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Spatial and environmental drivers of macrophyte diversity and community composition in temperate and tropical calcareous rivers

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Abstract

The hypothesis was examined that sources of variation in macrophyte species richness (alpha-diversity: S) and community composition (“species-set”), attributable to spatial and environmental, variables, may differ in importance between tropical and temperate calcareous rivers (>10 mg $CaCO_3$ L^{-1}). To test this hypothesis geographic, environmental, and aquatic vegetation data were acquired for 1151 sites on calcareous rivers within the British Isles, supporting 106 macrophyte species (mean S: 3.1 species per sample), and 203 sites from Zambian calcareous rivers, supporting 255 macrophyte species (mean S: 8.3 species per sample). The data were analysed using an eigenfunction spatial analysis procedure, Moran’s Eigenvector Maps (MEM), to assess spatial variation of species richness and community composition at large regional scale (>10^5 km^2: British Isles and Zambia); and at medium catchment scale (10^4 – 10^5 km^2: British Isles only). Variation-partitioning was undertaken using multiple regression for species richness data, and partial redundancy analysis (pRDA) for community data. For the British Isles, spatial and environmental variables both significantly contributed to explaining variation in both species richness and community composition. In addition, a substantial amount of the variation in community composition, for the British Isles as a whole and for some RBUs, was accounted for by spatially-structured environmental variables. In Zambia, species richness was explained only by pure spatial variables, but environmental and spatially-structured environmental variables also explained a significant part of the variation for community composition. At medium-scale, in the British Isles, species richness was explained by spatial variables, and only for four of the six RBUs.

Keywords: Biodiversity; Macroecology; Spatial scale; Hard-water rivers; Aquatic macrophytes; Landscape; Partitioning of variance; Species richness; Alpha-diversity; Spatially-structured factors.

Footnote

Abbreviations: MEM (Moran’s Eigenvector Maps: an eigenfunction spatial analysis procedure which is a generalization of Principal Coordinates of Neighbor Matrices, PCNM); RBU (River Basin Units)

Highlights

- We analysed the aquatic vegetation of 1354 tropical and temperate river sites
- MEM, multiple regression and pRDA were used to analyse the datasets
- Spatial and environmental variables were both significant driving factors
- Species richness (S) in tropical rivers was only driven by spatial factors
- In temperate rivers S was driven by both spatial and environmental variables

1. Introduction

Understanding the causes of geographic patterns of species and biodiversity distribution is central to ecology. As with other groups of biota, the spatial distribution of freshwater macrophytes (”aquatic photosynthetic organisms, large enough to see with the naked eye, that actively grow permanently or periodically submerged below, floating on, or growing up through the water surface”: Chambers et al., 2008) varies considerably in terms of both species richness and community composition at different spatial scales across the world (e.g. Jones et al., 2003). Recently, considerable progress has been made toward documenting large-scale patterns of species richness (e.g., Hillebrand, 2004), and macrophytes pose no exception to the many suggestions made, for different biota, to try to explain observed geographical and temporal patterns of variation in species richness and community composition (e.g., Hawksworth, 1995; Murphy et al., 2003; Varandas Martins et al., 2013).

Factors potentially influencing macrophyte community distribution, and variation in alpha-diversity, in freshwater systems have been considered at various scales (Hawksworth, 1995). First, there is the large, regional scale (e.g., Murphy, 2002) where these community characteristics are usually primarily driven by geography-related factors (e.g. temperate versus tropical climate: Crow, 1993). Second is medium, or catchment scale, where, for example, hydrological and chemical variation in the system may be important (e.g., Varandas Martins et al., 2013; Spink et al., 1997; Vestergaard and Sand-Jensen, 2000). Third is small scale, related to environmental features of specific habitats and communities, and the biological interactions which go on at this level, such as herbivory and competition (e.g., Lacoul and Freeman, 2006).

Both community composition and diversity are primarily affected by the sum and interactions of the numerous processes occurring at these various spatial scales (Borcard et al., 2004). Modelling spatial patterns in plant communities at multiple temporal and spatial scales can hence be a useful approach to improve understanding of community characteristics, and their potential future response to environmental change (Borcard et al., 2004), but has only rarely been carried out previously in river research (e.g., Poff, 1997).

Rivers are hierarchically structured, from source to mouth, meaning that spatio-temporal variation in the species richness and composition of the macrophyte communities which they support is influenced by a combination of local in-stream variables, regional environmental factors, and catchment characteristics. Only a few studies have so far attempted to assess the relationships between environmental factors and richness of aquatic macrophyte assemblages on a large spatial scale (e.g., Rørslett, 1991; Crow, 1993; Baattrup-Pedersen et al., 2006; Chambers et al., 2008). However several previous studies, undertaken at smaller scales, have shown similarities in the main environmental gradients underlying the species-environment model for river vegetation. For instance slope, substrate characteristics, dissolved oxygen and nitrate have all been found to be of varying importance in driving river macrophyte species distribution (Dodkins et al., 2005). Other driving variables that have been identified in this context include calcium concentration and flow regime (Wilby et al., 1998; Varandas Martins et al., 2013).

In this paper we address questions related to how environmental factors varying at medium scales (in this case, within individual river basins of the British Isles, at a unit size of approximately 10^4 – 10^5 km^2), such as alkalinity and altitude; and factors varying at a regional, large scale (e.g. temperature and precipitation regimes), in both the British Isles and Zambia (each with unit size >10^5 km^2), may interact with each other, and with spatial location data (i.e., latitude and longitude of the sampling sites), to help explain observed variation in patterns of river macrophyte species richness and community composition (species presence/absence across sites).

These questions were posed for a closely-defined type of freshwater habitat, namely calcareous (“hard-water”) rivers and streams, located within two target regions of the world: one temperate (the British Isles) and the other tropical (Zambia). Hard-water systems are here minimally defined (Tapia Grimaldo, 2013) as 10 – 19.9 mg L^{-1} $CaCO_3$ concentration ("marginally hard-waters"), through to a maximum of rivers with >200 mg L^{-1} $CaCO_3$ concentration ("very hard-waters").

Combined analysis of spatial and environmental factors has hitherto only rarely been applied to aquatic macrophyte communities (e.g., Capers et al., 2009; O'Hare et al., 2012). The inclusion of geographic location as a predictor can help improve understanding of whether species richness and/or community composition is spatially-structured (examples of underlying causal factors which may influence such observed spatial pattern include biological limits upon dispersal in individual species, and climatic constraints on species survival: Borcard et al., 1992).

