The arrow points north – endemic areas and post-Devensian assembly of the British Empidoidea fauna (Insecta: Diptera)

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Received 4 August 2016; revised 13 September 2016; accepted for publication 31 October 2016

Large-scale patterns of species richness, assemblage composition, β-diversity, and endemism in Britain were studied in the Diptera superfamily Empidoidea. Overall species richness was greatest in the south, but two areas of elevated richness in East Anglia and the Northeast Grampian Mountains corresponded with ‘hotspots’ of elevated endemism. Assemblage similarity decayed and species turnover increased along predominantly north–south geographical gradients and between inland and coastal localities. Dispersal direction probability vectors were anisotropic, suggesting that the assembly of northerly British assemblages may have been influenced by dispersal from the south, and eastern English ones by dispersal from continental Europe. Parsimony analysis of endemism retrieved northern localities in ‘basal’ positions with more southerly and European areas in progressively more distal positions in the trees. We propose that British communities were assembled as follows: (1) Early Phase dispersal northwards of cold-adapted taxa between the Devensian Late Glacial Maximum and ~15 Kyr; (2) Mid-Phase colonization by eurythermic taxa at 15–8 Kyr; and (3) Assembly was largely completed by severance of the land bridge with Europe at 8 Kyr with a Late Phase (8 Kyr – present) involving continued northwards dispersal within Britain and partitioning of taxa into geographically restricted habitat refugia.


INTRODUCTION

A fundamental problem in ecology and biogeography is to identify large-scale patterns in diversity and assemblage composition of regional biotas and to understand their historical origins and the processes by which they are sustained. Endemism is the extent to which taxa are unique to a particular area and is hence dependent on the area scale considered. Certain geographical regions support many endemic taxa, and understanding such centres of endemicity or endemism ‘hotspots’ at various spatial scales is fundamental to explanations of Earth history based on biological patterns (Linder, 2001). Delimiting areas of endemism is essential not only in historical biogeography, but also in recognizing areas of conservation importance (Kerr & Burky, 2002), especially as range restriction is an important component of extinction risk (Purvis et al., 2000; Harvey, 2002).
The mechanisms shaping regional diversity include fine-scale biotic processes – such as speciation, extinction, dispersal, and species interactions – and broad-scale geographic/geological processes including plate tectonics, changes in sea level or climate, and the formation of topographical barriers to dispersal (Hedges et al., 1996). Broad-scale processes influencing the assembly of British biota have been intensively studied over recent decades. During the last (Devensian) glaciation, probably only southernmost Britain remained ice free (McCabe & Clark, 1998; Clark et al., 2012), and there is general consensus that the major animal and plant colonizations occurred subsequently, driven by glacial retreat and climatic amelioration (Dennis, 1977, 1993; Lowe & Walker, 1984; Roberts, 1989; Coles, 1998; Montgomery et al., 2014) with polewards extension of species’ distributions continuing to this day (Parmesan & Yohe, 2003; Mason et al., 2015). Postglacial colonization of Britain has also been documented for insects, especially Coleoptera (Coope, 1975, 1977; Atkinson, Briffa & Coope, 1987) and to a lesser extent Diptera, which have been widely used as palaeoclimatic indicators to characterize historical assemblages in archaeological and sedimentary deposits (Skidmore, 1996; Panagiotakopulu, 2004). The persistence of relict populations of insects in range-restricted areas of Britain but which occur elsewhere in similar ecological or climatic conditions has often been used to infer colonization history of taxa. For example, species of many orders of insects with contemporary distributions restricted to northern British mountains (Horsfield & MacGowan, 1997; Falk & Chandler, 2005; Hill et al., 2010; Ball et al., 2011) but which occur elsewhere in Europe at high latitude or high elevation have been considered boreal, boreo-alpine, or boreomontane relicts. Historically changing climate and availability of habitat have resulted in contraction of ranges with the taxa becoming ‘marooned’ in isolated areas of suitable habitat.

The Diptera superfamily Empidoidea comprises the families Empididae, Hybotidae, Dolichopodidae, Atelestidae, and Brachystomatidae. They are highly speciose in Britain with c. 700 species, representing c. 10% of British Diptera diversity (based on data in Chandler, 1998) and can be abundant and a conspicuous element of the Diptera fauna. Although formal distribution atlases are not available, inspection of 138 394 unique records collated by the British Empididae & Dolichopodidae Recording Scheme (Stubbs, 2010) used in this study indicates multiple types of range distributions occur including cosmopolitan species and those with regional and local range restrictions and eurytopic or stenotypic habitat preferences in terrestrial, aquatic, and littoral environments (Plant, 2003, 2004; Pollet, 2009). With the exception of the dolichopodid Thrypticus Gerstäcker, all species have predatory immature stages present mostly in soils and a wide range of decaying organic material and adults of many are predators of other arthropods and/or nectar feeders. Their near ubiquity and diversity of ecologies and life-history traits suggests wider utility in studies of patterns of diversity in Diptera as a whole.

In this study, we investigate the distribution of endemism, assemblage structure, and species turnover of Empidoidea along geographical gradients in Britain. Spatial correlations with area clades retrieved by parsimony analysis of endemism (PAE) and probabilities of dispersal between adjacent areas in Britain and near continental Europe then allow historical colonization routes to be hypothesized that are reconcilable with the post-Devensian geographical and ecological history of north-western Europe.

