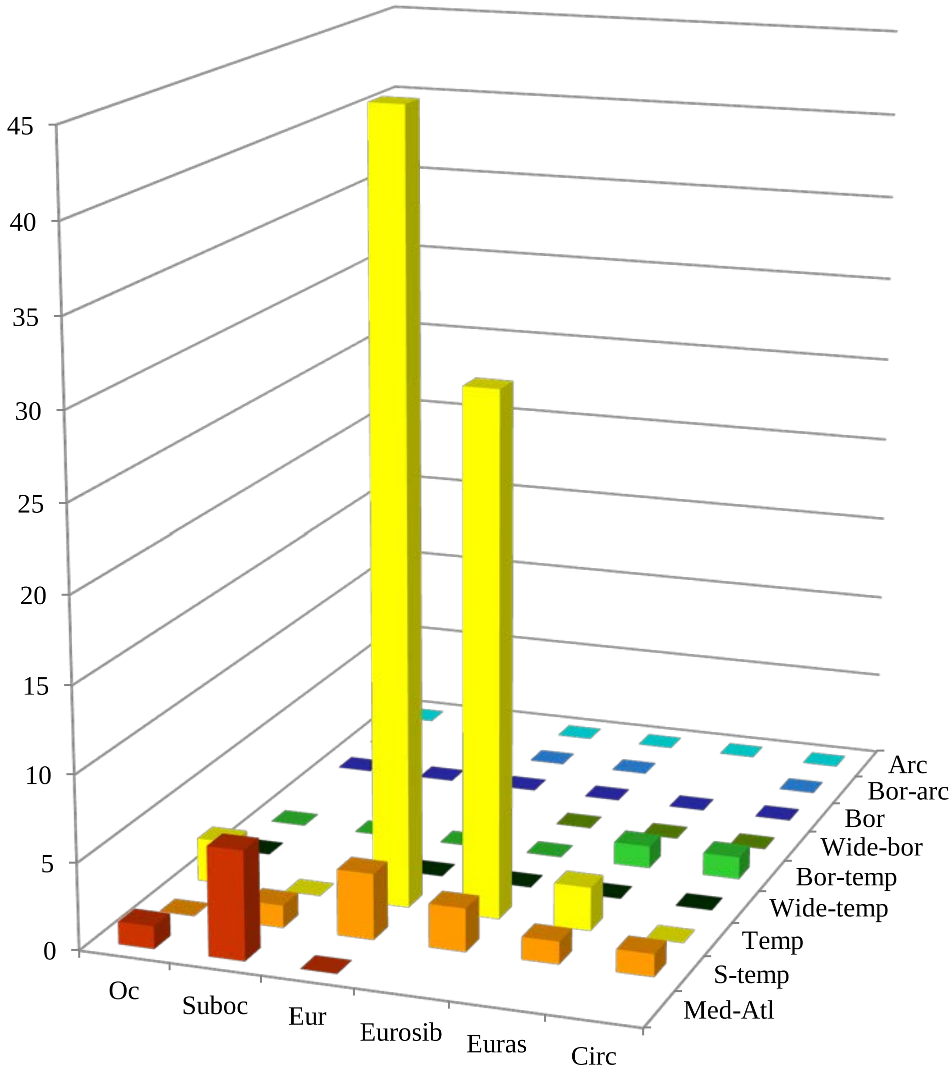

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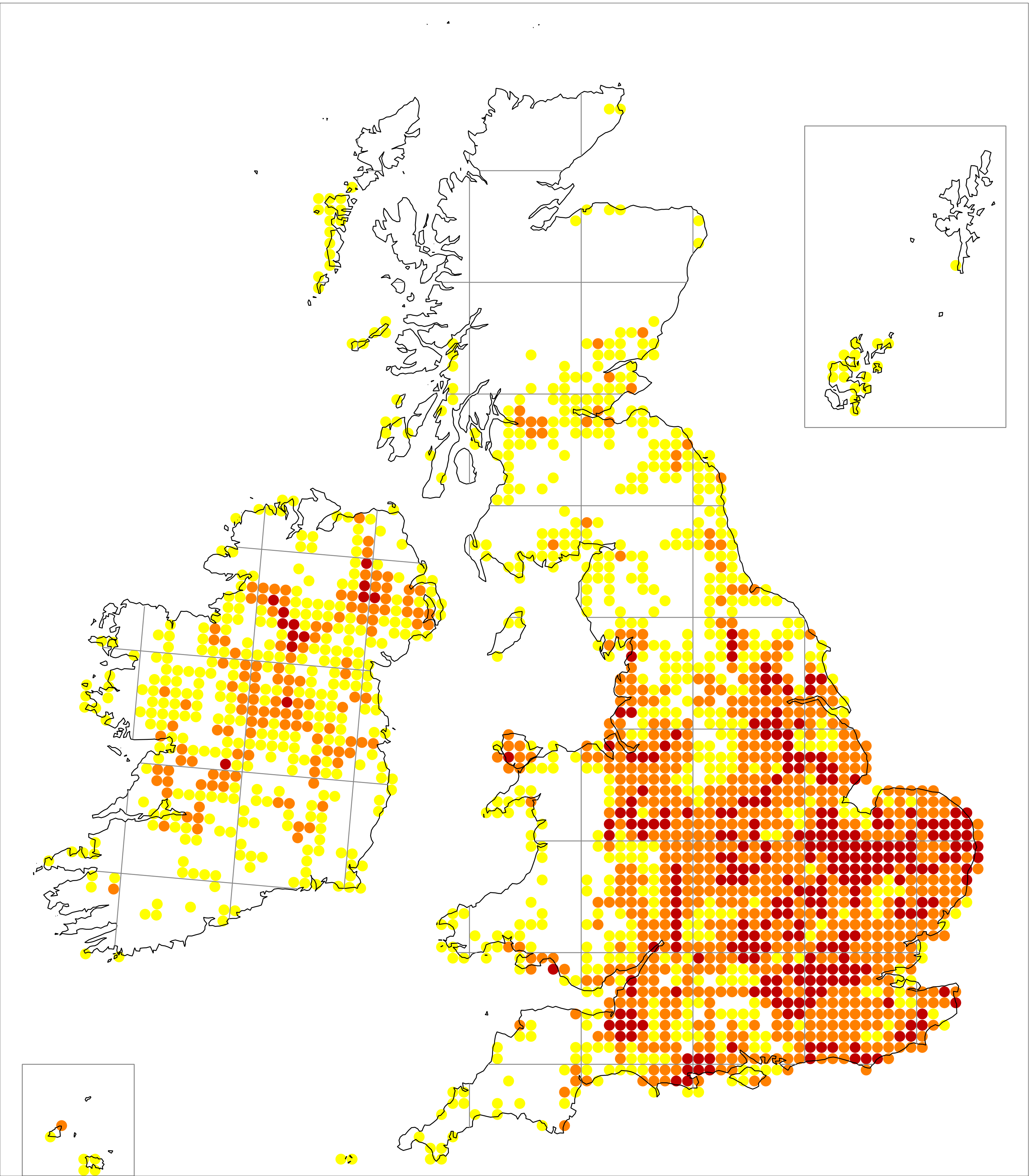
Figure 3E



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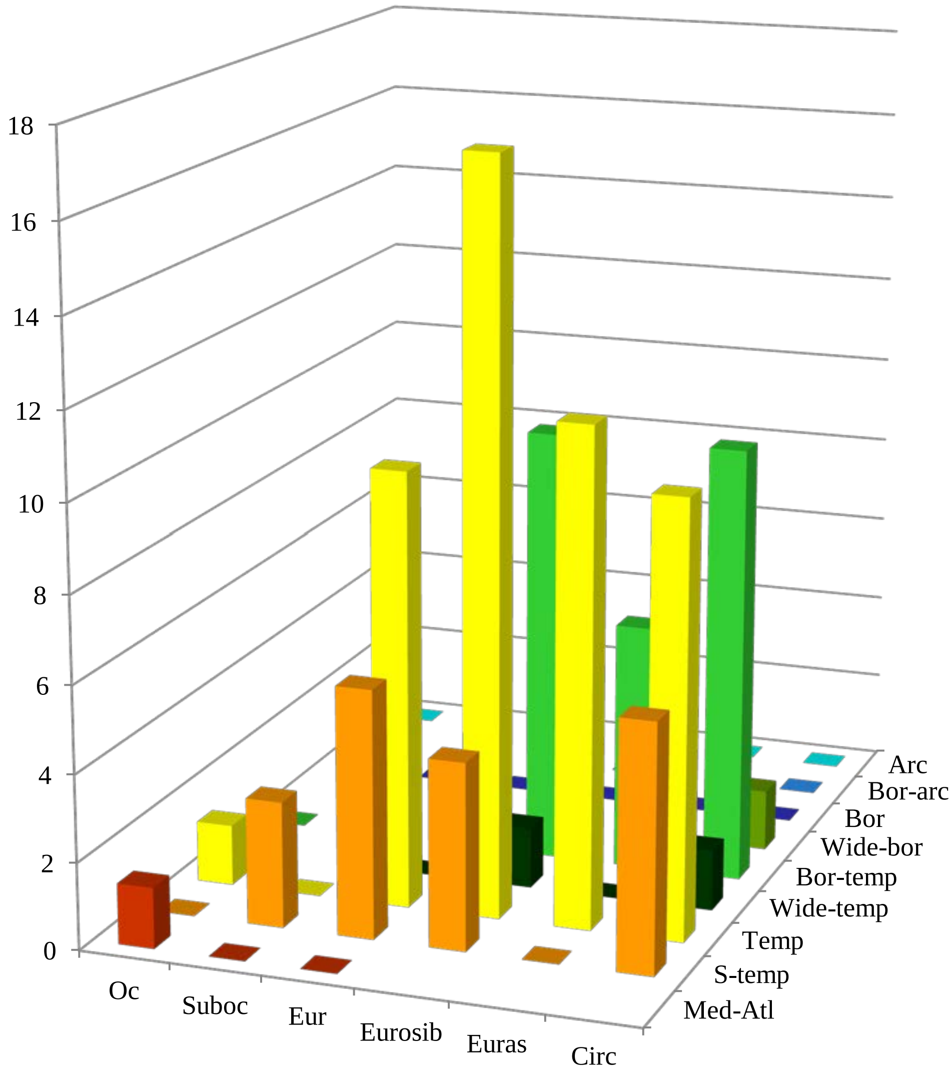

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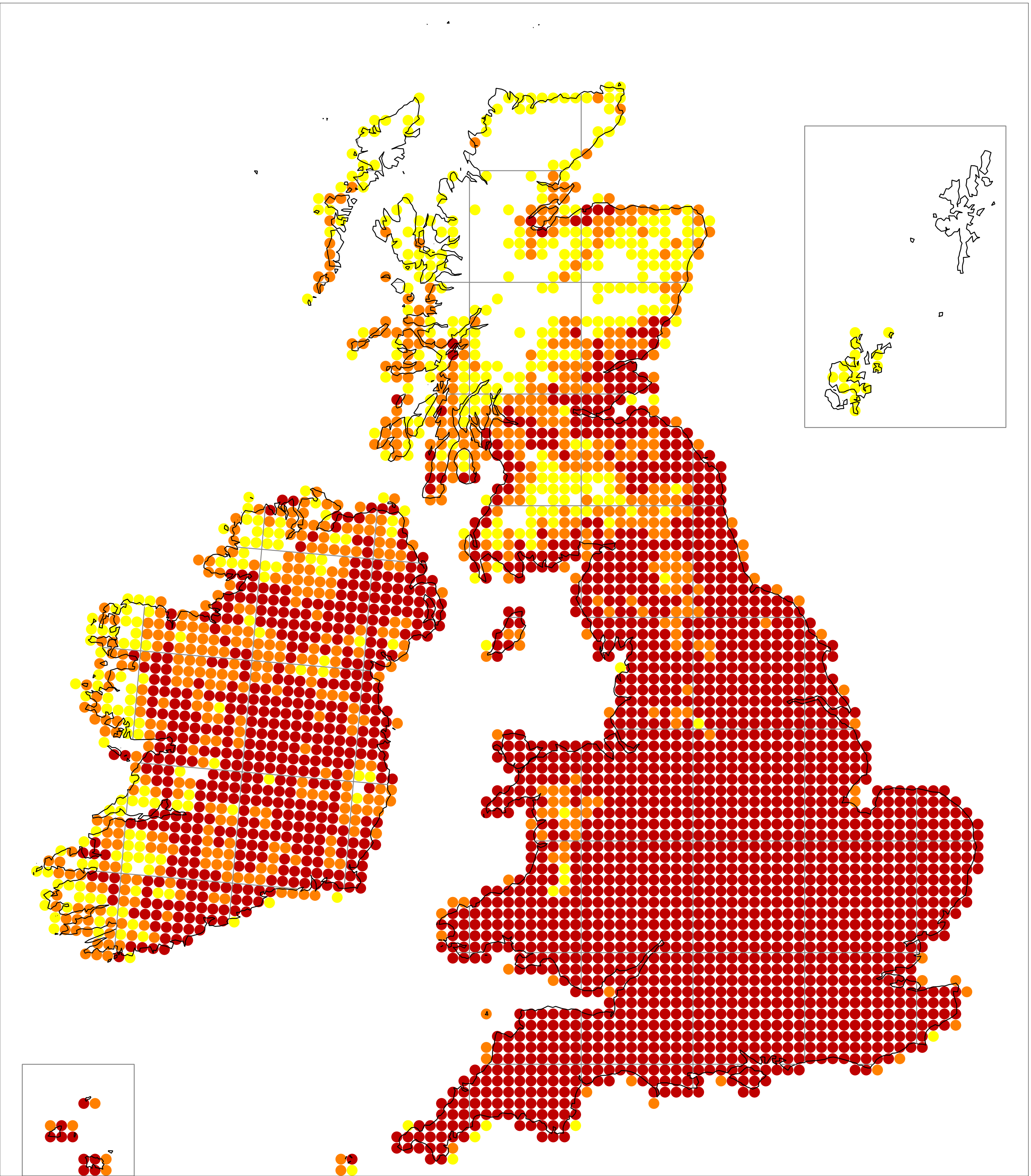
Figure 4A