Useful in such combined analyses are approaches based upon eigenfunction spatial analysis, such as Moran's Eigenvector Maps (MEM: Borcard and Legendre, 2002; Dray et al., 2006; Griffith and Peres Neto, 2006). MEM can quantify spatial patterns in species data (e.g., variation in richness and community composition) across a range of geographical scales (Borcard and Legendre 2002; Borcard et al., 2004), by generating spatial variables that could also account for unmeasured environmental variables (Peres-Neto and Legendre, 2010). A comprehensive account of the procedure, providing detailed interpretation of the meaning of MEM variables and scales represented by them, is provided by Dray et al. (2006), while Landeiro et al. (2011) also provide a succinct description of the primary characteristics of MEM and its outputs.

In this study we examined the hypothesis that sources of variation in macrophyte species richness (alpha-diversity) and community composition, attributable to spatial, environmental, and spatially-structured environmental variables, may differ in importance between tropical and temperate calcareous rivers.

2. Methods

2.1. Data collection

The analysis used data for 1151 sites located on hard-water rivers and smaller streams in the British Isles, supporting a total of 106 macrophyte species, together with a further 203 sites from Zambian calcareous rivers, supporting 255 macrophyte species. Vegetation species richness (S: number of species recorded per site) and community composition (presence/absence data across sites) were assessed per 100 m stretch at each site.

The data were obtained:

(i) by field survey, undertaken by the authors during 2006 - 2012: 54 sites in England, Scotland, and Ireland, and 203 Zambian sites, using an adapted version of the Mean Trophic Rank (MTR) field protocol developed in the United Kingdom to acquire vegetation data for river quality bioassessment (Holmes et al., 1999; WFD-UKTAG, 2014; Kennedy et al., 2015);

(ii) by extraction of information for sites located on hard-water rivers, from a large pre-existing dataset held by the authors (MTR data: collected since 2000 using the standard MTR protocol, as above). This dataset formed the bulk of the British Isles data analysed, comprising 1051 sites; and

(iii) from two older datasets for hard-water Irish and UK rivers, extracted from information in Caffrey (1990), Spink (1992), and Spink et al. (1997) comprising a further 46 sites.

The taxonomic resolution for the data used here was 85% to species level and the remaining 15% to genus level, across the different surveys contributing to the dataset.

Alkalinity (ALK: mg $CaCO_3$ L^{-1}) was measured by standard Gran titration procedure for water samples taken from each site (Neal, 2001). The MTR data set includes information on water alkalinity for the 1051 sites taken from this database. Data for climatic variables, as mean values for 1950 – 2000, for the British Isles and Zambia were obtained from the global climate database Worldclim (Hijmans et al., 2005; www.worldclim.org/bioclim). These variables were: annual evapotranspiration (EVAP: mm); annual mean temperature (AMT: °C); temperature seasonality (TS: standard deviation*100); maximum temperature of warmest month (MAXTW: °C); minimum temperature of coldest month (MINTC: °C); mean temperature of wettest quarter (MTWeQ: °C); mean temperature of driest quarter (MTDQ: °C); annual precipitation (AP: mm); precipitation seasonality (PS: coefficient of variation); precipitation of wettest quarter (PWeQ: mm); precipitation of warmest quarter (PWQ: mm); and precipitation of coldest quarter (PCQ: mm).

Altitude (ALT: m above mean sea level) was also recorded for each site, along with site coordinates (latitude (LAT) and longitude (LONG): both in decimal degrees). These data were acquired either using GPS equipment in the field, or from large-scale (1:50.000) maps.

2.2. Data analysis

Spatial variation of datasets for macrophyte species richness and community composition variation in hard-water streams was evaluated at two spatial extents: (i) regional, large scale (>10^5 km^2: British Isles; Zambia); and (ii) medium (catchment) scale (approximately 10^4 – 10^5 km^2: for the British Isles only), within River Basin Units (RBUs), of which six non-political entities (some crossing national borders) cover the British Isles. RBUs individually comprise sets of River Basin Districts (RBDs), established primarily around the catchments of the major river systems of the British Isles. The six RBUs are: Scotland (Scotland, and Solway Tweed RBDs), Northern England (Northumbria, and North West RBDs), South East England (Anglian, Thames, and South East RBDs), South West England and Wales (South West, Severn, Dee, and Western Wales RBDs), Northern Ireland (North Eastern, Neagh Bann, and North Western RBDs), and Southern Ireland (Western, Shannon, Eastern, South Eastern, and South Western RBDs). Further details and maps showing boundaries of RBDs in the British Isles are available from the websites of the Environment Agency (England and

Wales) www.wildswimming.co.uk/wp-content/uploads/2013/08/River_Basin_District_Map_LIT_8050_75c4b2-724x1024.jpg; Scottish Environment Protection Agency: www.gis.sepa.org.uk/rbmp; and the Geological Survey of Ireland: www.gsi.ie/NR/rdonlyres/780BFC43-AF88-4969-8B08-029840C7FF6F/0/River_Basin_Districts_1.jpg.

Because of the lower sample size for Zambia, analysis was undertaken only at regional (whole country) scale for that dataset.

To evaluate spatial patterns in species richness and community composition, in separate analyses for the British Isles and Zambia, spatial variables were created using the eigenfunction spatial analysis procedure Moran's Eigenvector Maps (MEM), which is fully described by Borcard and Legendre (2002), Griffith and Peres Neto (2006) and Dray et al. (2006). Before the development of eigenfunction spatial analyses, spatial patterns in biodiversity data were modelled using simple trend-surface analysis (TSA; i.e., a multiple regression analysis allowing for latitude and longitude of the sampling sites or for polynomial expansion of these coordinates: Borcard and Legendre, 2002). The problem with TSA is that it is suitable to model only simple spatial patterns (e.g., trends and parabolas) and, therefore, more complex patterns of spatial variation, so common in nature, may pass undetected with this method (Borcard and Legendre, 2002). Also, the monomials (e.g., Latitude and Latitude^2) are not orthogonal. On the other hand, MEM creates orthogonal explanatory variables (eigenvectors = spatial variables), representing different patterns of spatial relationships between sampling sites, which are potentially able to model complex spatial patterns of a response variable (e.g., species richness; see Fig. 2 of Griffith and Peres-Neto, 2006). These spatial variables are obtained by computing the eigenvectors of a connectivity matrix, which in its turn is derived from the geographical position of the sampling sites (see Fig. 1 of Griffith and Peres-Neto, 2006). The first eigenvectors associated with large, positive eigenvalues represent coarse spatial patterns and positive spatial autocorrelation. The last eigenvectors, associated with small eigenvalues, represent fine spatial structures (Griffith and Peres-Neto, 2006). In short, instead of using simple latitude and longitude (or polynomial expansions of these), some of the eigenvector maps, along with the environmental variables, are used as explanatory variables in statistical models (see below).