MATERIALS AND METHODS

INCLUDED TAXA

A total of 827 species of Diptera Empidoidea were sampled (Table S1) comprising Dolichopodidae 376, Empididae 235, Hybotidae 209, Brachystomatidae 3, and Atelestidae 2 species. The genera Iteaphila Zett., and Anthepiscopus Becker each here represented by single species, have not been confidently assigned to any family, and are regarded as incertae sedis in Empidoidea. Data on 678 species were available from Gt Britain – Dolichopodidae 291, Empididae 206, Hybotidae 176, Brachystomatidae 3, and Atelestidae 2 – and on 678 species from continental Europe (Belgium, Germany, and Norway) – Dolichopodidae 327, Empididae 173, Hybotidae 173, Brachystomatidae 2, Atelestidae 1, Iteaphila 1, and Anthepiscopus 1. A total of 149 taxa were present in continental Europe but not in Britain and the 149 were recorded only in Gt Britain.

SAMPLING METHODOLOGY

Data on occurrence of Empidoidea in Great Britain (excluding the Orkney, Shetland, and Scilly islands but including the Hebrides, Isle of Man, Anglesey, and Isle of Wight; hereafter referred to as ‘Britain’) were collated from a database held by the UK Empid and Dolichopodid Recording Scheme (Stubbs, 2010) comprising 138 394 unique taxon/locality/date records of the 678 species. Although all data from 1850 to 2015 were included, 95.07% of records were relatively recent and collected between 1975 and 2015. Data from Belgium, Germany, and Norway were collated from databases held by the authors from records made mostly between 1975 and 2015. The raw data from both Britain and continental Europe register the occurrence of taxa in grid squares at variable spatial scales between 10 × 10 m and 10 × 10 km. Analysis of
local endemism requires careful choice of spatial scale, the operational geographical unit (OGU), in order to limit geographical recording biases, to minimize overlap across the boundaries of neighbouring local biomes or across restricted range boundaries, and to ensure that data are sufficiently dense to support the grid size (Laffan & Crisp, 2003; Plant, 2014a, Mason et al., 2015). Meaningful analysis is unlikely at a scale of, for example, 10 × 10 km, at which species richness of British Empidoidea varied from 1 to 223 with a mean of just 29.1, a very low figure compared with the approximately 700 species known from Britain, even assuming high levels of patchiness and range restriction. The present study routinely analysed the occurrence of Empidoidea using grids of 50 × 50 km as OGU (1–413 species, mean 152.3), but in certain cases where density of data was insufficient to support analysis (detailed in Results section), neighbouring grids were pooled together into larger area OGUs. Each British 50 × 50 km OGU was aligned with the British Ordnance Survey (OS) grid reference system and was assigned a two-letter prefix code referring to the 100 × 100 km OS map reference square in which it occurs and numbered 1–4 clockwise from the north-west quadrant of that square (see Fig. 1). Belgian OGUs were aligned with the UTM grid and were designated as follows: B1, Coastal Western Flanders (bounded at NW by UTM grid DS77, at SE by ES13); B2, Inland Western Flanders (ES37, ES73); B3, Central Flanders (ES93, FR39); and B4, Eastern Flanders (FS58, FS94). Norwegian and German OGUs were referenced by latitude and longitude coordinates, not necessarily aligned with the UTM grid. The single Norwegian grid (designated N1) at the head of Oslofjord was bounded approximately by 59.924°N, 9.985°E (NW corner) and 59.480°N, 10.811°E (SE corner). The three German grids were all situated in Schleswig-Holstein. They were designated (approximate coordinates of NW and SE extremities indicated in parenthesis) as follows: G1, Sönke-Nissen-Koog NW of Bredstedt, Groß-Jörl NW of Schleswig, Flensburg (54.949°N, 8.697°E; 54.509°N, 9.379°E); G2, Kiel, Flintbek, Preetz, Lütjenburg, Howachter-Bucht, Neumünster, Bornhöved-Seenkette N Bornhöved, Plön, Eutin, Bad-Segeberg (54.379°N, 10.013°E; 53.921°N, 10.715°E); and G3, Grüne Insel Eider Estuary SW of Tönning, Alte Sorgeschleife S Bergenhusen, Meldorf-Bucht W Meldorf (54.396°N,
8.701°E; 53.947°N, 9.445°E). The location of all grids is shown in Fig. 1.

A matrix was constructed recording only presence or absence of taxa, ignoring multiple occurrences at different locations or dates within any particular OGU, resulting in a total of 19,888 (Britain), 1,373 (Belgium), 623 (Germany), and 349 (Norway) unique occurrences in 50 × 50 km OGUs.

**General statistical treatment and graphic presentation**

Univariate statistics, cluster analysis, and nonmetric multidimensional scaling (MDS) were performed in PAST version 3.0 (Hammer, Harper & Ryan, 2001). Contour maps of diversity and endemism parameters in Britain were prepared by spatial interpolation using the multiquadric gridding algorithm in the gridding module of PAST and the results were superimposed on outline map outputs from Mapmate Version 2.4.0 (MapMate, 2016) and DMAP Version 7.2f (Morton, 2016) using image editing software.

**Reciprocal weighted endemism**

Reciprocal weighted endemism was calculated using a modification (Plant, 2014a; Ivković & Plant, 2015) of the method of Moir, Brennen, and Harvey (2009). The number of OGUs within which each species occurred was counted. Each species was then assigned a value based on this number, with species known from only one OGU being given the highest value of 1, species occurring in two OGUs given a value of 0.5, species occurring in three OGUs given value of 0.333, and so forth. Total reciprocal weighted endemism for each OGU was then calculated as the sum of values for all species whose range overlapped that OGU. Mean reciprocal weighted endemism was calculated as the total weighted endemism for each OGU divided by the species richness of that OGU.