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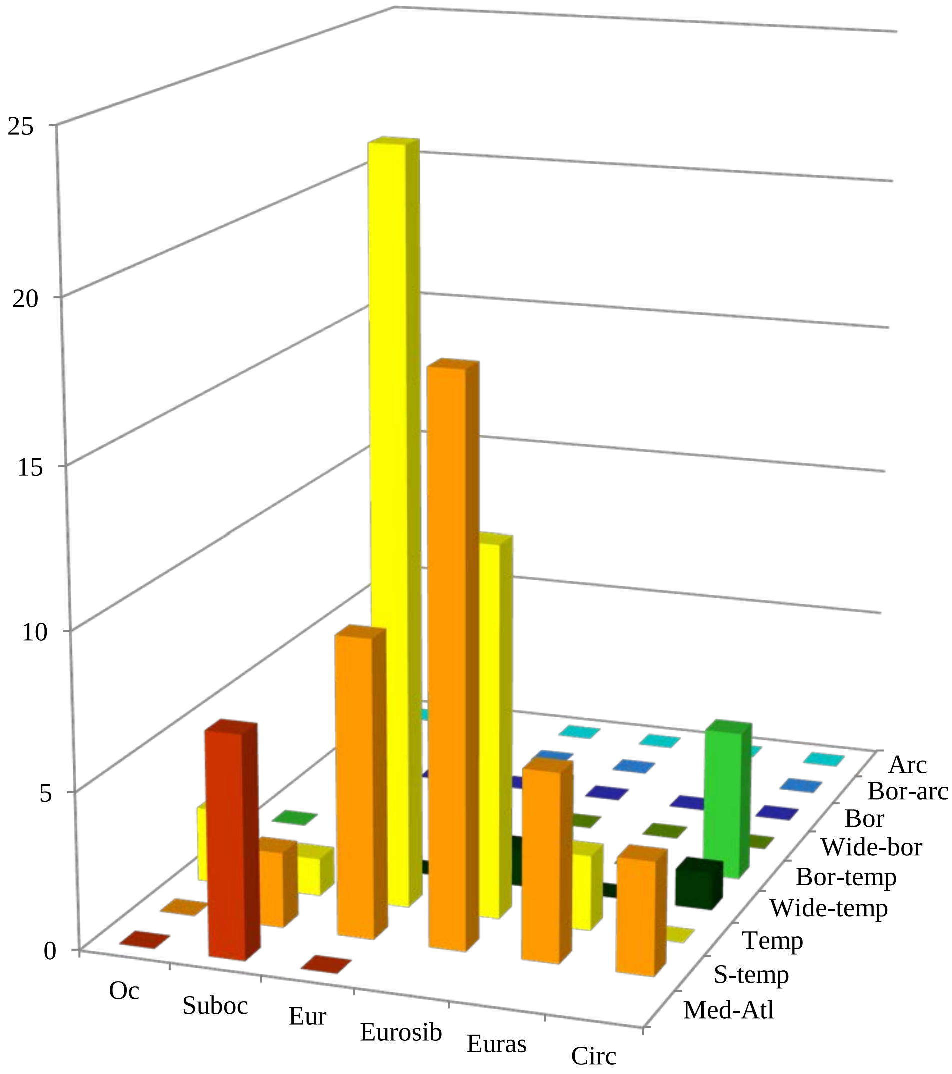
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Figure 4C

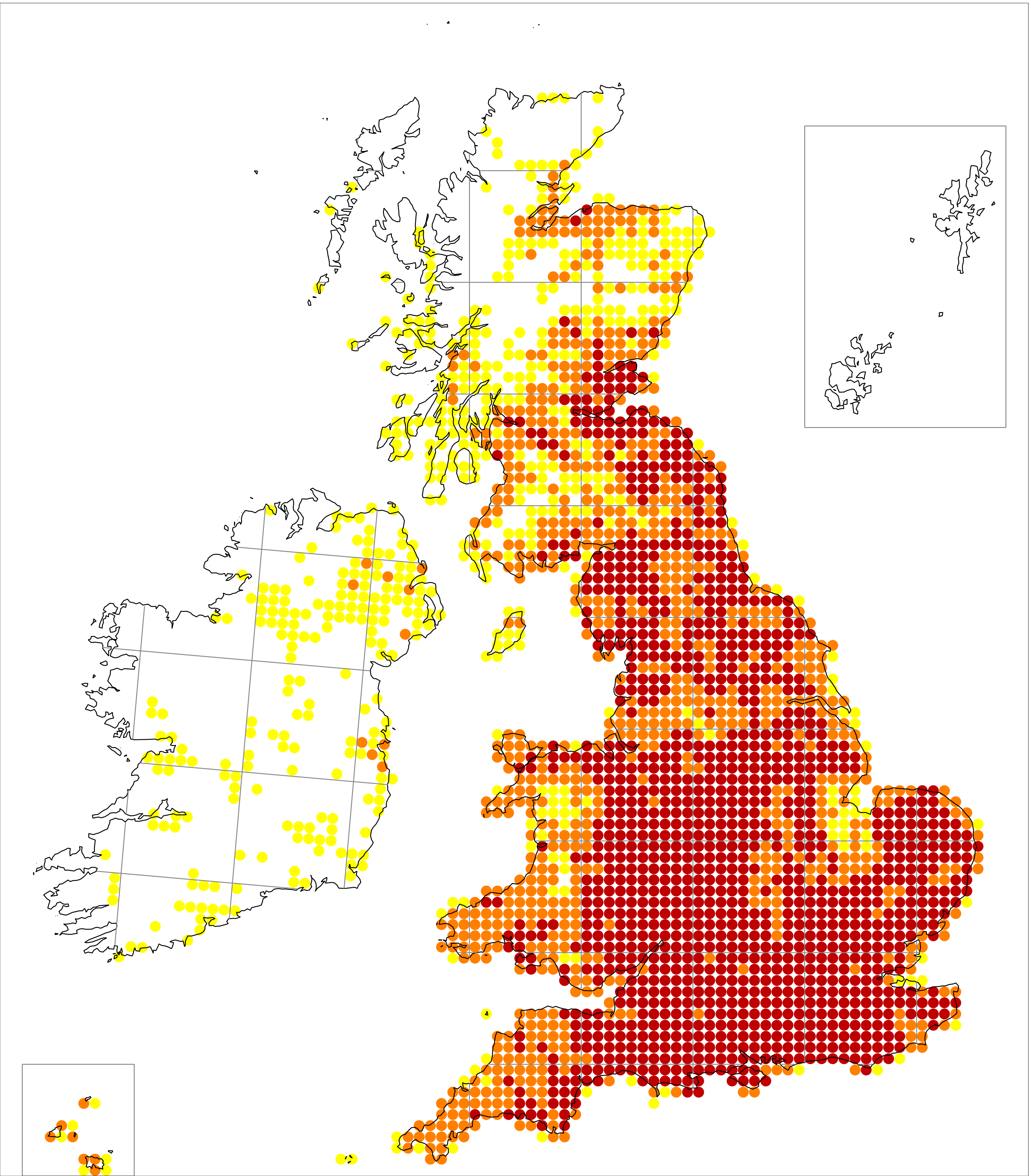

Figure 4D

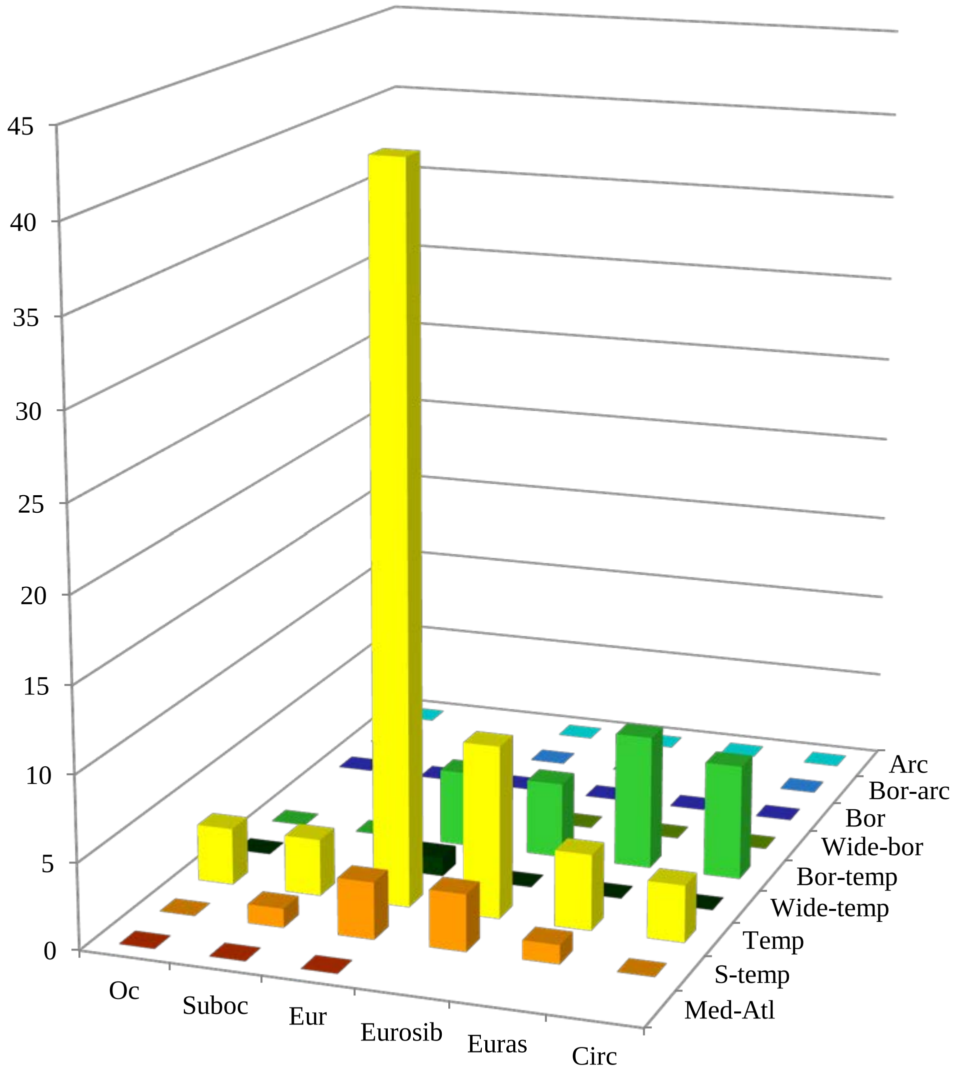
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Figure 4E