To model species richness and species presence-absence data (community composition), as functions of spatial and environmental variables, we used multiple regression analysis and partial Redundancy Analysis (pRDA; Legendre and Legendre, 2012), respectively. Explanatory variables (both spatial and environmental) were selected for inclusion in the final models using the forward selection procedure proposed by Blanchet et al. (2008). This method consists of first running a global test with all explanatory variables. The forward procedure continues only when this test is significant. The interest of this method is that usual significance levels and adjusted coefficients of determination are other two criteria used, which avoid overfitting.

In both cases (multiple regression and pRDA) we used variation-partitioning (Peres Neto et al., 2006) to determine the relative importance of environmental and spatial variables in explaining variation in macrophyte species richness and community composition at each spatial extent in the target locations. This approach split the total variation explained by each analysis outcome into four components: (i) variation explained exclusively by environmental variables (pure environmental variation); (ii) variation explained exclusively by spatial variables (pure spatial variation); and (iii) variation that can be explained by both environmental and spatial variables (shared fraction), also termed spatially-structured environmental variation (Blanchet et al., 2008). The fourth component was residual (unexplained) variation. We used adjusted R^2 (adj-R^2) values, which correct for unequal ratio between number of observations and explanatory variables, to perform the variation-partitioning (Peres-Neto et al. 2006).

3. Results

The findings provide evidence for the existence of spatial patterns in both macrophyte alpha-diversity and community composition in temperate and tropical calcareous rivers. There were substantial differences in mean values of alpha-diversity (S) between the British Isles (3.1 species per sample) and Zambia (8.3 species per sample), and also between RBUs within the British Isles (Table 1).

3.1. British Isles

3.1.1. Regional/ large scale species richness

Gamma-diversity for macrophyte species recorded from the sampling sites in temperate calcareous rivers of the British Isles comprised 58 emergent, 14 floating, and 34 submerged species, giving a total of 106 species. The mean alpha-diversity for macrophytes at sample sites for the British Isles as a whole was 3.1 species per sample (Table 1). Distribution of hard-water river macrophyte diversity across the British Isles is shown in Fig. 1. Only 2.1% of the variation in diversity was accounted for by pure environmental effects (e.g. alkalinity, temperature seasonality: see Fig. 2). Variation in macrophyte species richness was best explained by spatially-structured environmental factors (11.4%), and pure spatial variables (8.8%). These acted primarily at three spatial scales: broad, intermediate and fine, represented by MEMs 4, 20, and 100 (together with a number of MEMs of lesser importance, within these three scale ranges: see Table 1 and Fig. 3).

3.1.2. Regional/ large scale: community composition

Variation in macrophyte community composition was best explained by pure spatial variables (MEMs), but the variation accounted for was low (5.4%; Table 2). Spatially-structured environmental factors accounted for a further 3.9% of variation, while pure environmental factors (e.g. annual precipitation, minimum temperature of coldest month, precipitation of warmest quarter: see Fig. 2) taken together accounted only for 1.1% of the variation.

3.1.3. Medium (River Basin Unit) scale: species richness

There were substantial differences (Table 1) in average macrophyte alpha-diversity between RBUs, with southern Ireland having the highest, at 7.1 species per sample and Scotland the lowest, at 2.2 species per sample. Macrophyte richness variation in hard-water rivers within each of the six individual RBUs comprising the British Isles (Table 1) was explained only by spatial variables, and only for four of the six RBUs. Species richness variation in Scotland and Southern Ireland was not accounted for by any of the explanatory variables (environmental or spatial). The proportion of variation explained ranged from 5.9% (for South East England) to 14.4% (Northern England). Environmental and spatially-structured environmental adjusted R^2 values were negligible in all RBUs. Species richness for Northern England and South East England was explained by MEMs representing patterns at intermediate to fine spatial scales. Conversely South West England and Wales, and Northern Ireland retained low-order MEMs indicating broad spatial patterns of diversity in these RBUs.

3.1.4. Medium (River Basin Unit) scale: community composition

In contrast to the results for medium-scale richness within the British Isles, macrophyte community composition variation at medium scale (Table 2) was partially explained by all three sets of variables (spatial, environmental and spatially-structured environmental variation) within individual RBUs, but the relative importance of each differed between RBUs. In Scotland and Northern England, variation in community composition was best explained by spatially-structured environmental variables (6.9% and 4.5% respectively). However in South East England, and South West England and Wales, spatial variables were of primary importance in this respect (accounting for 7.1% and 4.2% of variation, respectively. In both Northern and Southern Ireland spatial variables were of sole importance in explaining variation in community composition. In all RBUs the pure environmental component (e.g. alkalinity, temperature seasonality, and minimum temperature of coldest month) was always of little or no importance (accounting for zero to 2.8% of variation). In all RBUs with significant spatial patterns, the order of influential MEMs was low to intermediate (e.g., for Scotland: MEMs 3, 1, 4, 28: see Table 2), suggesting that spatial patterns of variation in macrophyte community composition are operating mainly at broad scales.

3.2. Zambia

3.2.1. Regional/ large scale: species richness

The total number of macrophyte species recorded from the Zambian sites (gamma-diversity) was 255, consisting of 186 emergent, 18 floating and 51 submerged species. Mean species richness (alpha-diversity) at individual sites in Zambia sampled during 2009 – 2011 was 8.3 species per site, substantially higher than for the British Isles dataset. Macrophyte species richness variation, within Zambian streams (Table 1, Fig.4) was accounted for solely by the pure spatial component, which explained 25.8% of variation. Influential MEM orders were low, indicating broad-scale patterns of spatial variation.

3.2.2. Regional/ large scale: community composition

In contrast to the results for species richness, spatial, environmental and spatially-structured environmental variables all influenced the variation in macrophyte community composition observed in Zambian hard-water rivers (Table 2). The spatially-structured environmental component was of greatest importance, explaining 4.6% of the variation. The pure spatial component (with MEMs representing broad-scale spatial patterns) accounted for a further 3.8%, and pure environmental variables explained a further 2.7% of the variation, with both being statistically significant. Environmental variables that best explained the variation observed in macrophyte community composition were annual precipitation, precipitation seasonality, evapotranspiration, altitude and alkalinity. Fig. 5 shows the distribution of three of these variables across Zambia.