**Parsimony analysis of endemism**

Parsimony analysis of endemism (Rosen, 1988) was performed in TNT Version 1.1 (Goloboff, Farris & Nixon, 2008) with sufficient memory being allocated to hold 10,000 trees and general RAM set to 2000 Mb. Traditional parsimony-based searches employed 100 random-addition replicates using tree bisection reconnection (TBR) branch swapping, retaining 10 trees per replication with ‘characters’ uniformly weighted (prior-weighted) and unordered. Bootstrap support was calculated using 1000, replicates, and consistency index (CI) and retention index (RI) were determined by running the stats.run script. Taxa present in only one OGU were removed from the analysis (they do not inform the result, behaving as do autapomorphies in cladistics analysis). An outgroup with an all-0 score (all species absent) was arbitrarily established, but can be rationalized as the entire history of Empidoidea assemblages in Britain probably dates from after the last glacial maximum when the country was largely ice-covered and most species were likely absent. Although it would have been desirable to analyse patterns of local endemism at as high resolution as possible, initial trials using single 50 × 50 km grids as OGU resulted in highly polytomic tree topologies and poor bootstrap support for branches, probably because data were insufficiently dense and suffered from increased ‘noise’ from poorly recorded, relatively species-deficient grids. The problem of relative paucity and patchiness of data at smaller spatial scales was overcome by combining, where possible, four geographically adjacent 50 × 50 km grids together as OGUs for PAE. This ensured that areas analysed (indicated in Fig. 8) were large enough to provide increased data density and small enough to not markedly overlap the boundaries of zones of species richness (Fig. 3A), reciprocal weighted endemism (Fig. 3C), and assemblage similarity (Fig. 5) demonstrated elsewhere.

**Coefficient of dispersal direction**

The coefficient of species dispersal direction (DD1) was used as a measure of the probability of species dispersal between different geographic areas (Legendre & Legendre, 1984). If we identify two separate geographic areas $x_1$ and $x_2$, in which $a$ is the number of species in common, $b$ is the number of species restricted to $x_1$, and $c$ is the number of species restricted to $x_2$, then $DD1$ can be estimated by:

$$DD1(x_1 \rightarrow x_2) = \frac{a}{(a+b+c)} \frac{(b-c)}{(a+b+c)}$$

The term $a/(a+b+c)$ is the Jaccard coefficient of similarity. High values of $DD1$ result when $a$ is high and $b > c$ supporting the hypothesis of dispersal from $x_1$ to $x_2$. When $c > b$, the value of $DD1$ has negative sign, supporting the hypothesis of dispersal from $x_2$ to $x_1$ (Legendre & Legendre, 1998; Carrara & Flores, 2015). The geographical areas selected for dispersal studies were congruent with areas of assemblage similarity resolved by MDS (Fig. 5) and, where applicable, included hotspots of reciprocal weighted endemism (Fig. 3C). The included areas are indicated in Fig. 7 and designated as follows: East Anglia (zone A; comprising the following 50 × 50 km OGUs: TF3, TG3, TG4, TL2, TM1, TM2); south-east England (zone B; SU1, SU2, SU3, SU4, TQ1, TQ2, TQ3, TQ4, TR1, TR4, SZ1, SZ2, TV2); south-west England (zone C; SS2, SS3, SS4 ST1,
ST4, SX1, SW2, SX3, SY1); Wales (zone D; SH1, SH2, SH3, SH4, SN1, SN2, SN3, SM4, SM3); north-east England (zone E; NZ3, SE2, SE3, TA1, TA4, TF1, TF2); northern England (zone F; NY3, SD2, NZ4, SE1, SE4, SJ2, SK1); highlands of Scotland (zone G; NH1, NH2, NH3, NH4, NJ1, NJ2, NJ3, NJ4, NK1, NK2, NN1, NN2, NN3, NN4, NO1, NO2, NO3, NO4); and north-west highlands (zone H; NB1, NB2, NB3, NB4, NC1, NC2, NC3, NC4, ND1, ND4, NF2, NF3, NG1, NG2, NG3, NG4, NM1, NM2, NM3, NM4).

**B-Diversity**

Species turnover (β-diversity) was calculated using Whittaker’s measure $\beta_w$ (Whittaker, 1960) in PAST; $\beta_w = (S/\alpha) - 1$, where $S =$ the total number of species recorded and $\alpha =$ the mean sample diversity where each sample is a standard size (1 OGU) and diversity is measured as species richness. Values of $\beta_w$ range between 0 (complete identity) and 1 (complete non-identity).

**RESULTS**

**Patterns of diversity in Britain**

**Species richness**

Near complete sampling of British Empidoidea species was achieved from 138 394 unique taxon/locality/date records of the 678 species representing ~98.6% of all known British empidoid Diptera species. Sampling effort covered the entire country but was uneven with greater coverage from areas of southern and north-east England, parts of Wales and the Cairngorm Mountains, and Strathspey areas of Scotland for example, with regions of central England and many areas in Scotland which are less well covered (Fig. 2). Geographical bias is an inevitable consequence of data collected by biological recording schemes (Isaac & Pocock, 2015) as records are collected by volunteers of variable experience at times and places that suit them and tend to group around localities where volunteers live or places they target as being diverse or interesting in some other way. Recorder effort is thus neither systematic nor randomized and presents considerable problems of analysis. When species richness (number of species) was mapped at the scale of 50 × 50 km OGUs (Fig. 3A) and compared with geographical coverage (Fig. 2), some degree of correlation is observed although certain areas such as N Wales and NW England have fewer species than might be expected from the high level of coverage there. Failure to record a species does not of course preclude its presence, and although statistical occupancy models have been developed that can potentially ‘plug’ gaps in coverage (Hill, 2012; van Strien, van Swaay & Termaat, 2013; Isaac et al., 2014), they were not applied here. However, ‘cold-spots’ of species richness are almost certainly not due entirely to inadequate recording effort as ecological and habitat considerations lead us to expect that areas such as the uplands in the north or zones of extensive arable agriculture in the eastern English Midlands would have a depauperate fauna compared with, for example, ancient woodlands or landscapes with heterogeneous habitat elements found elsewhere.