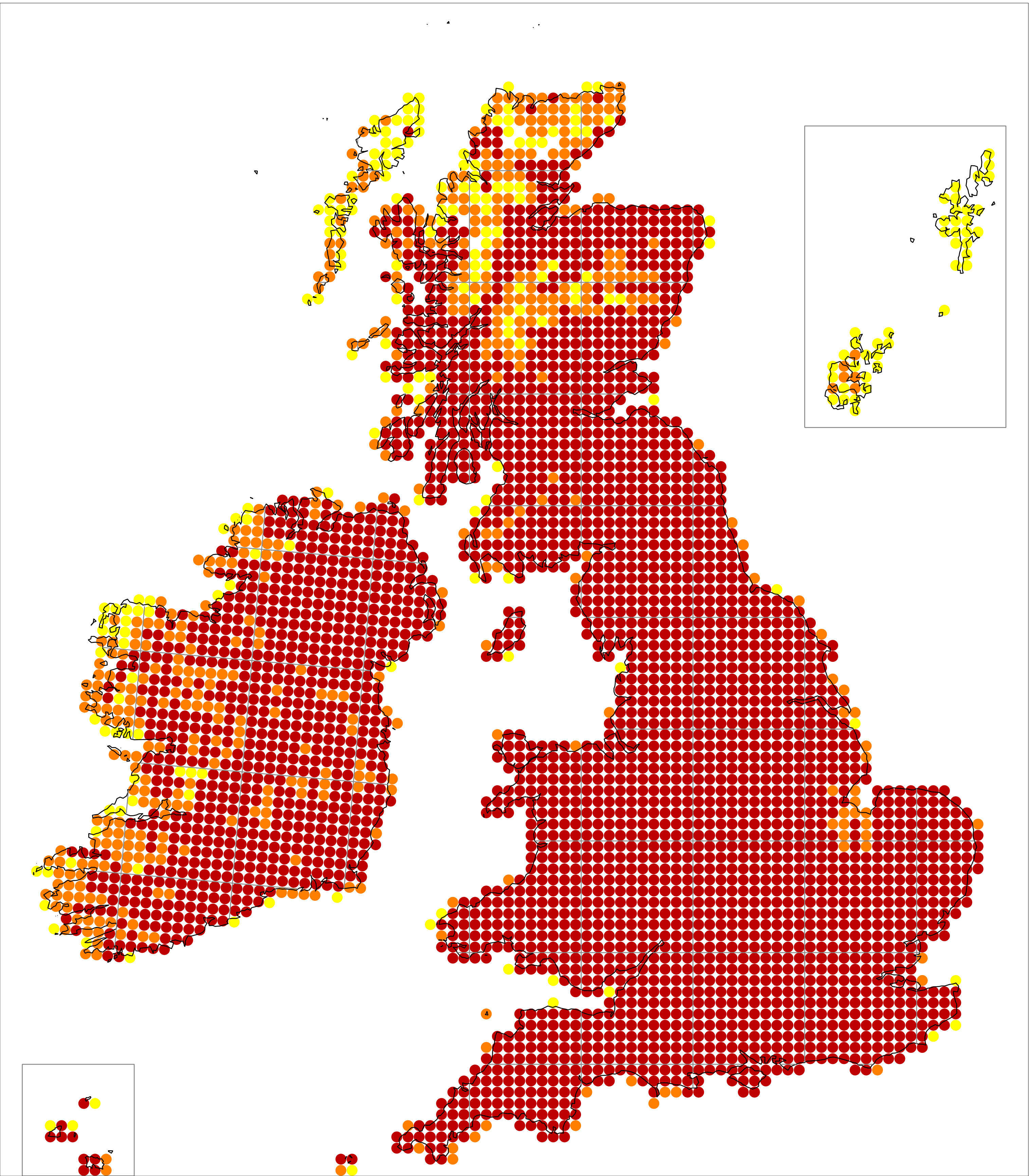

Figure 4F

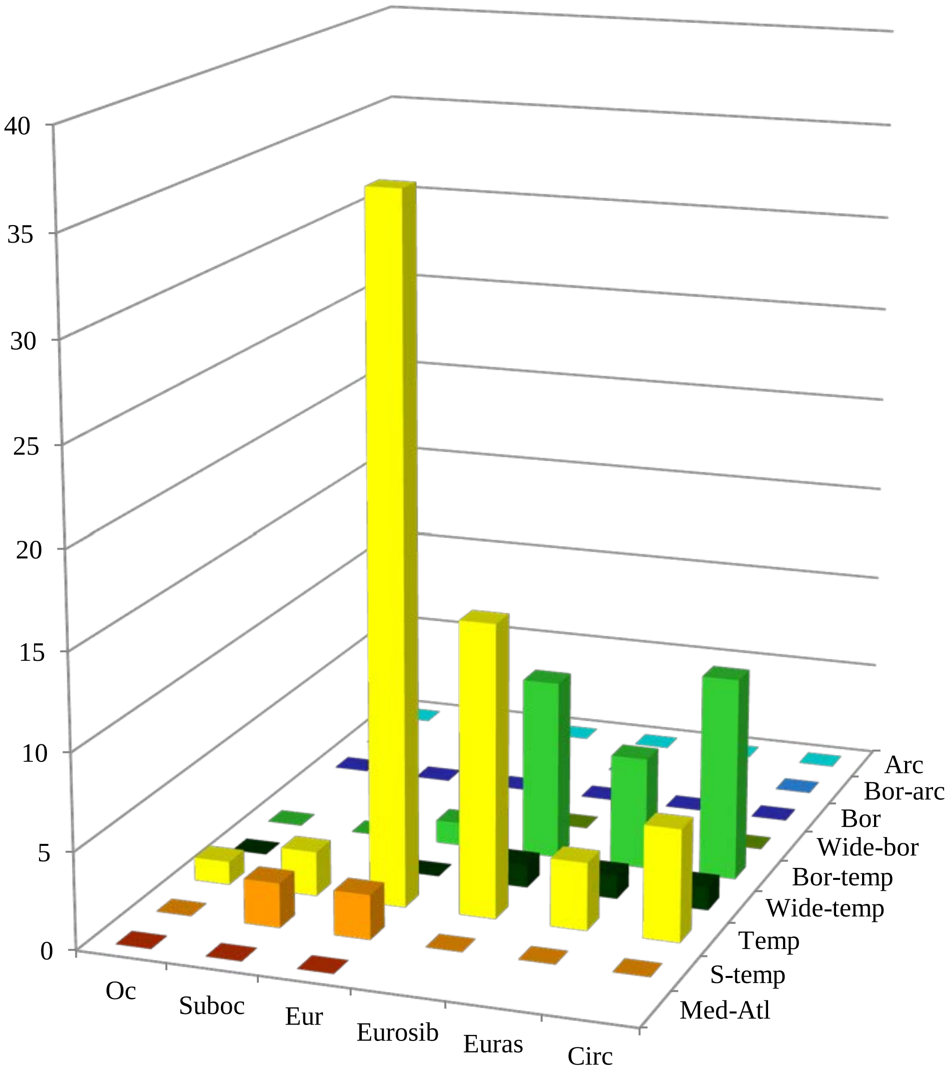

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Figure 5A

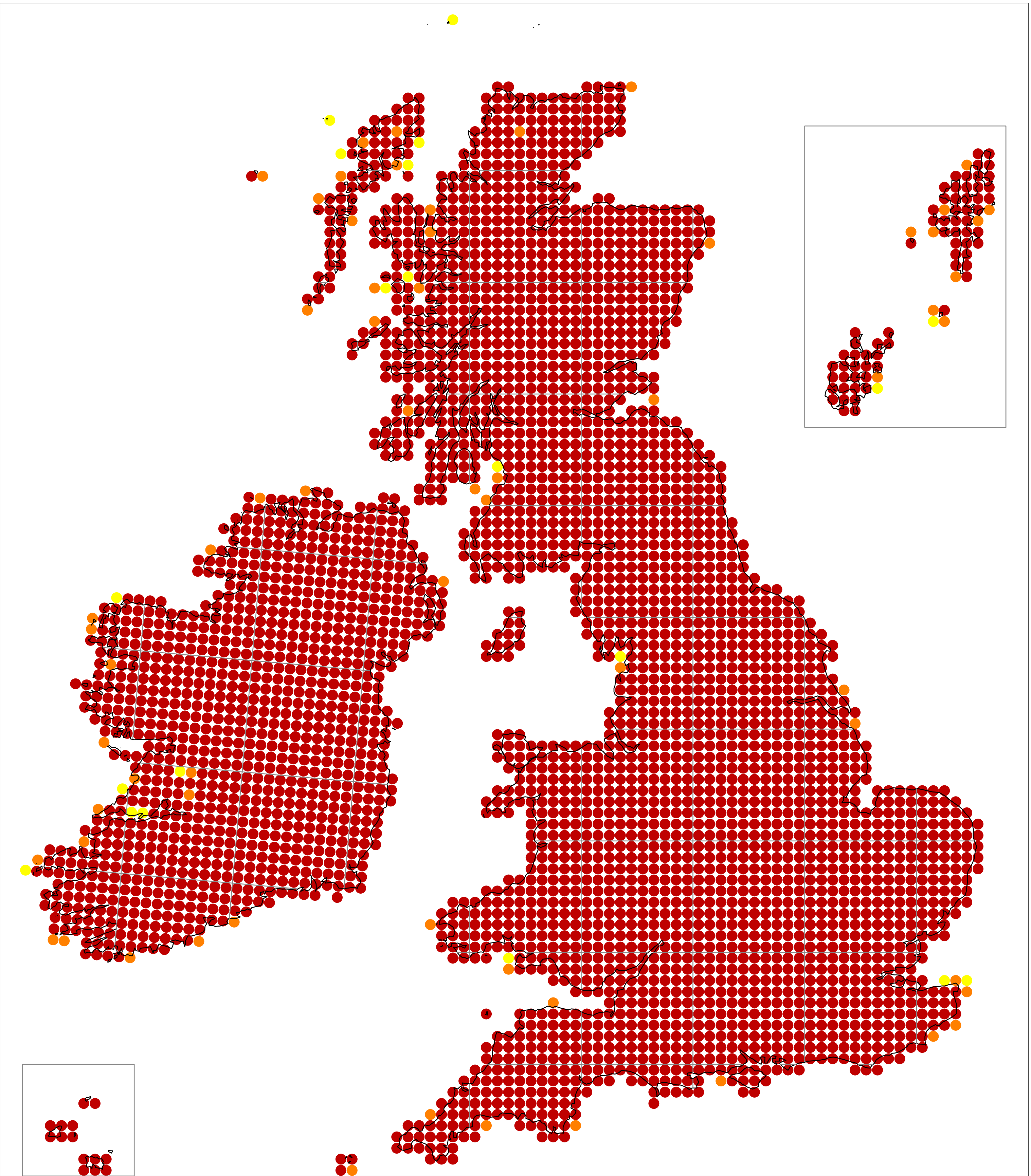

Figure 5B

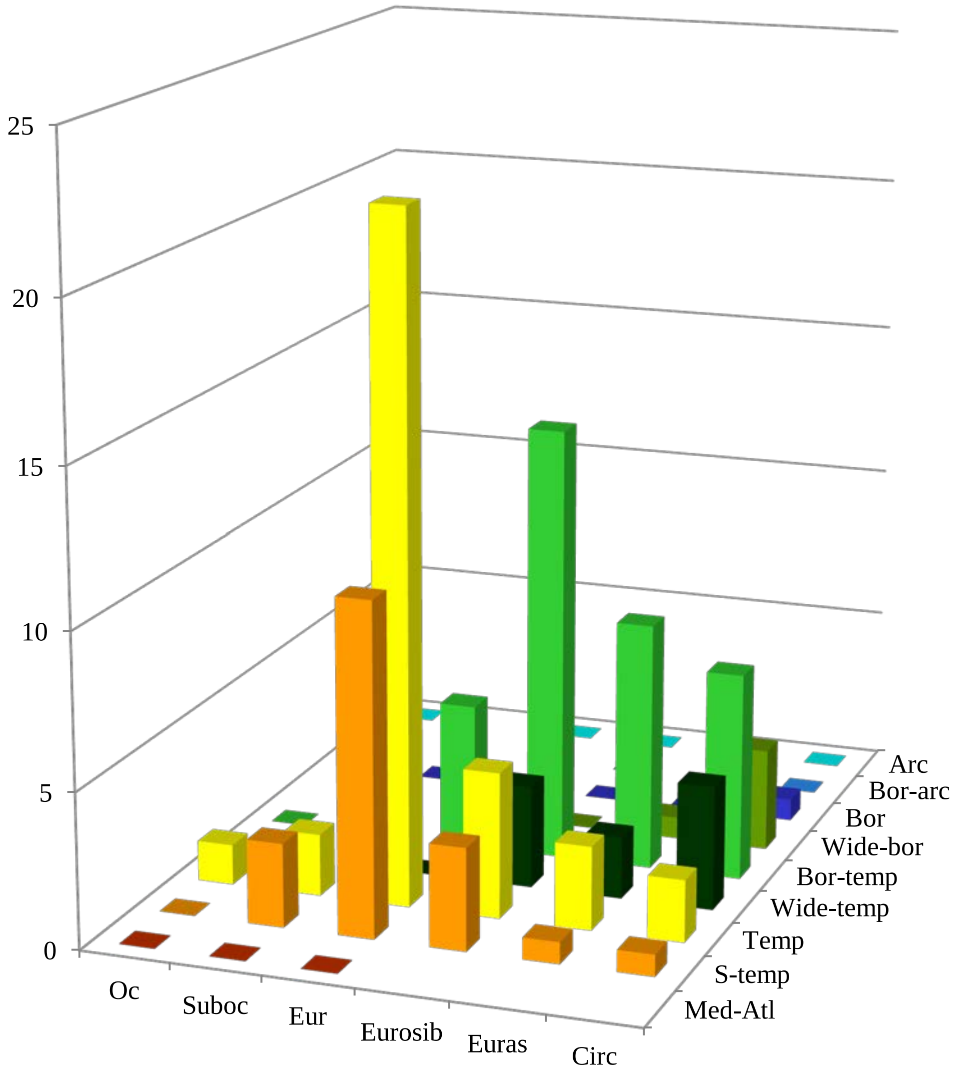

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Figure 5C