4. Discussion

Our results suggest that in the tropical calcareous rivers of Zambia only spatial factors were of importance (though quite strongly so) in explaining species richness variation, mainly acting at broad scales. In contrast, although a total fraction of the variation in species richness comparable to that seen for Zambia was explained by variables retained in the final model for the temperate rivers of the British Isles, this was made up not only of pure spatial factors, but also pure environmental (alkalinity, temperature seasonality, maximum temperature of warmest quarter, minimum temperature of coldest quarter, and mean temperature of wettest quarter) and spatially-structured environmental factors, whilst spatial factors operated across a wide range of scales from broad to finer-scale patterns. It is noteworthy that, in both cases, the inclusion of spatial factors in the analysis helped explain a significant proportion of the observed variation for species richness in calcareous river vegetation, demonstrating the importance of spatial processes (e.g., unmeasured environmental variables, dispersal) when analysing large-scale species diversity distributional patterns (see Legendre et al., 2009).

In terms of community composition, differences between the tropical and temperate outcomes are less marked than for the richness outcomes, with all three components (spatial, environmental and spatially-structured environmental) contributing to explain community variation, and a comparable total proportion of variation (ca. 10 – 11%) being accounted for in both target regions. Within this total proportion of variation explained there were minor differences in the importance of each component between the two regions, with spatial factors being of greater importance in the temperate rivers of the British Isles, and the spatially-structured environmental component being most important in tropical Zambian rivers. In both cases spatial patterns operating mainly at broad scales were suggested by the order of MEMs retained as of primary importance in the final models (Table 2).

Of the three environmental variables most strongly contributing to the outcomes for variation in regional community composition, annual precipitation was of primary importance in both Zambia and the British Isles. In both cases a further precipitation variable (precipitation of wettest quarter in the British Isles; precipitation seasonality in Zambia) was second in importance. However the third strongest variable was quite different between the target regions, being minimum temperature of coldest month in the British Isles, and annual evapotranspiration in Zambia. This may reflect the importance of cold winter temperatures in potentially stressing vegetation in temperate rivers, and the probable importance of evapotranspiration in contributing to water loss from aquatic systems in tropical rivers, again causing potential stress to river plants as their habitat dries out during the dry season.

The overall proportions of variation explained by the analysis of regional-scale species richness and community composition are undoubtedly low (see Tables 1 and 2). However, these outcomes are of comparable magnitude to those recorded from variation-partitioning analyses in similar studies elsewhere which have incorporated spatial analysis (e.g. Heino et al., 2009; Astorga et al., 2011; O'Hare et al., 2012; see also Soininen et al., 2014; 2016 for general quantitative reviews).

In order to improve the total explained variation it is likely that the inclusion of large-scale data for additional environmental factors (such as river flow regime, nutrient status, pH and other measures of water chemistry, and relevant catchment-scale factors such as land use) that are likely to influence river macrophyte richness and community would be helpful (e.g., Johnes et al., 1996; Kennedy et al., 2015). Such issues notwithstanding, our findings provide evidence to support the suggestion (e.g., Capers et al., 2009; O'Hare et al., 2012) that large regional-scale patterns in diversity are often strongly related to climate, though we also found that alkalinity and altitude were useful explanatory variables for community composition distribution (less so for species richness).

According to metacommunity theory, a significant environmental fraction provides evidence for the role of niche-based based processes (species sorting) in structuring communities (Leibold et al., 2004). Thus, in general, our results suggest the importance of species sorting processes in structuring local communities, despite the low values obtained for the pure environmental fractions.

Comparing the British Isles with Zambia, it is interesting to note that in both tropical and temperate rivers the primary environmental variable explaining community composition variation was annual precipitation. There are strong spatial gradients of annual precipitation in both regions: primarily increasing from east to west in the British Isles, and south to north in Zambia (Figs. 2, 5). These gradients are reflected in changing macrophyte community composition in rivers in both regions, with some examples detailed below.

In Zambia, Kennedy et al. (2015), using a dataset which included the data utilised in our study, but also including sites on non-calcareous rivers, found strong evidence that macrophyte community composition in rivers of the northern part of the country (primarily comprising the Bangweulu-Mweru freshwater ecoregion (Abell et al., 2008), which lies in the catchment of the Upper Congo, flowing to the Atlantic) shows substantial differences from rivers in the southern part of the country (in several freshwater ecoregions, but all within the Zambezi catchment, flowing to the Indian Ocean). For example a community type indicated by the presence of *Ottelia exserta* (Ridl.) Dandy, together with a number of less-common (within Zambia) macrophyte species such as *Potamogeton octandrus* Solms., *Aldrovanda vesiculosa* L., and *Ottelia cylindrica* (T.C.E.F. r.) Dandy, occurred only in upland calcareous streams of the Bangweulu-Mweru ecoregion in northern Zambia. The same study found that a very different community type, indicated by the presence of *Lagarosiphon ilicifolius* Oberm., *Ceratophyllum demersum* L., *Azolla filiculoides* Lam. and *Potamogeton schweinfurthii*

A. Benn., was characteristic only of sites on rivers located in low-lying valleys of the Zambezi catchment, in the southern part of Zambia.

Spatial vegetation trends in calcareous river macrophyte community composition have long been well documented for the British Isles along the well-known east – west precipitation gradient for this region (e.g., Butcher, 1933; Haslam, 1982; Caffrey, 1990; see also Fig. 2). A good example is the calcareous river macrophyte community type dominated by Batrachian *Ranunculus* spp., one variant of which (indicated by *Ranunculus penicillatus* subsp. *pseudofluitans* (Syme) S.D. Webster) tends to occur in more westerly, higher-flow rivers in the wetter parts of Britain, but which is much less common in the more sluggish calcareous rivers characteristic of lower-precipitation areas of eastern England (Holmes and Raven, 2014; see also information on the autecology of this plant, and a map of its British Isles distribution provided by the Online Atlas of the British Flora at: www.brc.ac.uk/plantatlas/index.php?q=node/1476). This illustrates the point that factors such as annual precipitation may not be the primary proximal cause of spatial variation in species distribution and hence community composition. In the case of annual precipitation other factors (such as topography) associated with the discharge and velocity of rivers (as well as a whole suite of other physico-chemical factors) will also strongly influence the ecology of these systems, and hence help determine what species they support. However, it is clear that spatially-structured environmental variables, such as annual precipitation, can act as a strong surrogate for a larger set of factors, in this case associated with flow regime, which influence river vegetation.