**Endemic areas**

Figure 3B shows how total reciprocal weighted endemism of Empidoidea varied across Gt Britain. High endemism was apparent in southern and north-east England, south-east Wales, and especially East Anglia (hereafter abbreviated to EAng, delimited here by grids TG, TM, and eastern TF and TL in Fig. 1) and the Northeast Grampian Mountains of the Scottish Highlands (hereafter abbreviated as NEGM, comprising grids NJ, NO, NN, and eastern NH in Fig. 1). Low
endemism was found in areas bordering the western seaboard, English Midlands, Scottish Lowlands, and the far-north of Scotland. Areas of high endemism were similarly distributed to those with high species richness (Fig. 3A), suggesting that high species richness correlates with high endemism. Alternatively, as areas of high endemism were also generally coincident with those with better observer coverage (Fig. 2), it is possible that detection of a larger number of endemic species might be a consequence of increased coverage. Mean reciprocal weighted endemism and species richness were indeed weakly correlated (Fig. 4), and it is interesting to note that positive 'outlier' OGUs with mean weighted endemism above that predicted by the regression line in Fig. 4 were distributed across the full range of variation in species richness and likely

Figure 3. Geographical distribution of species richness and endemicity of Empidoidea in Gt. Britain. (A), species richness (number of species present); (B), total reciprocal weighted endemism; (C), deviation of mean reciprocal weighted endemism from values predicted by a regression model of its relationship with species richness. Spatial interpolation of results for 50 x 50 km OGUs was performed in PAST using the multiquadric gridding algorithm.

Figure 4. Relationship between mean reciprocal weighted endemism and species richness in 50 x 50 km OGUs in Gt. Britain. Mean values ± standard error are indicated. Linear regression (r = 0.581) was fitted (dashed line) using the modelling module in PAST and 95% confidence intervals (unbroken lines) determined from 2000 bootstrap replicates. Strongly positive 'outlier' OGUs are indicated (see Fig. 1 for explanation of alphanumeric code).
represent OGUs with exceptionally high endemism. While coverage effects cannot be entirely excluded, a better representation of the geographical spread of endemism was obtained by mapping deviations in mean weighted endemism above and below the regression line in Fig. 4. The resulting map (Fig. 3C) thus shows areas with relative levels of endemism that deviate above or below which expected from their species richness (and concomitantly, coverage). In this treatment, the endemic areas of EAng and NEGM are again retrieved and a new endemic area in the far north of Scotland (grid NC in Fig. 1) is weakly apparent, but the southern and north-east English and south-east Wales ‘hotspots’ are greatly diminished in apparent importance.

Assemblage composition and species turnover
In order to examine similarities in Empidoidea assemblages present in endemic areas and elsewhere, we employed MDS using Jaccard index to compare only relatively data-rich 50 X 50 km OGUs (those with ≥125 species). The result was transformed into a more readily interpretable form by subjecting the data from the primary axis of the MDS result to cluster analysis using Euclidian distance (Fig. 5). Although assemblages represented by adjacent clusters were generally associated with adjacent geographical areas, those of Scotland (cluster 1 in Fig. 5) were distinctly different from those elsewhere in Britain, indicating that the species composition of assemblages differed greatly in the two areas. A group of East Anglian OGUs (cluster 2) had a sister-group relationship with other areas of England within which two clusters were retrieved: cluster 3 representing south-east England and cluster 4 including south-west and northern England and Wales. Overall, the results indicate zones of Empidoidea assemblage similarity orientated approximately along a south-east to north-west axis across Britain but with those associated with the Scottish Highlands and East Anglian endemic areas being more distinctly defined.

Variation in species turnover along geographical gradients was further investigated using Whittaker's measure of $\beta$-diversity, $\beta_w$ (Fig. 6). TG4 is an OGU at

![Figure 5. Assemblage similarities of British Empidoidea. (A), a two-dimension MDS matrix was calculated using Jaccard similarity in PAST (stress = 0.1608) utilizing only 50 × 50 km OGUs that have at least 125 species present. Data from the first axis of the MDS result were then analysed using unweighted pair-group average cluster analysis in PAST employing Euclidian distance. Numbers 1–5 indicate major clusters discussed in the text. (B), map of OGUs colour-coded to match major clusters in A.](image-url)
the centre of the EAng endemism hotspot, and pairwise comparison of $\beta_w$ between it with all other British OGUs revealed pronounced east-west and south-east–north-west gradients of dissimilarity (Fig. 6A). As species turnover measured as $\beta_w$ provides an accurate reflection of community turnover (Wilson & Shmida, 1984), it is clear that assemblage similarity decays with distance along these axes. The gradient of turnover at distance from NH3 in the NEGM hotspot was less pronounced (Fig. 6B) but with some similarity in assemblage composition likely being maintained through inland localities further south, while coastal areas in both the east and west were clearly very different. Turnover away from SU4 in central southern England had a strong north–south component and again, large differences were evident from coastal localities.