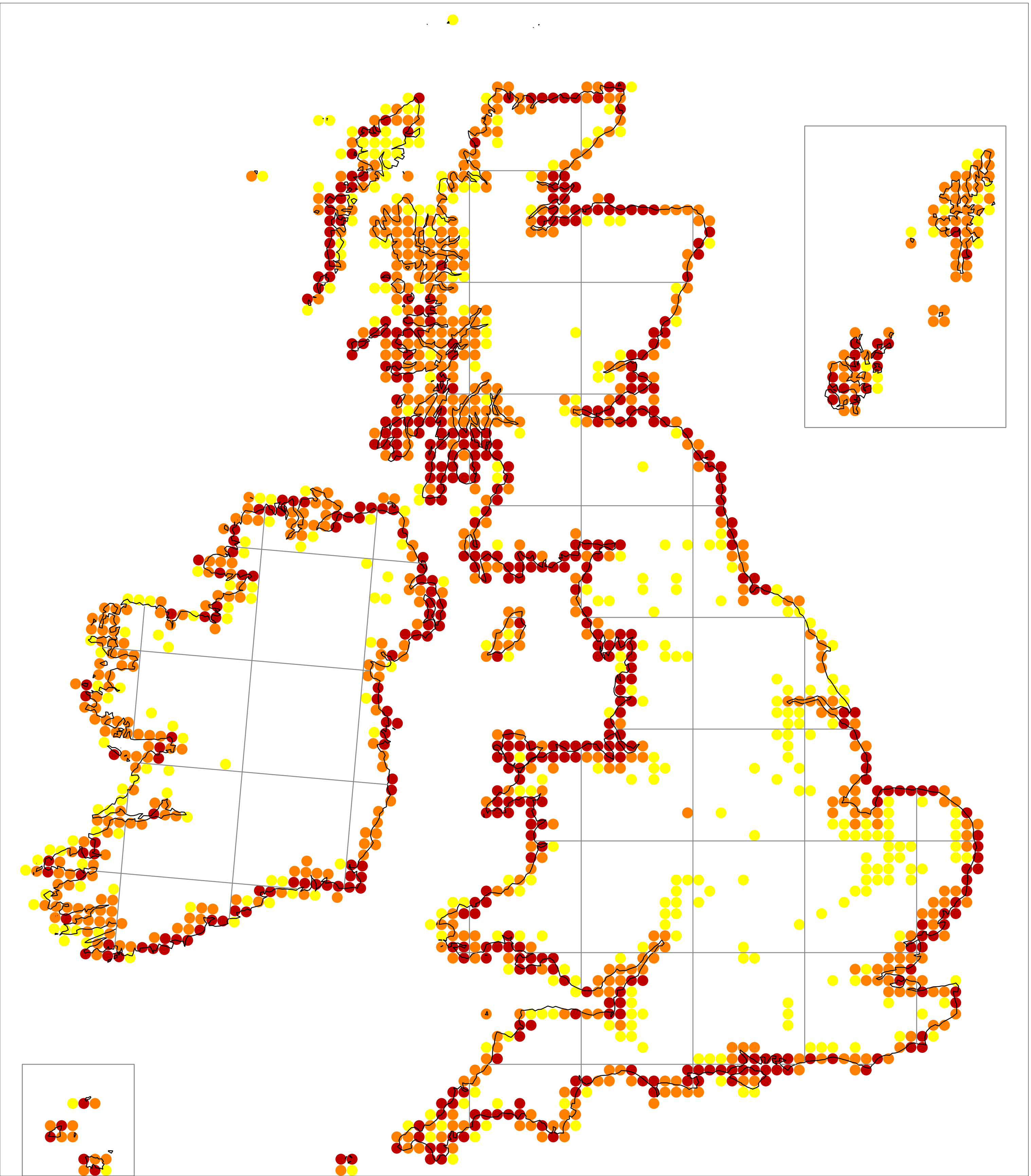

Figure 5D

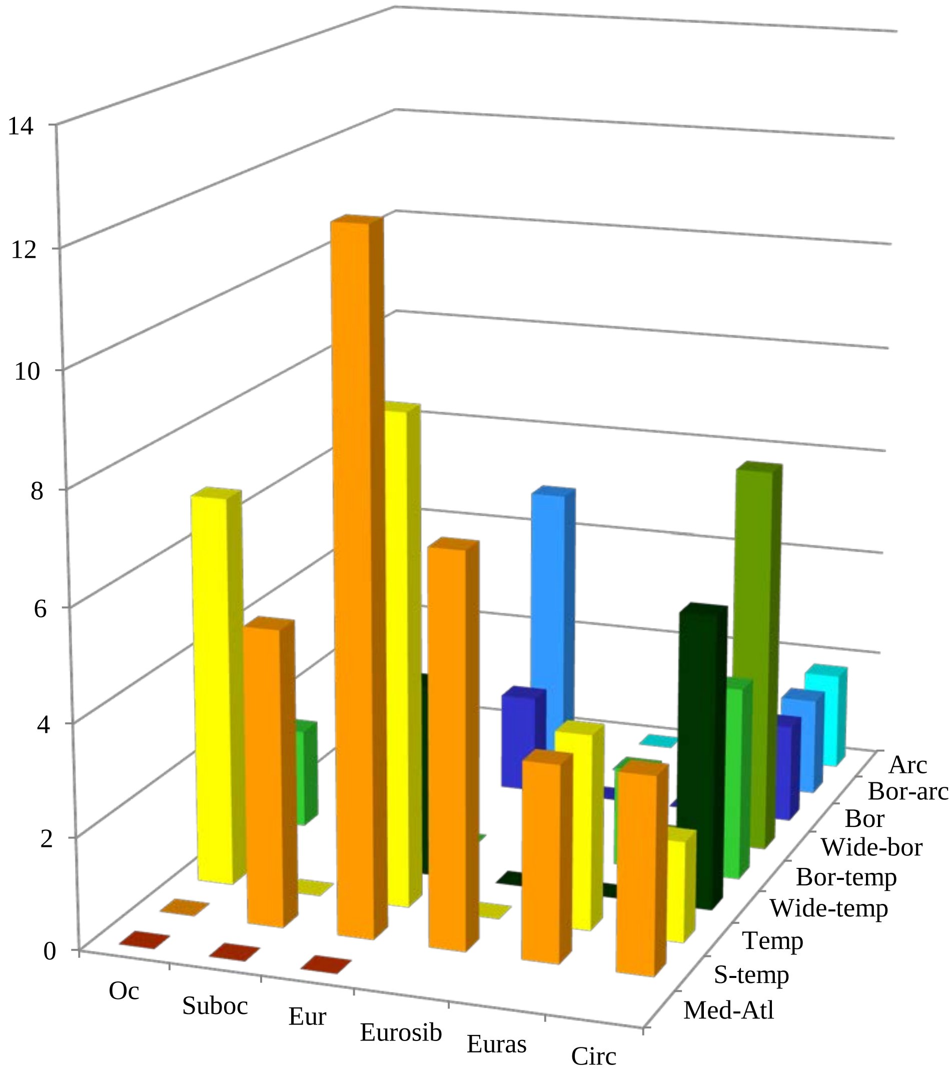
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Figure 5E

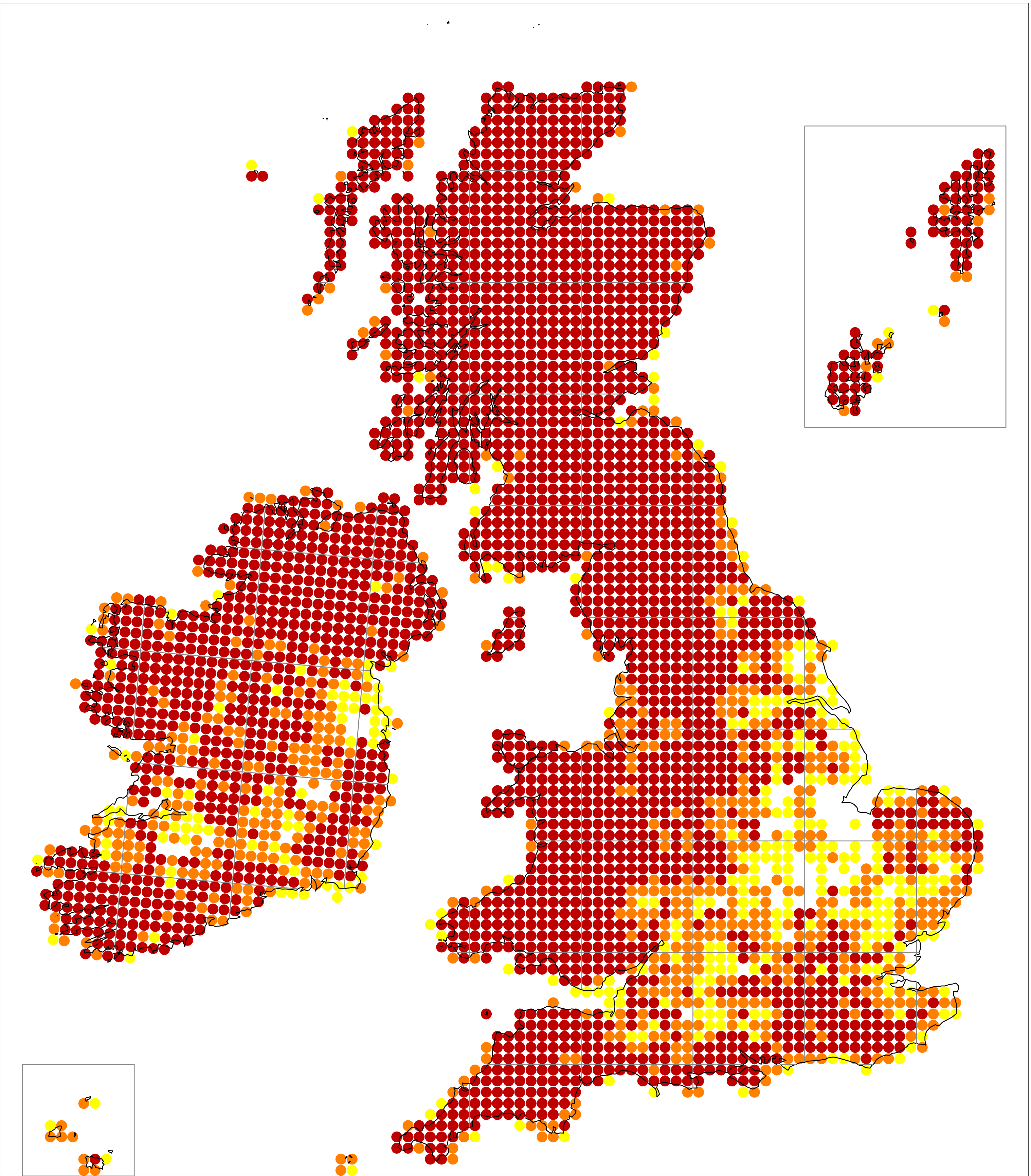

Figure 5F

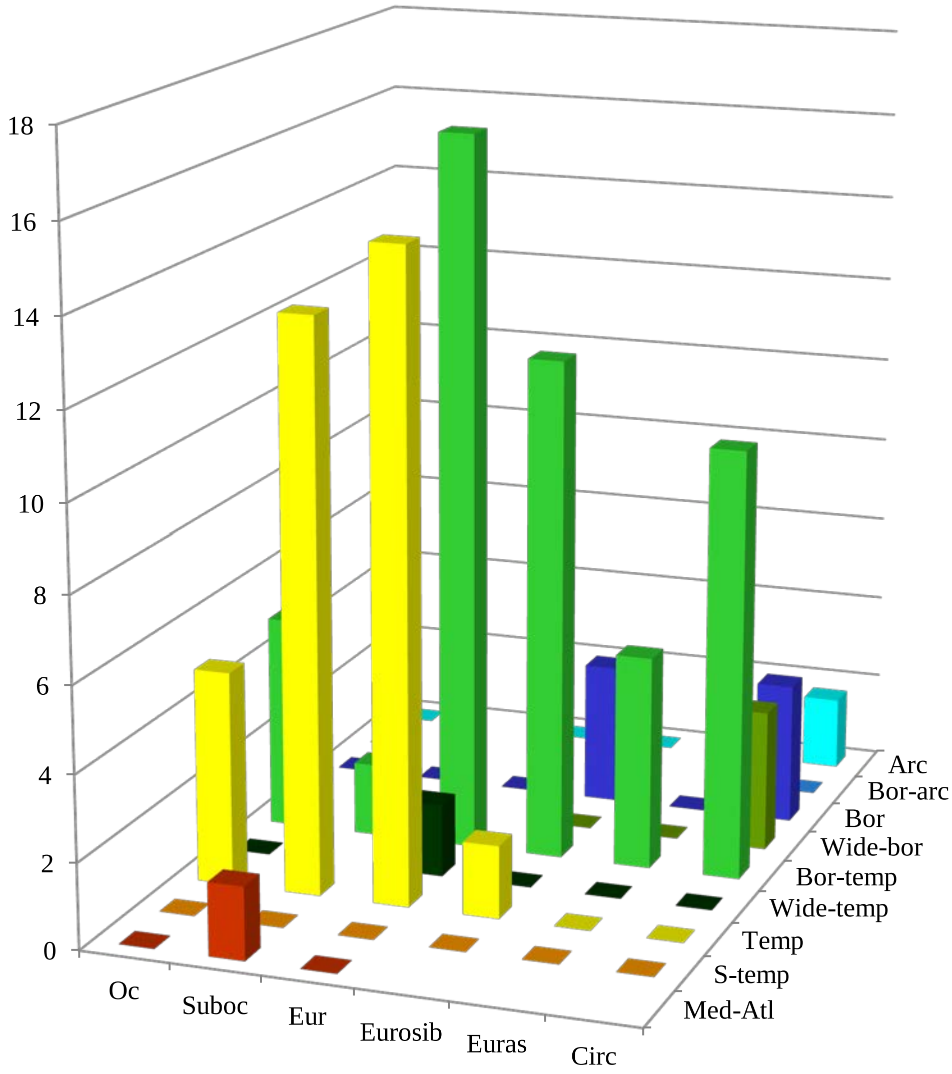
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Figure 6A