Overall, variation in calcareous river macrophyte community composition at regional scale in the British Isles, and at catchment scale in Great Britain (but not in Irish RBUs) was generally quite strongly attributable to spatially-structured environmental variables, though different variables were of greater or lesser importance within individual RBUs. Precipitation of coldest quarter was one such variable that was retained in the final model for every one of the RBUs in Great Britain.

Species richness variation was attributed to spatially-structured environmental variables at regional level, and this clearly mirrored well-documented climatic gradients which influence rivers in the British Isles and in Zambia. For instance hard-water river macrophyte species richness generally increased along a north-west to south-east gradient in the British Isles and in the opposite direction across Zambia (Figs. 1, 3). Several environmental variables such as temperature seasonality, and maximum temperature of warmest quarter vary spatially along a similar gradient in the British Isles (Fig. 2), while in Zambia precipitation seasonality and annual evapotranspiration show a clear south-west to north-east spatial gradient, mirroring the richness gradient (Fig. 5).

In this study we made no attempt to identify what the actual factors were, acting at different spatial scales upon river vegetation, which influenced the richness and community composition outcomes for spatial variation. Our results simply show that one or more such spatial factors, associated with each relevant MEM filter (as listed in Tables 1 and 2), differentially influenced variation in alpha-diversity and/or community composition of the macrophyte assemblages present at river sites in different parts of the British Isles and Zambia. A considerable amount of further work is needed to tease out what exactly is responsible for these observed results, but the observed outcomes are highly likely to be due to spatial structure (as indicated by MEMs).

5. Conclusions

Our results suggest that the sources of variation in macrophyte species richness and community composition in hard-water rivers, are, at least in part, spatially organized; implying the presence of spatial structure, termed induced spatial dependence (Peres Neto and Legendre, 2010), i.e. non-random organization across space of either species distribution or environmental processes, or both. Returning to our original hypothesis it is apparent that the variation in both richness and community composition attributable to spatial, environmental, and spatially-structured environmental factors, differs in detail rather than fundamentally, when comparing tropical and temperate calcareous rivers. We suggest that variation in both species richness and community composition for hard-water river macrophytes can (to a small but significant degree) be partially explained by the interaction of environmental and spatial processes (usually, but not always, operating primarily at broad scales) in both temperate and tropical systems. However, the detail of the driving processes (for both alpha-diversity and community composition) differed between tropical and temperate rivers.

The principal question arising from the outcomes of this study is whether the observed spatial variation is really mirroring differences in actual spatially-varying environmental drivers of calcareous river vegetation community characteristics, and if so in what way(s)? This question is beyond the scope of this study to address, and emphasises the need to include as wide a range as possible of environmental drivers potentially influencing river plant ecology (e.g., O'Hare et al., 2012), in future studies, but at least our results set out some possible directions for future work to address such issues.

Acknowledgements

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Table 1. Spatial and environmental models explaining macrophyte species richness (alpha-diversity, S: average number of species per sample) variation in the British Isles and Zambia, and for individual River Basin Units (RBUs) within the British Isles only. Order of listing of spatial and environmental variables follows their level of importance in the final model. Probability values (*p*: considered significant at $p<0.05$) are shown respectively for outcomes of analysis of environmental and spatial components, for the whole dataset (Global), and the partitioned dataset (Fractions): *p* Global Environmental (ENV); *p* Global Spatial (SP); *p* Fractions Environmental (ENV); *p* Fractions Spatial (SP). Adjusted R^2 values for partitioned variation are respectively for environmental (ENV), spatially-structured environmental (SSE) and pure spatial (SP) fractions: Adj R^2 Fractions ENV; Adj R^2 Fractions SSE; Adj R^2 Fractions SP. See Methods Section 2.1 for list of environmental variables codes.

Region	Environmental variables retained in final model	Spatial variables (MEM) in final model	*p* Global ENV	*p* Global SP	*p* Fractions ENV	*p* Fractions SP	Adj R^2 Fractions ENV	Adj R^2 Fractions SSE	Adj R^2 Fractions SP	Mean alpha-diversity (S)
British Isles	ALK, TS, MAXTW, MINTC, MTWeQ	4, 20, 100, 6, 16, 21, 8, 525, 166, 99, 23, 383, 42, 39, 101, 438, 135, 102, 320	0.0002	0.0002	0.0002	0.0002	0.021	0.114	0.088	3.1
Scotland	None	None	0.9016	0.6472	-	-	-	-	-	2.2
N England	None	81, 7, 16, 19, 65, 61, 75	0.0810	0.0344	-	0.0002	-	-	0.144	2.5
SE England	None	106	0.3656	0.0054	-	0.0002	-	-	0.059	3.6
SW England and Wales	None	1	0.1078	0.0002	-	0.0298	-	-	0.109	2.8
N Ireland	None	4, 6	0.1888	0.0004	-	0.001	-	-	0.138	3.1
S Ireland	None	None	0.4012	0.5122	-	-	-	-	-	7.1
Zambia	None	9, 7, 3, 8, 2, 1, 21	0.11	0.01	-	0.005	-	-	0.258	8.3

Table 2. Spatial and environmental models explaining macrophyte species community composition variation in the British Isles and Zambia, and for individual River Basin Units (RBUs) within the British Isles. Order of listing of spatial and environmental variables follows their level of importance in the final model. See Methods Section 2.1 for environmental variable codes, and caption to Table 1 for key to other abbreviations.