COMMUNITY HISTORY

Dispersal direction

Figure 7 summarizes measurement of the coefficient of dispersal direction, $DDI$, between regions of Britain and continental Europe. $DDI$ can be thought of as a measure of the probability that species in an assemblage in one area are derived from another (Legendre & Legendre, 1984). Values of $DDI$ were strongly asymmetric across different regions of Britain, indicating a common dispersal direction vector trending from southern areas toward the north or north-west. Strong dispersal vectors were also found directed from Belgium to East Anglia (EAng) (zone A in Fig. 7) and to Germany, but vectors for other trans-North Sea colonization possibilities (e.g. between Belgium and south-east England (zone B) or north-east England (zone E) and Germany) were weak. The finding of a prevalent anisotropic directional dispersal vector in Britain is consistent with the historical foundation of more northerly assemblages of Empidoidea by dispersal in a northerly or north-westerly direction from ‘founder’ assemblages further south. Assemblages in eastern England may have been influenced, at least in part, by colonization from regions that now form adjacent areas of the modern continental European landmass and those of northern Germany in Schleswig-Holstein have been shaped by dispersal from the south.

Parsimony analysis of endemism

PAE employing 650 taxa and 28 ingroup OGUs constructed by combining four geographically adjacent 50 × 50 km grids in Britain and one OGU comprising four 50 × 50 km grids in Belgium retrieved two equally parsimonious trees (CI = 0.236, RI = 0.519). Resampling support (Fig. 8A) was generally low, although a terminal area clade incorporating all southern localities (indicated by branches distal to the arrow in Fig. 8A) was very robust being supported by all bootstrap replicates. More northerly British OGUs were retrieved in ‘basal’ positions in the tree topology, whereas southern and eastern English and the Belgian OGUs were resolved in more terminal positions. German and Norwegian data were not included in the analysis above (Fig. 8A) because PAE ideally requires OGUs to have identical areas (Laffan & Crisp, 2003). It should
be noted, however, that geographical land area was not constant in British OGUs as all coastal OGUs inevitably had actual land areas reduced by the presence of sea. When the German (three 50 × 50 km grids) and Norwegian (one 50 × 50 km grid) data were grouped and included as OGUs, PAE (678 included taxa, 30 ingroup OGUs) retrieved 2 equally parsimonious trees (CI = 0.219, RI = 0.494), and the bootstrap consensus (Fig. 8C) had similar topology and branch support to that obtained when German and Norwegian data were excluded. The German and Norwegian localities were retrieved in a terminal area clade that also included southern localities. The results suggest that the historical assembly of communities now represented by modern assemblages in the north of Britain may have preceded the assembly of those further south with tree topology implying a north–south gradient with older ancestry in the north and younger in the south.

DISCUSSION

This study has revealed that geographical areas of Britain with high species richness of Empidoidea generally correspond with the areas of range-restriction as measured by reciprocal weighted endemism (Fig. 3B). An association between high levels of endemism and species richness is perhaps not unexpected as it is reasonable to suppose that rarer range-restricted species are more likely to persist in ecologically ‘intact’ and varied areas that provide greater ecological opportunity and are able to support a greater number of
species. Indeed, correlations between hotspots of local endemism (measured as rarity) and elevated species richness have also been reported in Britain for other taxa, for example birds (Gibbons et al., 1996), and elsewhere for Diptera (Ivković & Plant, 2015). The topographical delimitation of areas of local endemism was robust and endured when geographical bias in recording effort was moderated by considering only deviations above the expected relationship between mean reciprocal weighted endemism and species richness (Fig. 4) as indications of local endemic areas (Fig. 3C). Two principal areas of local endemism were recovered, in EAng in eastern England and the NEGM of the Scottish Highlands, with less significant zones associated with southern England and the far north of Scotland. The areas identified here are coincident with those identified by Plant (2014b) employing a much smaller number of species (205) of just one empidoid family (Empididae). Tables 1 and 2 list Empidoidea taxa considered as narrow range endemics in a British context and characteristic of the EAng and NEGM hotspots, respectively. Species with core ranges centred within these two areas but demonstrating distinct geographic range disjunctions or with ranges partially overlapping adjacent areas are also indicated. Species composition of Scottish Empidoidea assemblages as assessed by MDS was markedly dissimilar from that in the rest of Britain (Fig. 5, cluster 1) although NEGM assemblages were not well resolved from others in Scotland. The EAng assemblage of Empidoidea (Fig. 5, cluster 2) was clearly structured differently from others in England and Wales, which were otherwise

Figure 8. Parsimony analysis of endemism of British and continental European Empidoidea. (A), bootstrap consensus of two equally parsimonious trees resolved by PAE using 650 taxa, and 28 OGUs comprising four pooled adjacent 50 × 50 km grids in Britain and Belgium, CI = 0.236, RI = 0.519; (B), geographical alphanumeric codes V1–V27 identifying British OGUs used in the analysis; (C), terminal part of bootstrap consensus of two equally parsimonious trees resolved by PAE using 678 taxa, and 30 OGUs comprising four pooled adjacent 50 × 50 km grids in Britain and Belgium, three pooled grids from Germany, and a single grid from Norway, CI = 0.219, RI = 0.494. The basal part of the tree (basal to the arrow in A and C) had identical topology as in A. Bootstrap support (1000 replicates) is indicated at the nodes.
Resolved by MDS into two groups (Fig. 5, clusters 3 & 4), one occupying much of central England and the other extending from south-west England through Wales into northern England. Thus, disparate species composition of the EAng and NEGM centres of endemism is also supported by ordination.