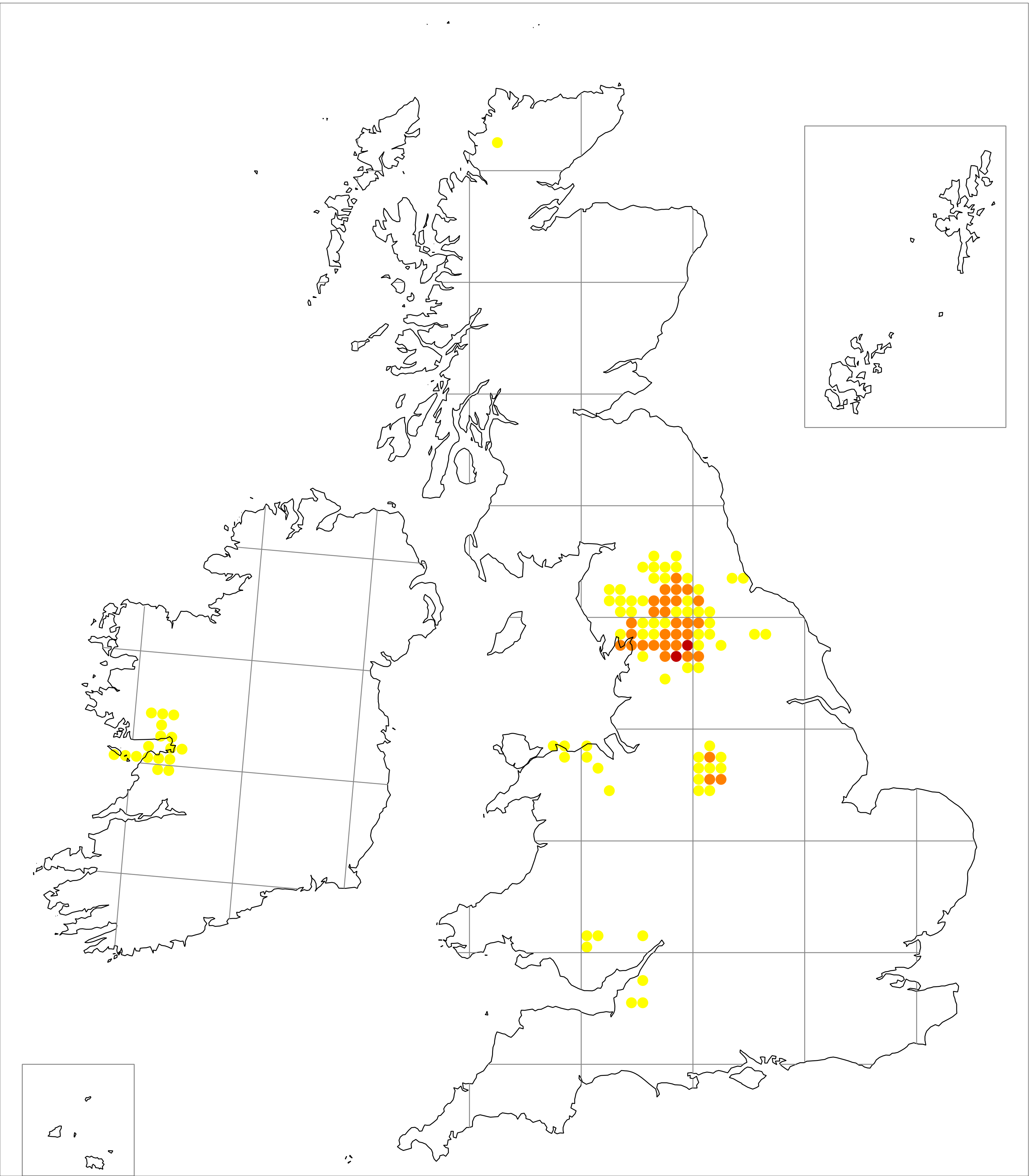

Figure 6B

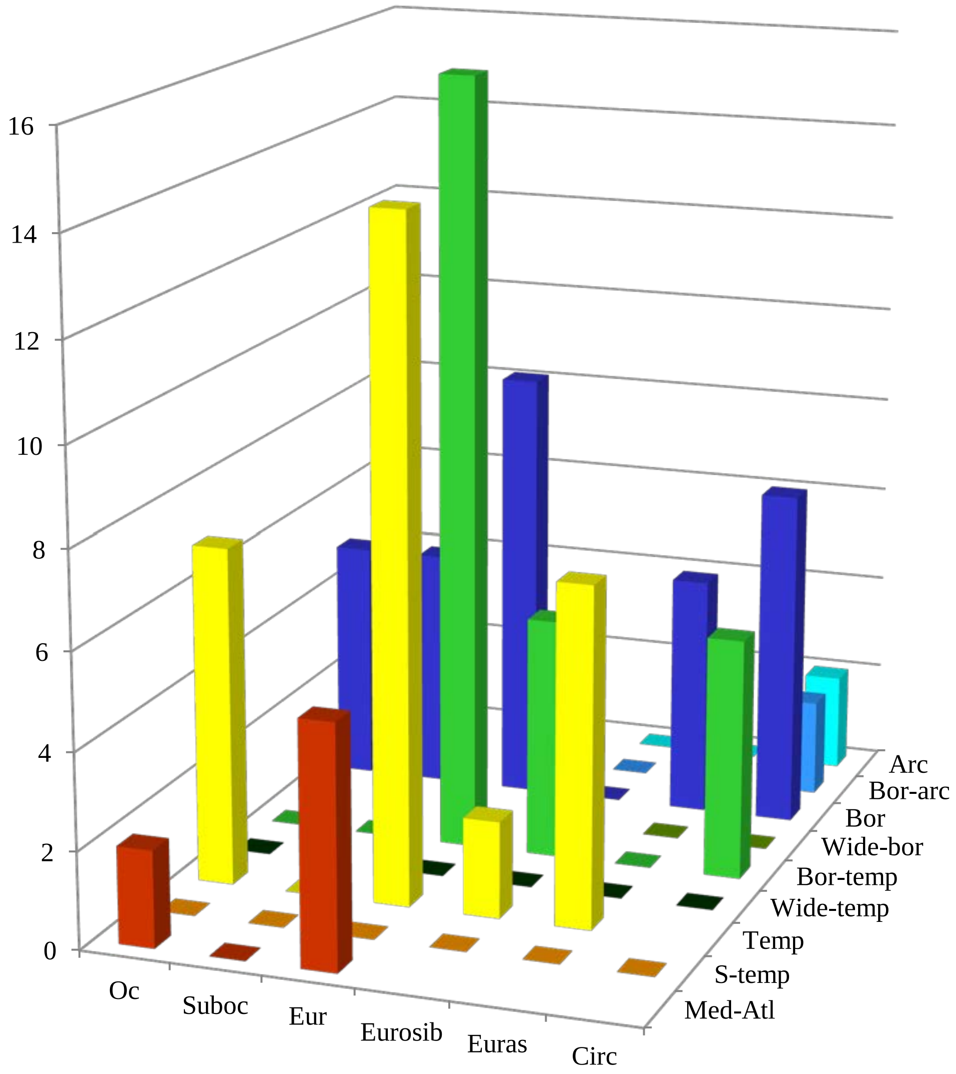

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Figure 6C

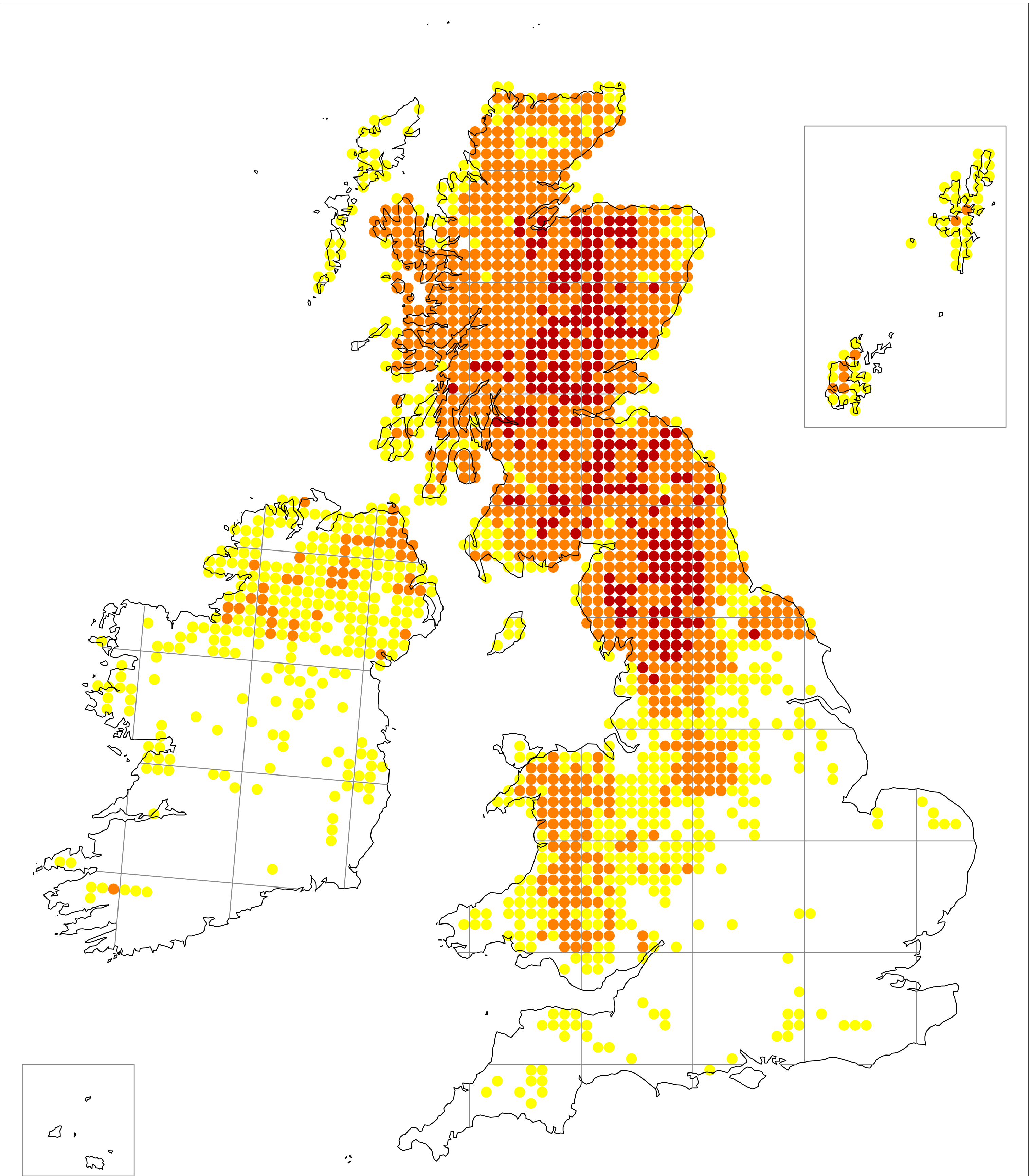

Figure 6D

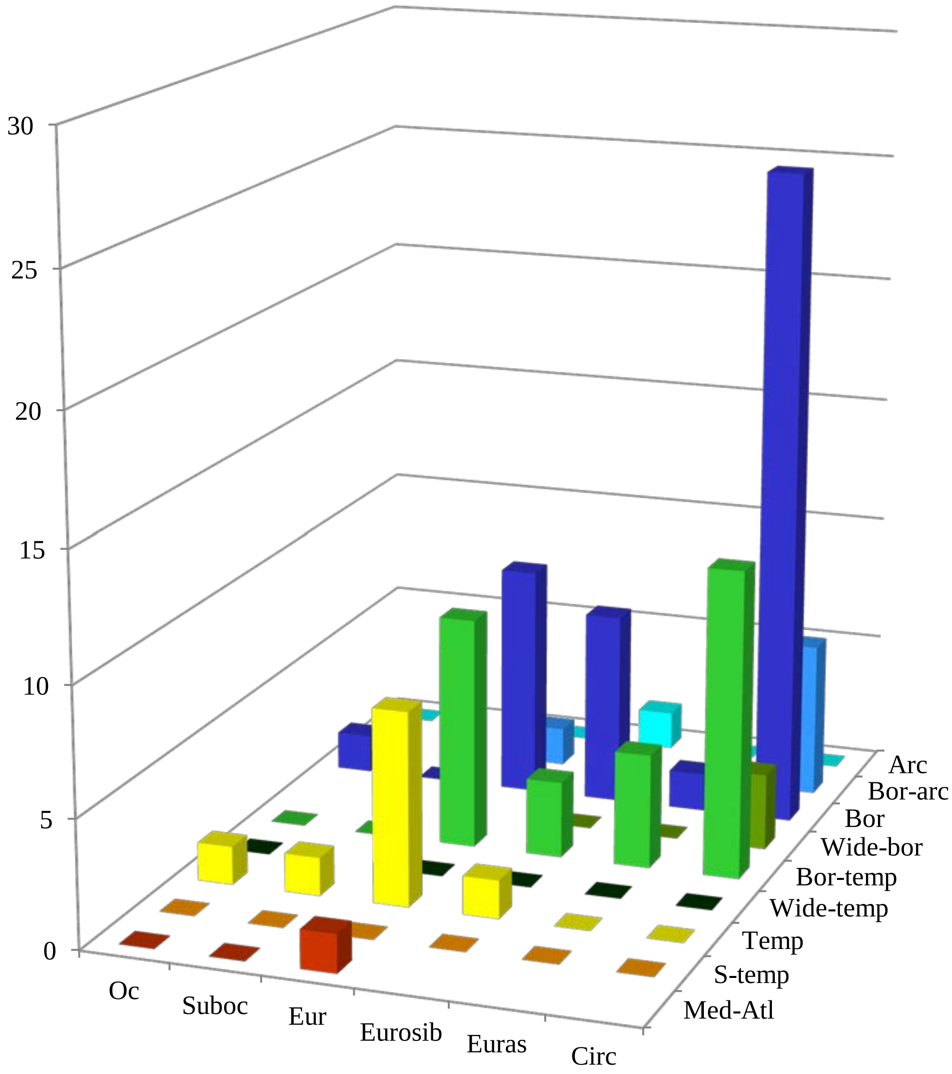

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Figure 6E

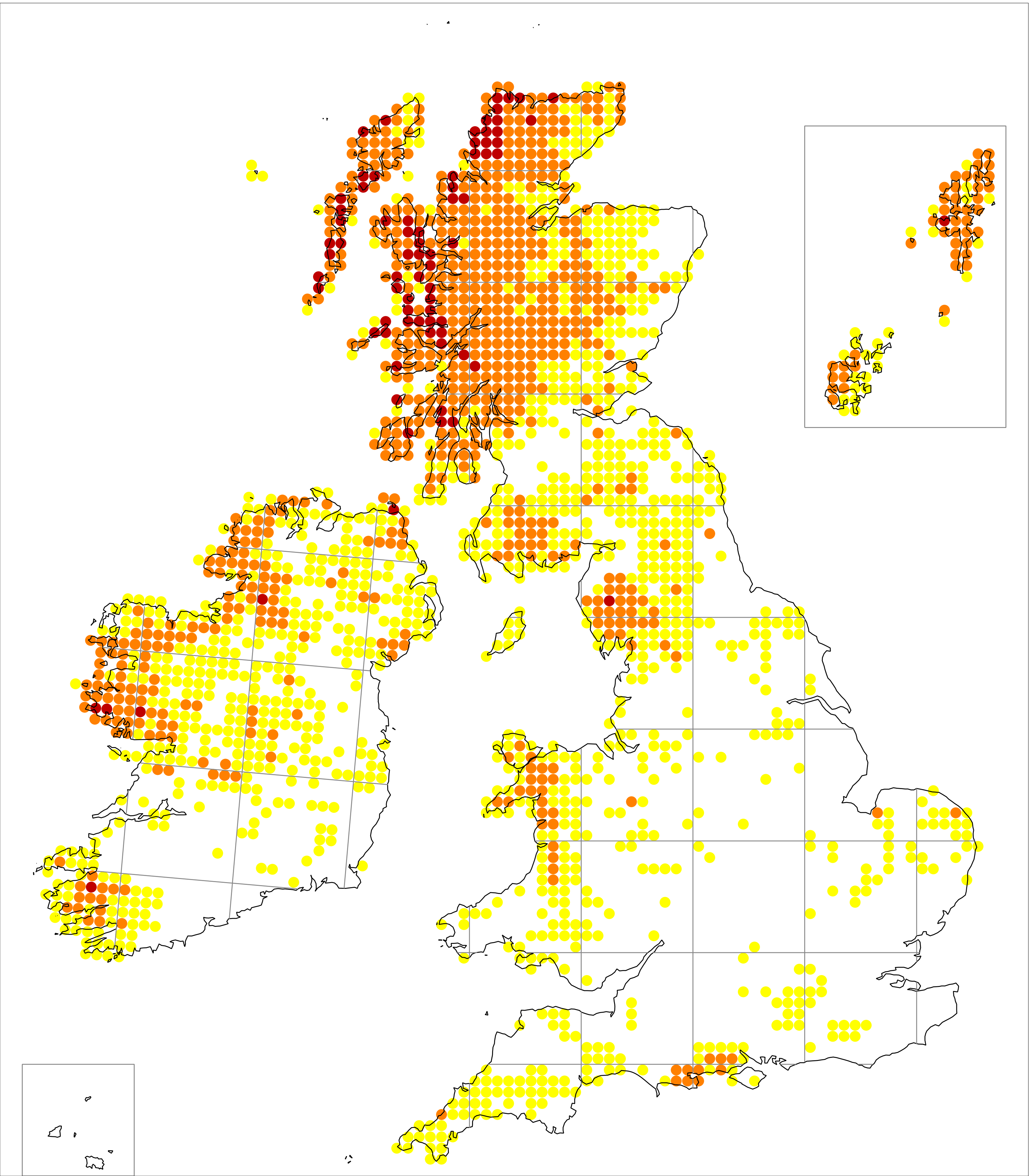

Figure 6F

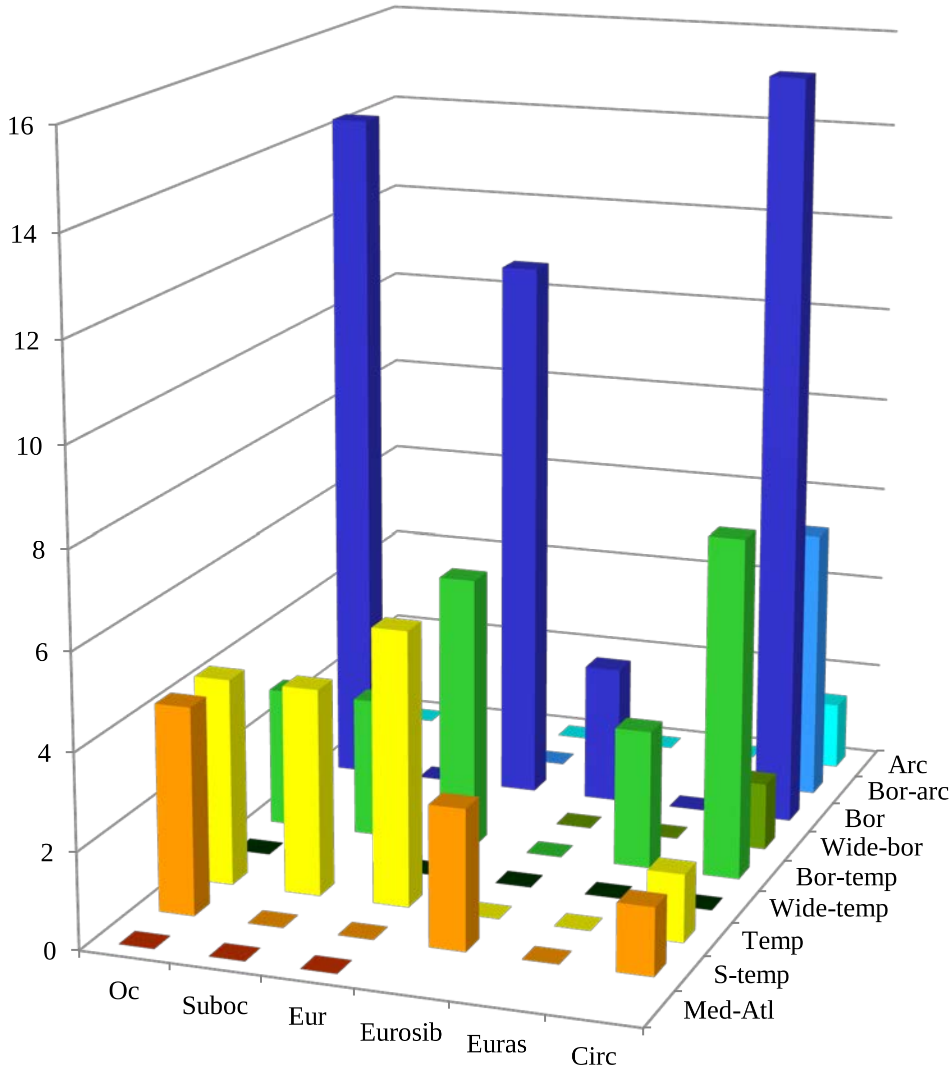

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Figure 7A

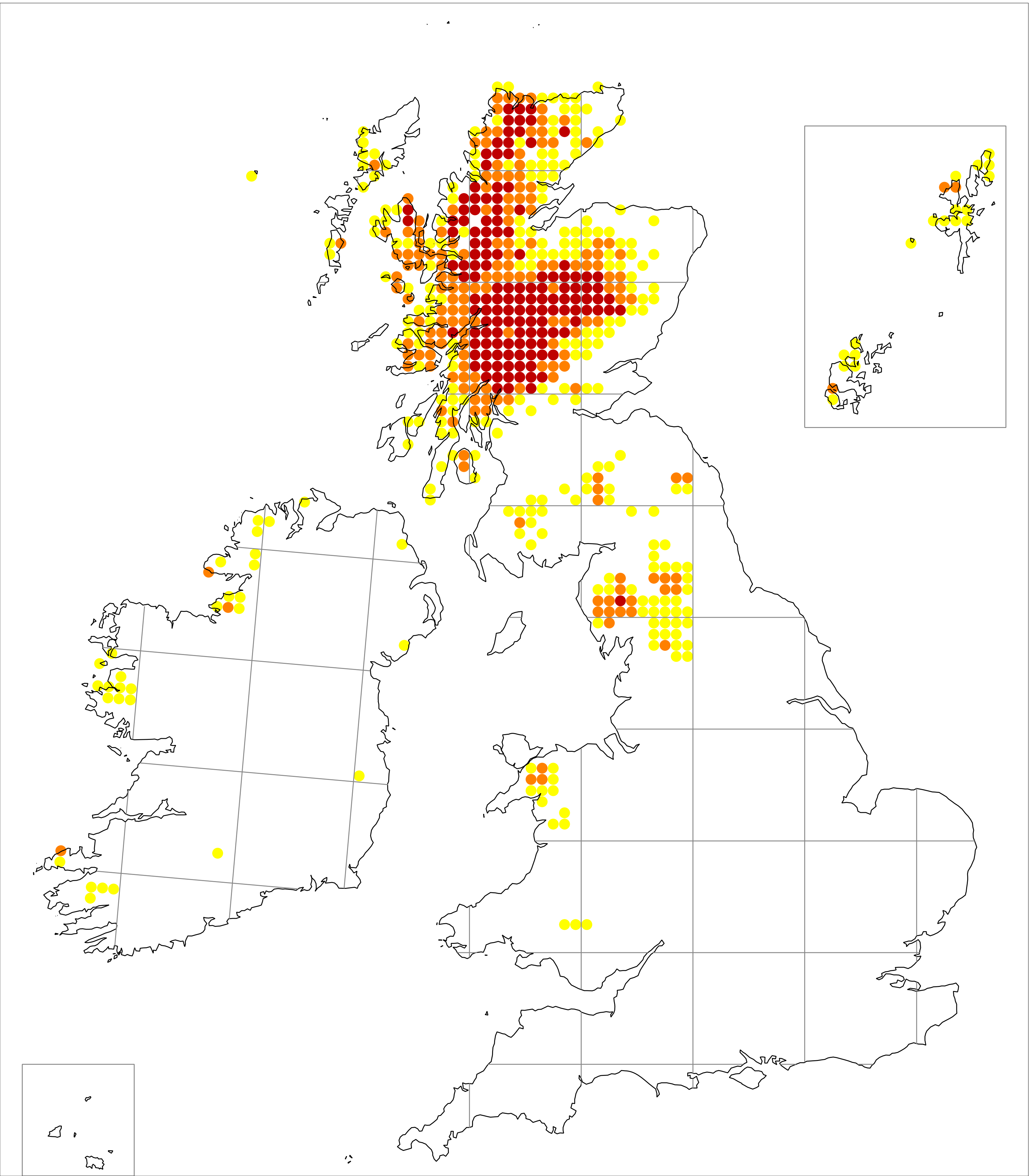

Figure 7B

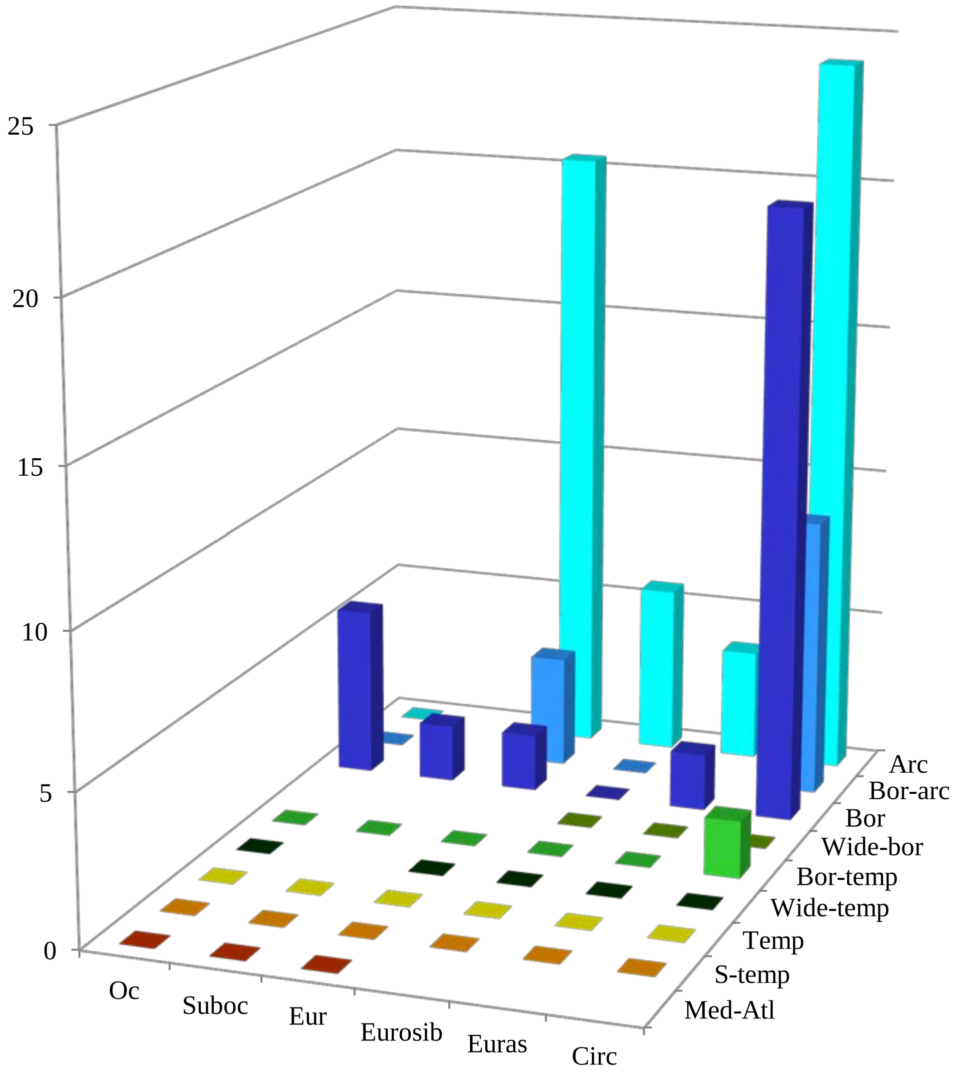

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Figure 7C

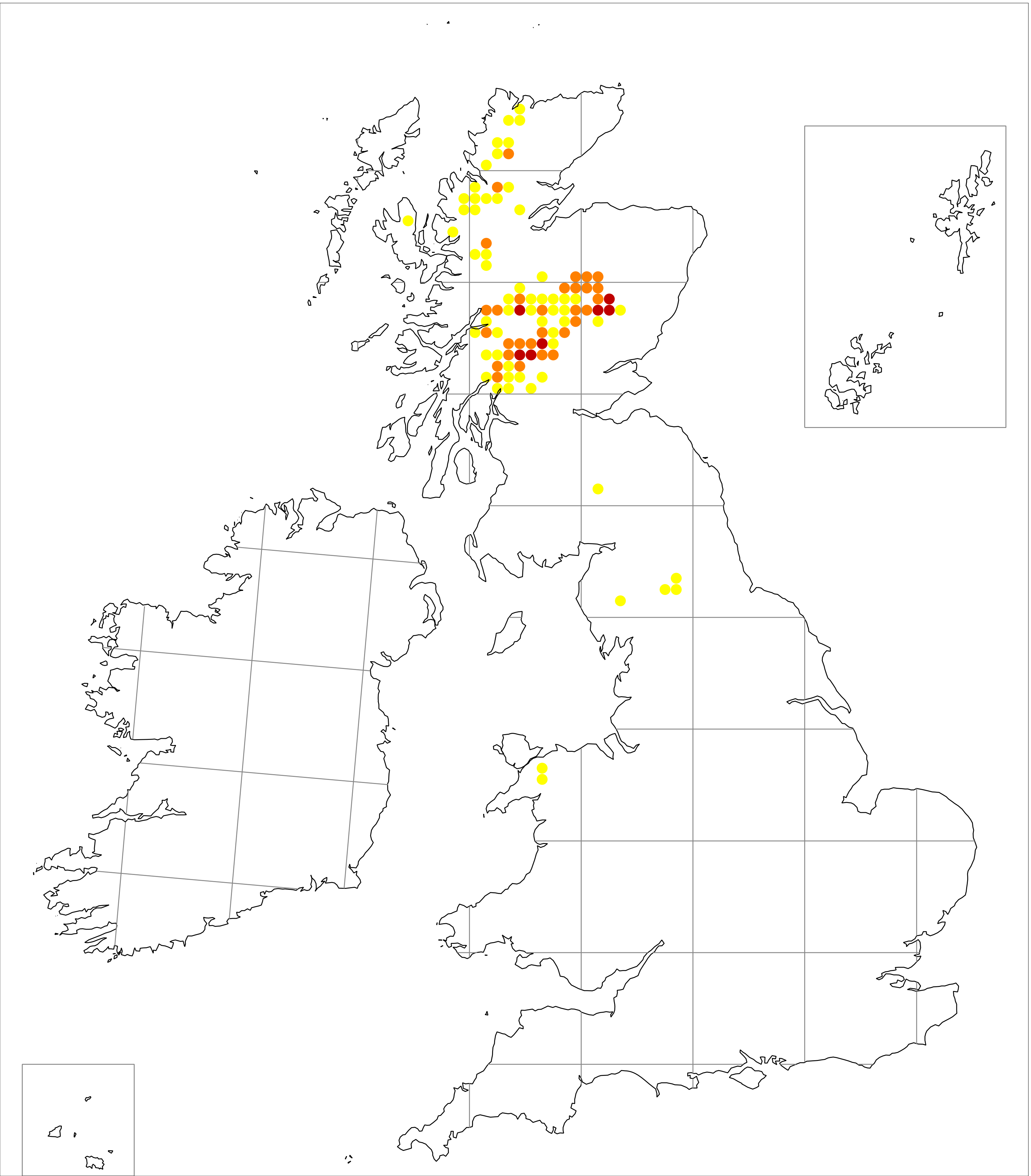