Region	Environmental variables retained in final model	Spatial variables (MEM) in final model	*p* Global ENV	*p* Global SP	*p* Fractions ENV	*p* Fractions SP	Adj R^2 Fractions ENV	Adj R^2 Fractions SSE	Adj R^2 Fractions SP
British Isles	AP, PWQ, MINTC, TS, MAXTW, ALT, ALK, PS, MTWeQ, PCQ, PCQ, AMT, EVAP.	1, 4, 2, 3, 5, 20, 10, 9, 6, 16, 7, 14, 12, 8, 11, 15, 19, 18, 24, 193, 21, 22, 17, 28, 53, 25, 54, 27, 47, 45, 23, 41, 338, 56, 65, 387, 26, 522, 51	0.005	0.005	0.005	0.005	0.011	0.039	0.054
Scotland	ALK, TS, MINTC, MTWeQ, PCQ	3, 1, 4, 28	0.028	0.005	0.018	0.103	0.028	0.069	0.013
N England	MAXTW, ALT, MINTC, TS, MTWeQ, ALK, PS, PCQ, PWQ, AP	1, 6, 4, 11, 9, 14, 3, 13, 7, 2, 15, 52	0.005	0.005	0.005	0.005	0.025	0.045	0.036
SE England	PCQ, MAXTW, PS, ALT, ALK, TS, MTDQ, AP, MINTC	8, 1, 21, 2, 7, 13, 18, 19, 30, 10, 3, 120, 6, 147, 108, 11, 24, 97, 23, 31, 9, 52, 25	0.005	0.005	0.005	0.005	0.013	0.021	0.071
SW England and Wales	PWQ, PCQ, ALT, MAXTW, AP, ALK	2, 1, 8, 6, 47, 4, 37, 89, 3, 5, 130, 7, 94, 67, 54	0.005	0.005	0.005	0.005	0.015	0.023	0.042
N Ireland	None	4, 1, 2	0.082	0.005	-	0.005	0	0	0.041
S Ireland	None	none	0.22	0.65	-	-	0	0	0.031
Zambia	AP, PS, EVAP, ALT, ALK.	1, 2, 7, 4, 34, 6, 41, 32, 24, 39	0.005	0.005	0.005	0.005	0.027	0.046	0.038

List of Figures.

Figure 1. Macrophyte species richness (S) plotted at sample sites across the British Isles

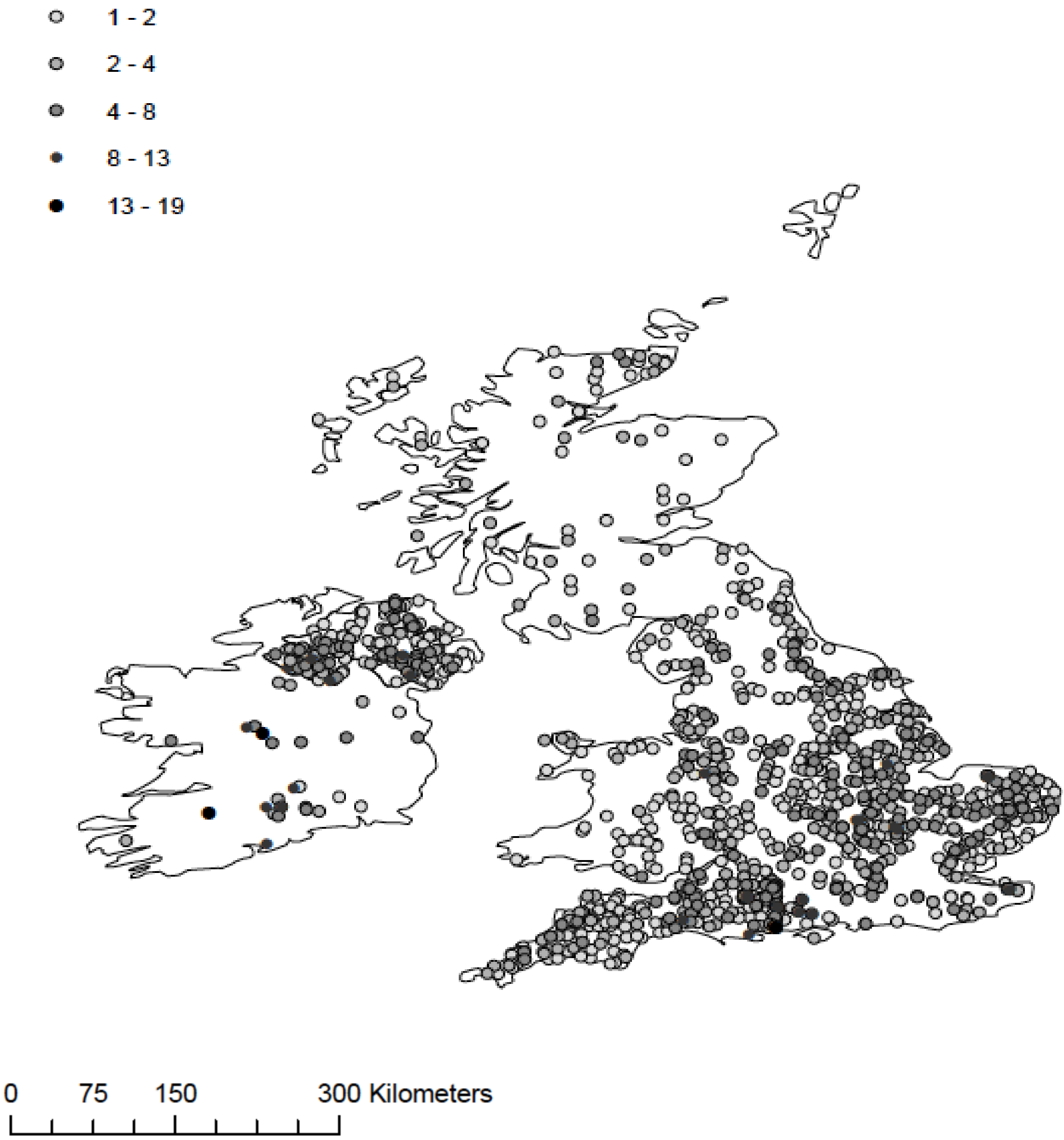
Figure 2. Selected environmental variables plotted at sample sites across the British Isles: (a) ALK: alkalinity (mg L^{-1}); TS: temperature seasonality (standard deviation * 100); (b) MAXTW: maximum temperature of warmest month (°C); MINTC: minimum temperature of coldest month (°C); (c) AP: annual precipitation (mm); PWQ: precipitation of wettest quarter (mm); (d) ALT: altitude (m above sea level).

Figure 3. Broad and intermediate scale geographic patterns (plotted as eigenvector values: range of values as shown for each map) within the British Isles associated with the fourth and twentieth MEMs: (a) MEM 4 and MEM 20; compared with finer-scale geographic pattern shown by the hundredth MEM: (b) MEM 100.