Species turnover (measured as $\beta_w$) increased along spatial gradients away from the EAng (Fig. 6A), NEGM (Fig. 6B) and southern English (Fig. 6C) centres of endemism. Decay of community similarity with distance is well known as a scale-dependent effect (Keil et al., 2012) generally attributed to environmental and climatic dissimilarities along geographical gradients (Nekola & White, 1999; Hawkins et al., 2003; Field et al., 2009) influencing both niche- and dispersal-based community assembly mechanisms (Sokol et al., 2011). Our data revealed decay in species similarity of Empidoidea assemblages orientated predominantly along south-east to north-west gradients and between coastal and inland localities, which are patterns of variation that are widespread in the British biota (Hill, 1991; Harrison, Ross & Lawton, 1992). Gradients were not uniform as, for example, upland areas of northern England and Wales were less dissimilar to the NEGM area than were adjacent lowland areas (Fig. 6B), indicating that local-scale environmental conditions are likely superimposed on the form of wider-scale geographic gradients.

PAE retrieved a nested set of area clades with more northerly British OGUs recovered in ‘basal’ positions and more southerly British and continental European localities in progressively more distal positions in the tree topology (Fig. 8). Branch support was generally low although much stronger for the terminal area clade including all southern localities (indicated by the arrow in Figs 8A, C), which emulates a corresponding geographical separation between Scottish assemblages and those of the rest of Britain found by ordination with MDS. There was general geographical correspondence between tree topology and area clades found by PAE with areas of elevated reciprocal weighted endemism and assemblage similarity. We interpret the results as evidence that historical community assembly processes that gave rise to contemporary northern assemblages in Britain preceded those that eventually gave rise to more southerly communities. Biotic connections shared by southern assemblages are more recent than those further north. Furthermore, a tree topology lacking in deep branches suggests that all modern British assemblages are descendants of a single early pioneer community (or at least that if multiple pioneer events occurred, they must have been at an early time in the history of Empidoidea being present in Britain). The results imply a north–south gradient between early ‘founder’ assemblages in the north and southern

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<th>Taxon</th>
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<td>Dolichopodidae</td>
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<tr>
<td><em>Dolichopus nigripes</em> Fallén</td>
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<td><em>Dolichopus plumiparsis</em> Fallén</td>
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<td><em>Hercostomus verbekei</em> Pollet</td>
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<tr>
<td><em>Empis prodromus</em> Loew</td>
<td>Empididae</td>
<td>W</td>
</tr>
<tr>
<td><em>Platypalpus caroli</em> Grootaert</td>
<td>Hybotidae</td>
<td>W</td>
</tr>
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<td>W</td>
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<tr>
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<td><em>Telmaturgus tumidulus</em> (Raddatz)</td>
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Distribution status; N, narrow-range endemic confined to the EAng hotspot; W, distribution centred on the EAng hotspot but encroaching on adjacent areas; D, disjunct distribution including the EAng hotspot and distant areas.
assemblages influenced by more recent events. PAE has been widely used as a method to generate historical hypotheses of biogeographical area relationships (García-Barros et al., 2002; Navarro et al., 2007; Plant, 2014a; Ivković & Plant, 2015). The technique has attracted criticism including a perceived inability to distinguish between areas sharing similar ecologies and those with similar history (Rosen, 1988) and questions as to the relative strength and importance of geographical patterns generated by vicariance and by dispersal (see Nihei, 2006 for discussion). A major limitation of PAE is that it ignores phylogenetic relationships (Humphries, 1989, 2000), but there can be greater confidence that the results reflect historical events if they can be corroborated with the results of traditional cladistic biogeography based on a sound knowledge of phylogeny (unavailable for Empidoidea) or if geographical patterns among groups of organisms can be reconciled with geological evidence or palaeoecological data (Rosen, 1988).

Climate changes in Europe during Pleistocene glacial episodes were associated with periodic expansion and contraction of northern temperate taxa which survived in refugia during glacial maxima and extended their ranges during interglacials (Montgomery et al., 2014). During the Devensian Late Glacial Maximum (LGM) 26.5–19 Kyr, much of Britain and Ireland was covered by ice (McCabe & Clark, 1998; Clark et al., 2012) with limited exposure of land (Rolfe et al., 2012; Clark et al., 2012) and only a very restricted fauna of cold-adapted species is likely to have persisted in southern Britain. Following the LGM, a period ensued of rapid changes in ice extent, sea levels, and climate followed by steady warming from 15 Kyr, punctuated by the cooler Younger Dryas (12.8–11.5 Kyr). From the

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Family</th>
<th>Distribution status</th>
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<tr>
<td>Hilara hybrida Collin</td>
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<td>Rhamphomyia hirtula Zett.</td>
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<td>Rhamphomyia ignobilis Zett.</td>
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<td>Rhamphomyia vesiculosa (Fallén)</td>
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<td>Tachypeza truncorum (Fallén)</td>
<td>Hybotidae</td>
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<td>Wiedemannia simplex (Loew)</td>
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<tr>
<td>Rhamphomyia murina Collin</td>
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</table>

Distribution status; N, narrow-range endemic confined to the NEGM; S, distribution centred on the NEGM but encroaching on adjacent areas; D, disjunct distribution including the NEGM and distant areas.