Figure 7D

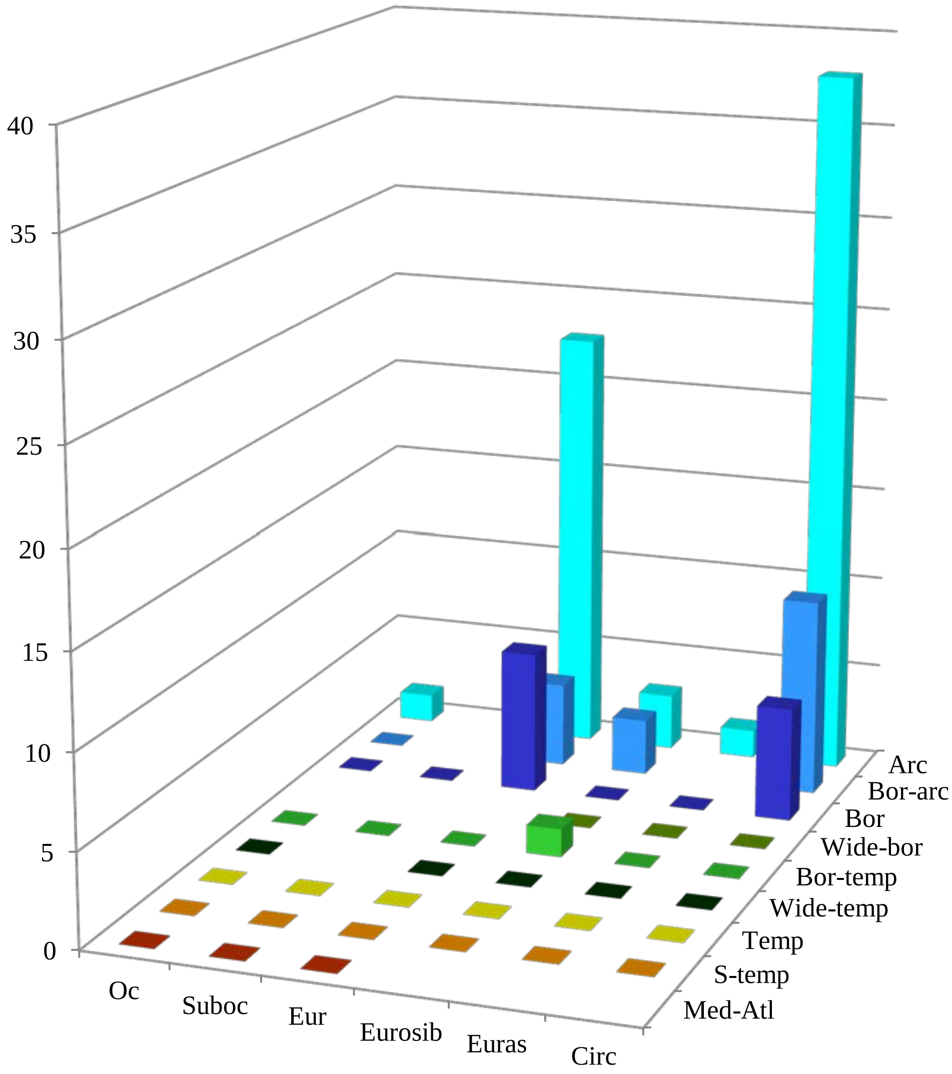

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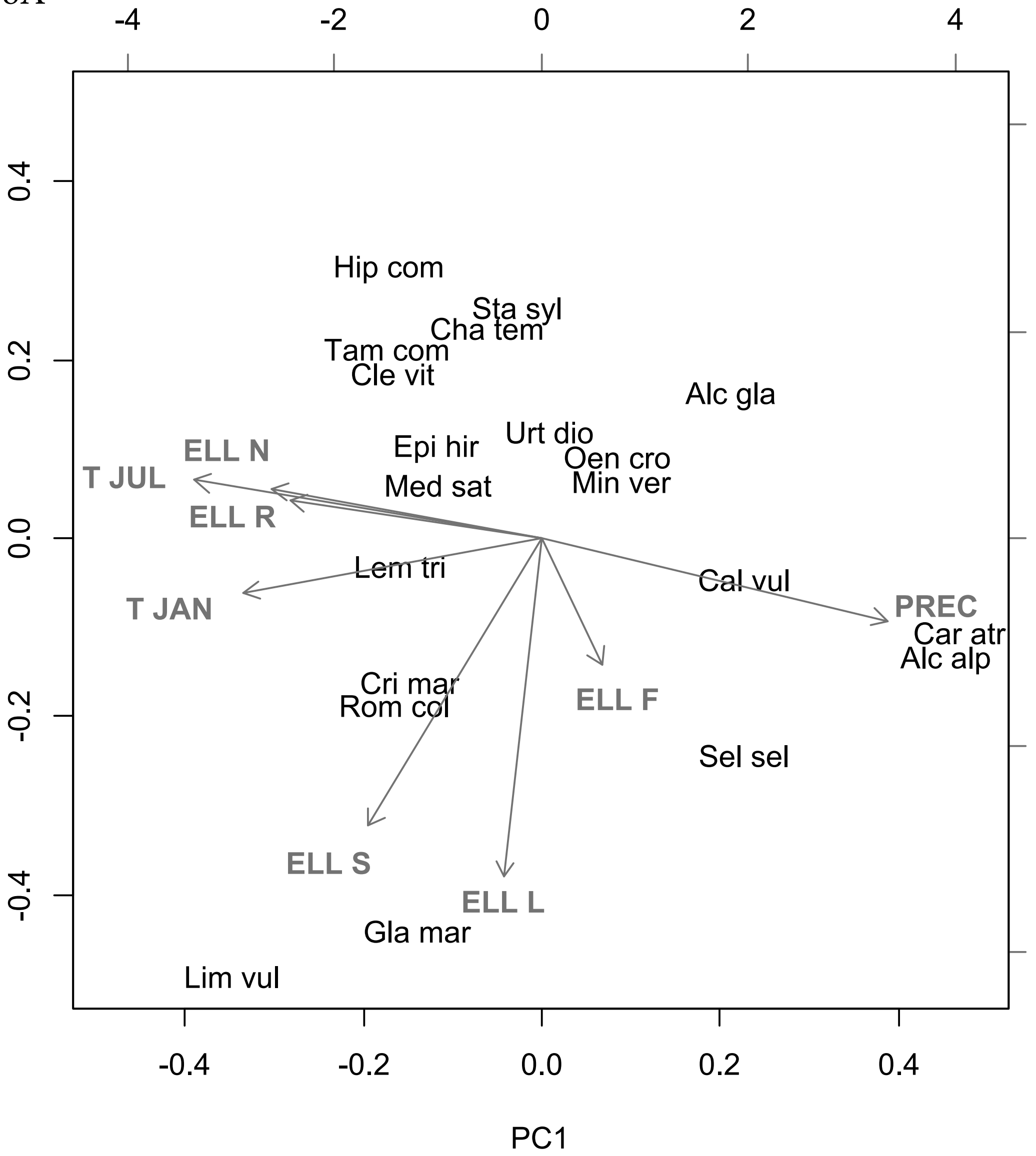
Figure 8A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PC2
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PC1
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Cha tem
Tam com
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Alc gla
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Epi hir
Oen cro
Min ver
Med sat
ELL N
T JUL
ELL R
Lem tri
Cal vul
T JAN
PREC
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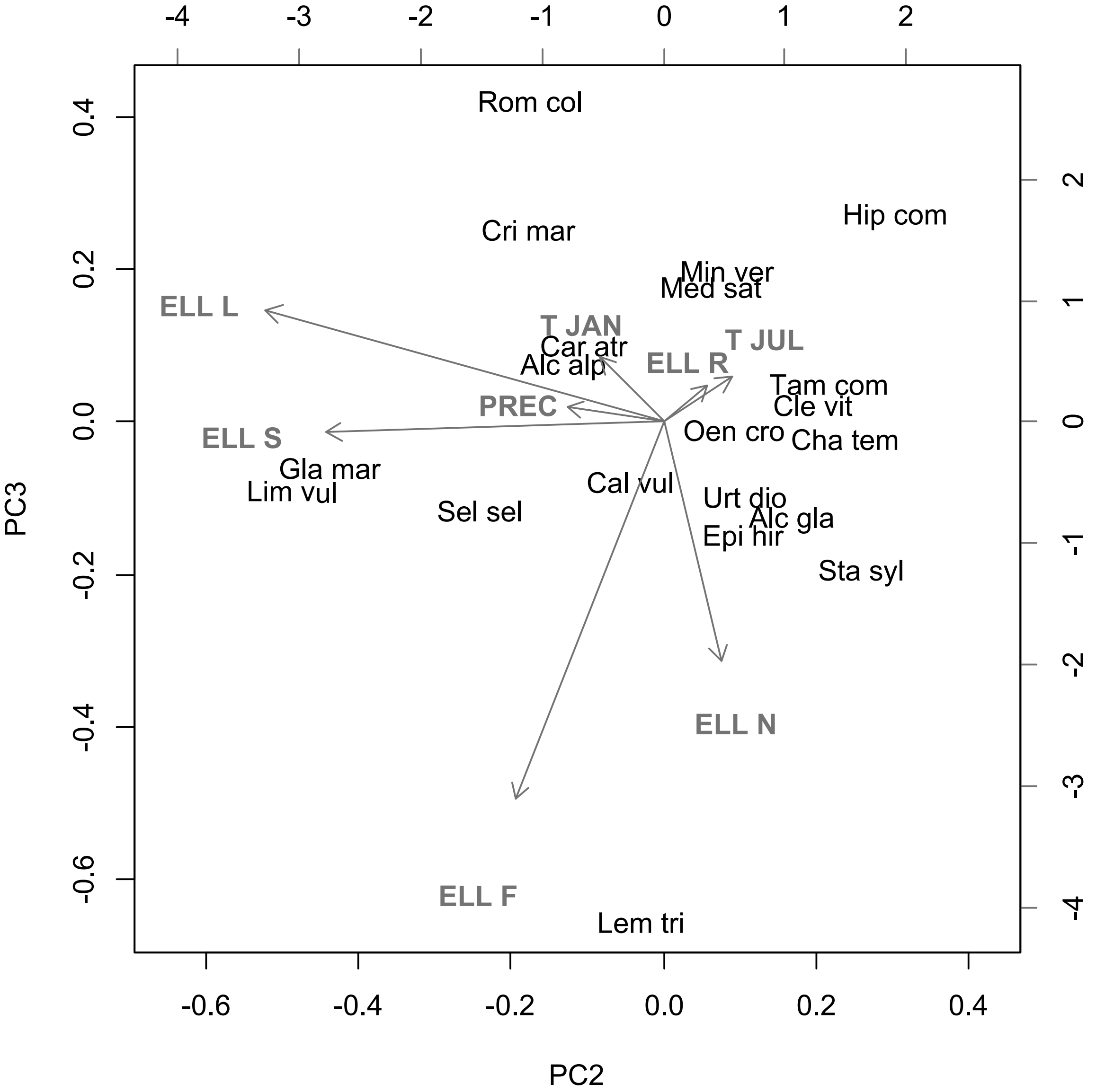
Cri mar
Rom col
ELL F
Sel sel
ELL S
ELL L