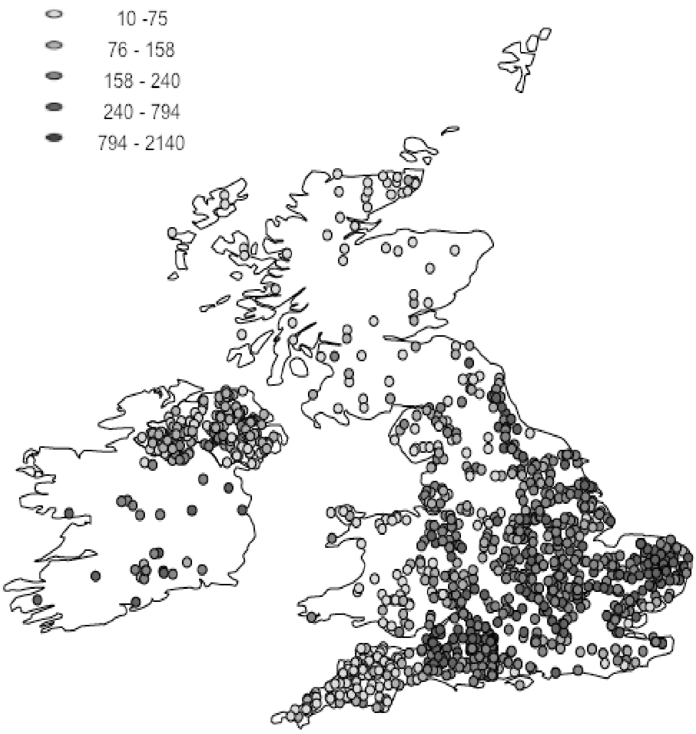
Figure 4. Macrophyte species richness (S) plotted at sample sites across Zambia.

Figure 5. Selected environmental variables plotted at sample sites across Zambia: (a) AP: annual precipitation (mm); PS: precipitation seasonality (coefficient of variation); (b) EVAP: annual evapotranspiration (mm).

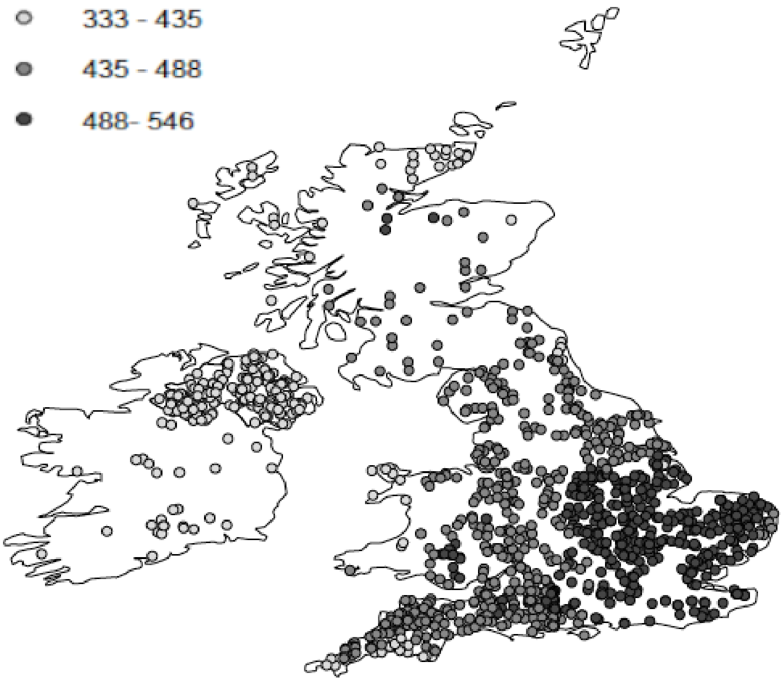
Macrophyte species richness per 100m (S)



ALK mg L^{-1}

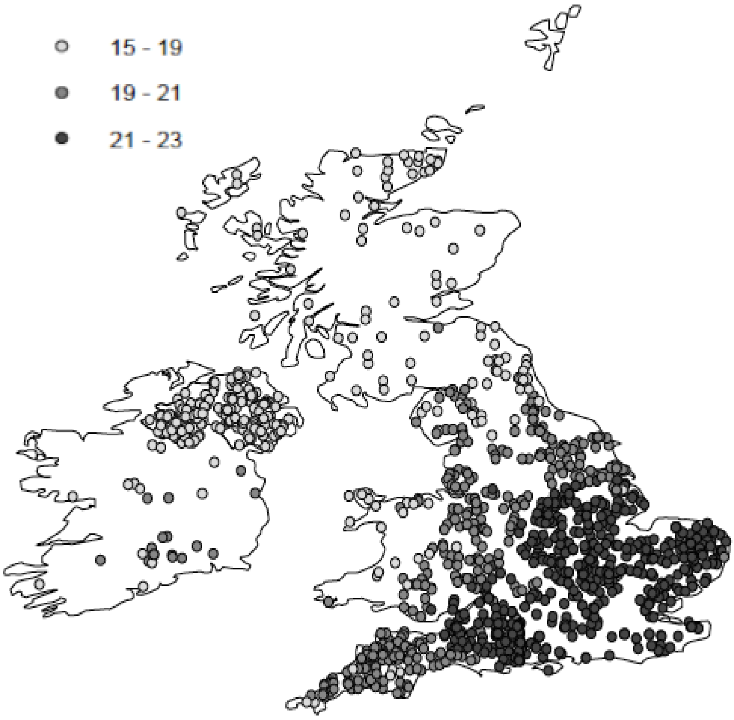


TS (SD * 100)

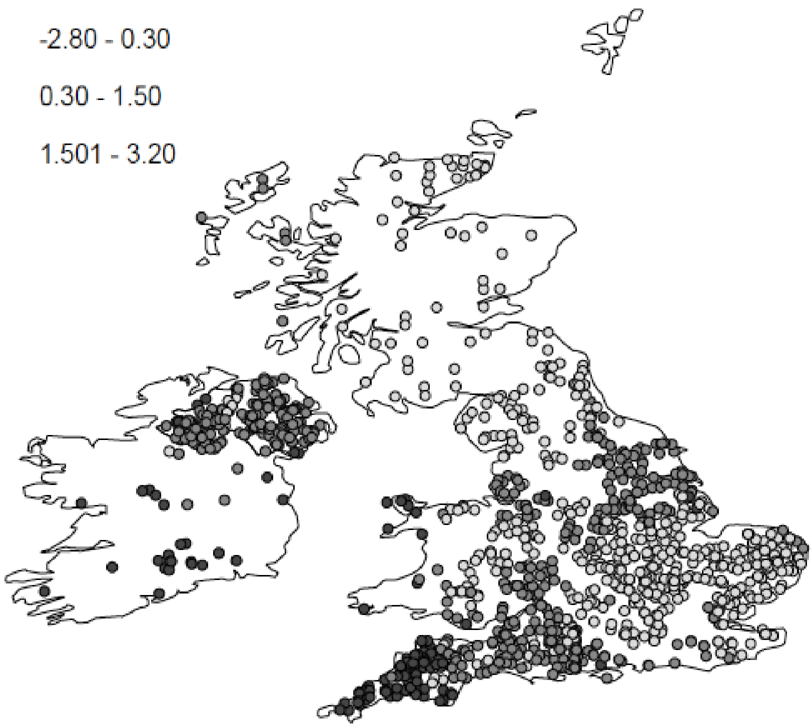


(a)