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start of the Holocene (11.5 Kyr), a more stable climate ensued, continuing to the present day (Montgomery et al., 2014). Land connectivity between eastern Britain and Europe via Doggerland persisted until c. 8 Kyr when the land bridge between Britain and the Netherlands and Belgium was inundated (Coles, 1998; Montgomery et al., 2014). As temperatures rose, less cold-tolerant species, which had been restricted to southerly refugia (Stewart et al., 2010), would have dispersed out of these areas to colonize Britain and north-western Europe, and there is abundant evidence from the palynological and archaeobiological records, sedimentary fossil deposits, and phylogeographic studies, of major colonizations of Britain and Doggerland by plants and animals during this period (Lowe & Walker, 1984; Coles, 1998; Montgomery et al., 2014) before severing of the land bridge presented a barrier to dispersal.

Our PAE results reveal that the historical assembly of Empidoidea communities now represented by modern assemblages in much of Scotland likely took place at an early stage in the origination of the British fauna. This does not imply, of course, that the composition of modern northern assemblages actually matches that of their progenitors, but rather that it was derived from them. A consistent south to north vector of historical dispersal direction probabilities (Fig. 7) together with a similarly orientated decay in assemblage similarity may be linked to Holocene climatic amelioration allowing northward migration of eurythermic taxa, which would, in effect, have diluted the signal of early cold-adapted pioneer communities which themselves would have retreated northwards as the climate warmed. Early British and continental European Empidoidea shared a common origin as judged by PAE as Belgian, German, and Norwegian assemblages were retrieved in terminal nested area clades of the tree (Fig. 8). Our data are consistent with a model in which British and continental assemblages were derived from common ancestral communities which probably came to occupy ice-free land in north-western Europe following the end of the Devensian glaciation and at a time before the land-bridge between Britain and Europe was lost. Northward dispersal of more southerly communities would have continued into at least the mid-Holocene. The lack of any deep branching in PAE tree topology reveals no evidence consistent with a vicariant separation of the British fauna that might be attributed to the relatively recent (8 Kyr) loss of land connectivity with Europe, suggesting that the assembly of the British fauna was largely complete by the time the land-bridge was inundated.

Empidoidea exhibit very varied ecologies and environmental tolerances, and some cold-tolerant taxa, at least, were likely to have persisted in southernmost Britain through the LGM and the following 5000–7000 years characterized by fluctuating but generally cool climates when ice-free habitat may have been available at different places at different times (Montgomery et al., 2014). Diptera are a dominant component of many modern high Arctic arthropod communities (Danks, Kukal & Ring, 1994; Brodo, 2000) and, for example, many genera of the empidid subfamily Empidinae, especially Rhamphomyia Mg. are speciose and numerous at high latitudes and at high elevations where they can be important pollinators (Lefebvre et al., 2014; Vajda, 2015). Whereas species of the empidine genera Rhamphomyia and Hilara Mg. comprise only c. 17% of the total British Empidoidea, they constituted 45% of narrow range endemic taxa here considered characteristic of the NEGM endemism hotspot (Table 2). While knowledge of global ranges of these species is limited, all appear to have northern European distributions, sometimes with disjunct populations in central European mountain ranges, and might properly be considered as boreal or boreo-montane taxa. These species (and indeed other non-empidine taxa listed in Table 2) may be relicts of an Early Phase of Diptera colonization of Britain by cold-adapted stenotherms dating to the early post-Devensian (between the LGM and 14–15 Kyr) or even to the LGM, although a later colonization during cold climatic periods such as the Younger Dryas cannot be discounted. The Grampian Mountains, especially their included areas of Strathspey and the Cairngorm Mountains, are well known as loci of range-restricted species of many Diptera families including Heleomyzidae, Calliphoridae, Scatophagidae, Anthomyiidae, Muscidae (Horsfield & MacGowan, 1997), Mycetophilidae, Phoridae, Pipunculidae (Falk & Chandler, 2005), Syrphidae (Ball et al., 2011), and other orders of insects including Lepidoptera (Hill et al., 2010), Odonata (Merritt, Moore & Eversham, 1996), and Neuroptera (Kirby, 1991). Many Grampian range-restricted species are confined to montane habitats such as snowfield vegetation and tundra-like habitats (Horsfield & MacGowan, 1997; Horsfield, 2002; Sinclair, 2008) or associated with boreal woodland remnants of Populus tremula and Pinus sylvestris (Horsfield & MacGowan, 1997; MacGowan, 1997) and may be Early Phase colonists of Britain.

By 13 Kyr, the severe periglacial conditions of the Late Devensian were rapidly ameliorating, and notwithstanding the intercession of the cold Younger Dryas, there are indications that summer temperatures in much of Britain were little different from the present day (Lowe & Walker, 1984). Transition from Arctic conditions may have been abrupt at some sites as judged by biostatigraphic evidence of Coleoptera assemblages (Coope, 1975, 1977). Although at the start of the Holocene, Britain and Doggerland likely had only sparse woodland cover, perhaps on account of
the immaturity of soils, more extensive forests developed subsequently (Coles, 1998) and greater ecological opportunity would have allowed increased colonization by Diptera, especially Empidoidea, the majority of which have predatory immature stages found in well-developed soils and decaying organic matter. Ireland has been isolated as an island for perhaps twice as long as Britain and there is no evidence that a land bridge between these islands persisted after 15 Kyr (Edwards & Brooks, 2008). Although the Irish fauna was not studied here, it shares only 50.1% of its Empidoidea diversity with modern Britain (based on the data of Chandler, 1998). It thus seems likely that the Middle Phase of colonization of Britain by Empidoidea was underway by 15 Kyr and that major colonization of Britain continued after the loss of the Ireland-Wales land bridge and probably accounts for the assembly of the majority of nonboreal lowland communities now present. The middle phase would have been terminated by the inundation of Doggerland and loss of the land bridge between Britain and continental Europe at 8 Kyr, after which the presence of open marine environments would have presented barriers to further dispersal and colonization. The dispersal capabilities of Empidoidea are very poorly known, and we have no evidence to indicate to what extent they would have been able to penetrate Britain in the Late Phase once the land-bridge was lost, and can only speculate that colonization rate was likely much slower than during the preceding period.