Gla mar
Lim vul

Figure 8B



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ELL S
Oen cro
Cha tem
Gla mar
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Cal vul
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Alc gla
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PC3
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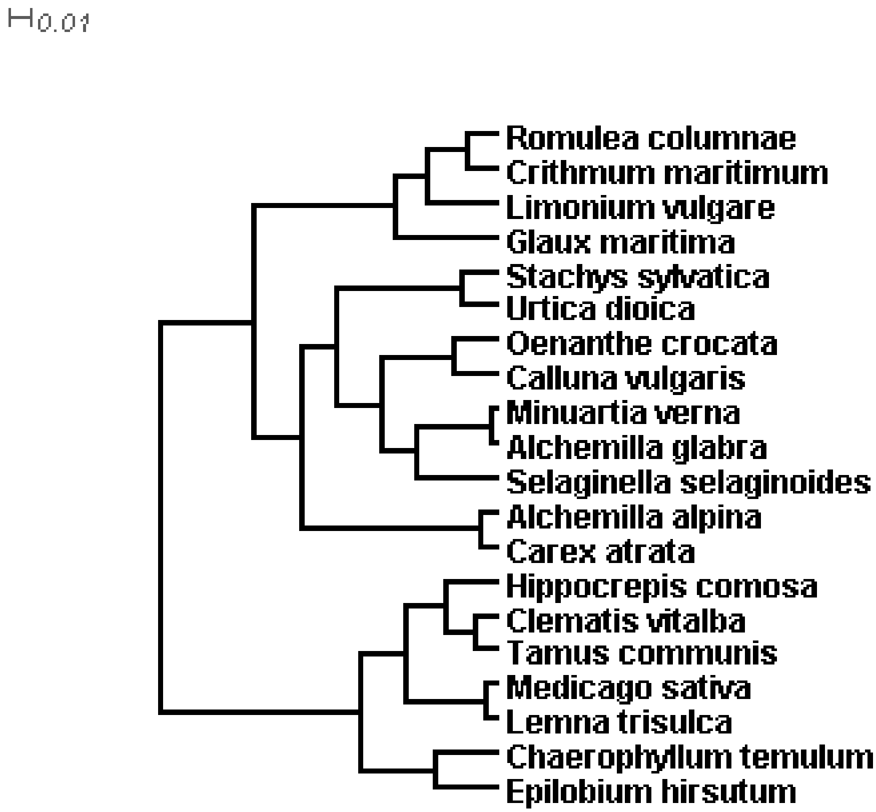
PC2

Figure 9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Crithmum maritimum
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Glaux maritima
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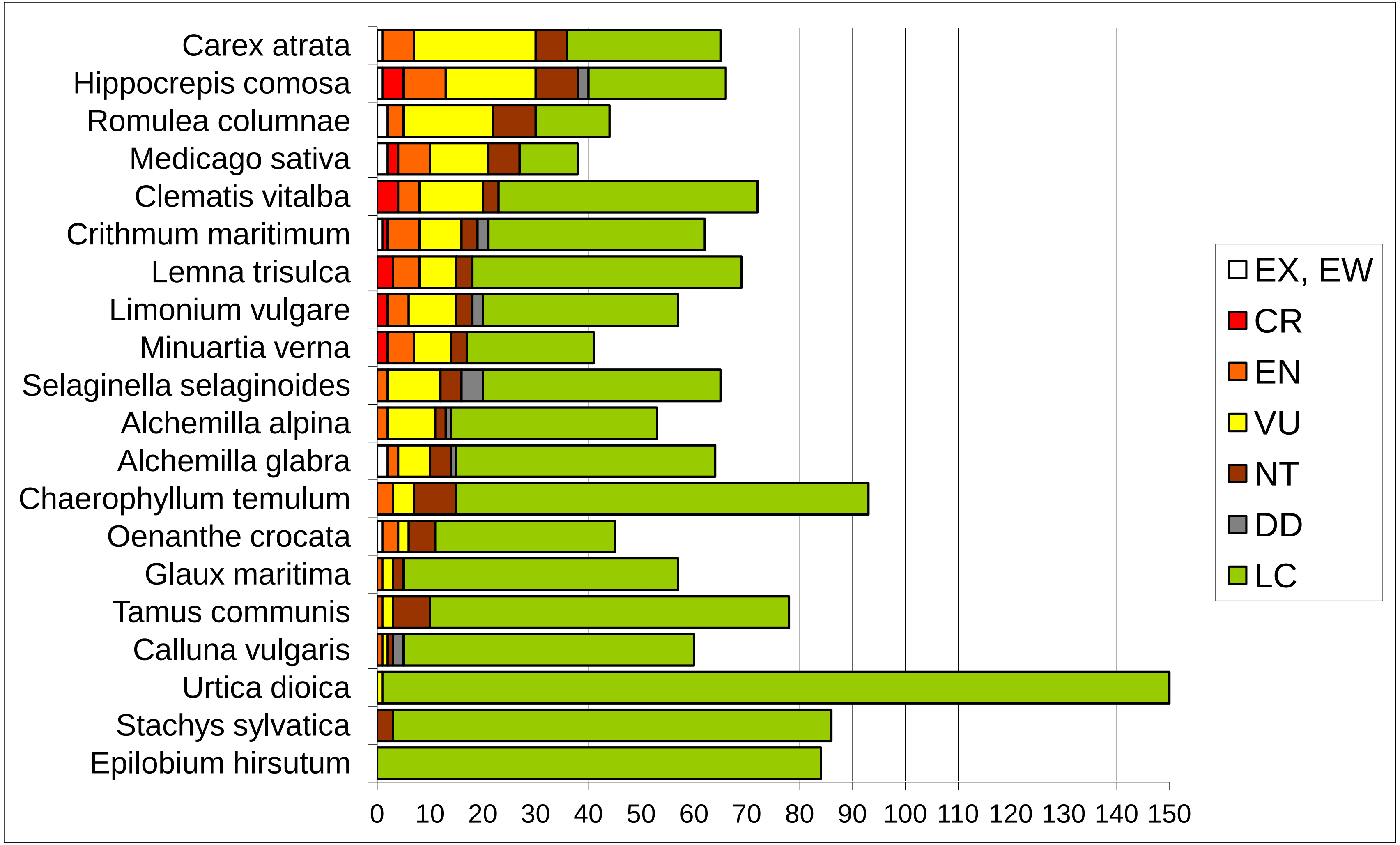
Calluna vulgaris
Minuartia verna
Alchemilla glabra
Selaginella selaginoides
Alchemilla alpina
Carex atrata
Hippocrepis comosa
Clematis vitalba
Tamus communis
Medicago sativa
Lemna trisulca
Chaerophyllum temulum
Epilobium hirsutum

Figure 10



Carex atrata
Hippocrepis comosa
Romulea columnae
Medicago sativa
Clematis vitalba
Crithmum maritimum
Lemna trisulca
Limonium vulgare
Minuartia verna
Selaginella selaginoides
Alchemilla alpina
Alchemilla glabra
Chaerophyllum temulum
Oenanthe crocata
Glaux maritima
Tamus communis
Calluna vulgaris
Urtica dioica
Stachys sylvatica
Epilobium hirsutum
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150
EX, EW
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