While the NEGM endemism hotspot might be understood as a montane refugial area into which cold-adapted Early Phase colonists retreated northwards in the face of climatic amelioration, origination of the EAng hotspot is less clear. The close terminal positions of East Anglian and Belgian OGUs in PAE trees (Fig. 8) suggest a relatively recent common origin, and dispersal direction vectors indicate that the assembly of East Anglian communities may have been considerably influenced by Belgian and south-east English faunas (Fig. 7). The alluvium-filled basins and surface sands and gravels of EAng (Greig, 1996) and similar surface topography, at least in the west of Belgium (Verbruggen, Denys & Kiden, 1966), sustain similar broad habitat types including fen and sandy heath or pseudo-steppe environments which were also likely present on Doggerland during the Holocene (Coles, 1998). The inundation of Doggerland at c. 8 Kyr marked the final loss of land connectivity between Britain and continental Europe and would have resulted in some components of the shared Doggerland biota becoming isolated in refugial areas on either side of the North Sea in EAng and Belgium.

Whereas the taxonomic composition of Empidoidea in the NEGM hotspot is dominated by cold-adapted Empididae and Hybotidae (Table 2), Dolichopodidae are the major components of the EAng hotspot (Table 1), and many of the included species have wetland or coastal affinities. The fen and breckland habitats of EAng are recognized as centres of distribution of many range-restricted taxa including certain aquatic Heteroptera (Huxley, 2003) and Odonata (Merritt et al., 1996) and species of the Diptera families Syrphidae (Ball et al., 2011) and Mycetophilidae (Falk & Chandler, 2005). Such habitats may formerly have been more widespread as some species with a core distribution in EAng have modern ranges that include geographically disjunct outlier populations elsewhere. For example several species of Diptera associated with Phragmites (often the dominant plant in fen habitats) have isolated populations in distant localities with abundant Phragmites in southern Britain and the fen and open water species Allodio protenta Laštovka & Matile (Mycetophilidae) and Anopheles algeriensis Theobald (Culicidae) are also known from similar habitats in Anglesey in Wales (Falk & Chandler, 2005). Interestingly, ordination of species composition of Empidoidea implies similarities between assemblages on Anglesey (Grid SH1) and part of EAng (Fig. 5, cluster 3a), both areas with extensive fen habitat. We suggest that although the EAng hotspot of endemism may have originated during mid-phase colonization of Britain, it was probably shaped and became more geographically restricted by subsequent habitat changes. Such changes were likely to have been substantial for fen species, which would have suffered massive loss of habitat through anthropogenic wetland draining during the late phase.

Disjunctions are also known between areas of the Scottish Highlands and English localities. These typically involve heathland species such as the Syrphidae Microdon analis (Macq.) (Ball et al., 2011) and may represent examples of populations becoming ‘marooned’ in isolated pockets of acidic healthy soils during historical edaphic or other environmental changes. We have no clear evidence for disjunct distributions among the many heathland specialist Empidoidea. However, ordination suggested similarities in assemblage composition between the Scottish Highlands and grid SO1 on the Welsh/English borders (Fig. 5, cluster 7a). Species characteristic of this disjunction include Hilara borbipes Frey, Hilara diversipes Strobl, Hilara pseudosartrix Strobl, and Platypalpus stigmatellus (Zett.); and assemblage similarity is also supported by a larger number of species such as Oedalea ringdahlii Chvála, Platypalpus melancholicus (Collin), and Dolichopus argyrotarsis Wahlberg that have essentially northern and western distributions but with relatively isolated and small populations not only on the Welsh borders, but also elsewhere in predominantly upland areas of England. Many of the species involved have associations with
extensive alluvial sands of periglacial origin present in the Grampian area and along rivers such as the Monnow and Usk in the borders area, and we conjecture that southern populations may have become isolated from those further north by persistence of local areas of suitable habitat as the environment changed during the Holocene.

The model presented here of how British communities of Empidoidea were assembled historically is one in which the arrows of colonization and dispersal point consistently northwards. Early Phase cold-adapted arrivals were followed by a greater diversity of more eurythermic taxa during a middle phase which probably ended when the land-bridge with Europe was severed. Thereafter, northward dispersal continued in response to continued climatic and environmental change with populations becoming fragmented in isolated relictual habitat types, resulting in local hotspots of elevated endemicity. The model is however only a broad outline, and further work will be needed to verify and refine it. The absence of a reliable phylogeny hinders the development of cladistic biogeographical interpretations and prevents assessment of how taxonomic composition might reflect potentially differing areas of origin of the different assemblages. In particular, molecular phylogeographic methods may be needed to elucidate dispersal trajectories and timing more accurately.

ACKNOWLEDGEMENTS

We would like to thank the many ‘amateur’ recorders who contributed data to the British Empididae & Dolichopodidae Recording Scheme without whom this analysis would not have been possible. Andreas Stark and Heather Pardoe are thanked for useful discussion. We thank two anonymous reviewers for their helpful comments.

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Morton A. 2016. *DMAP distribution mapping software*. Available at: www.dmap.co.uk


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article at the publisher’s website:

**Table S1.** List of taxa of Empidoidea included in analyses.