MAXTW °C

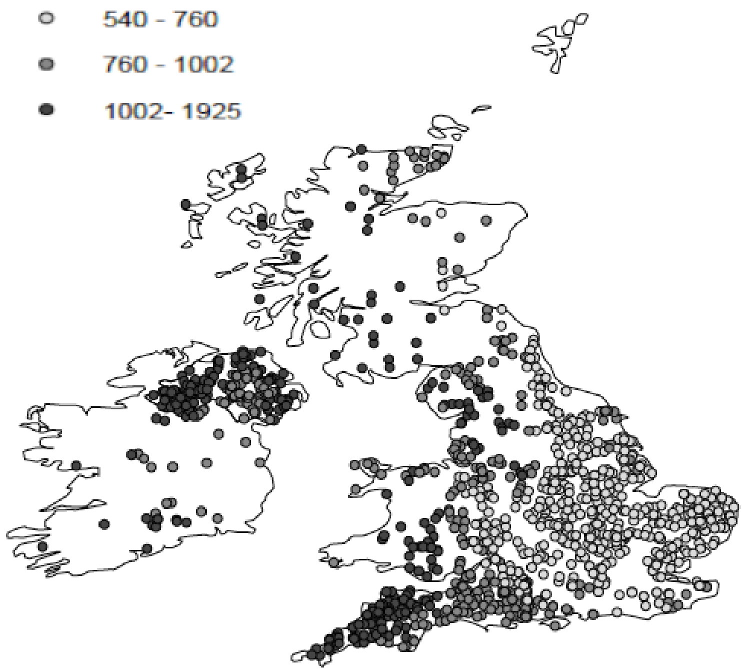


MINTC °C

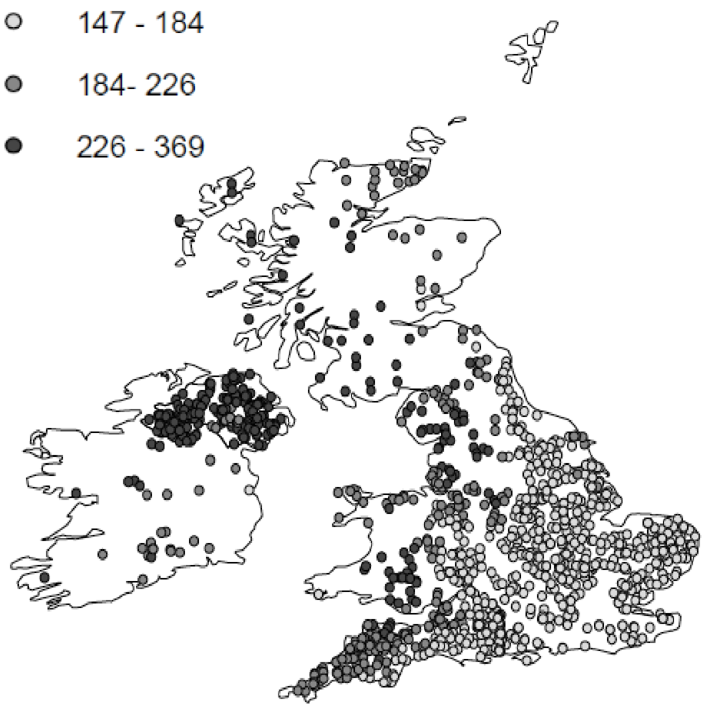


(b)

AP mm

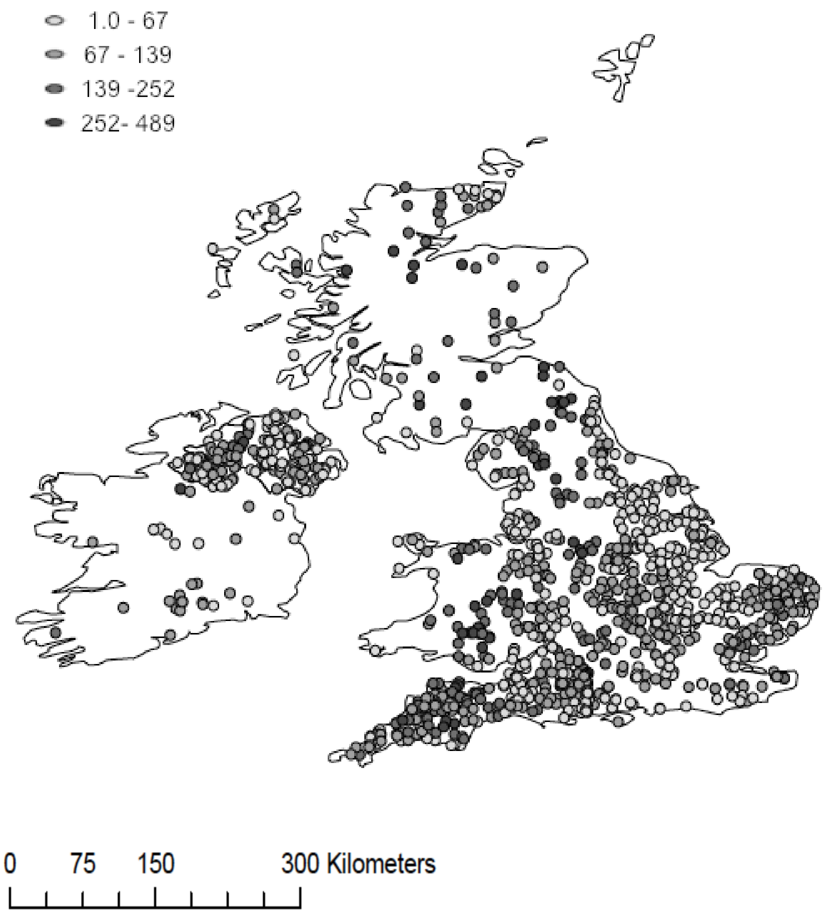


PWQ mm



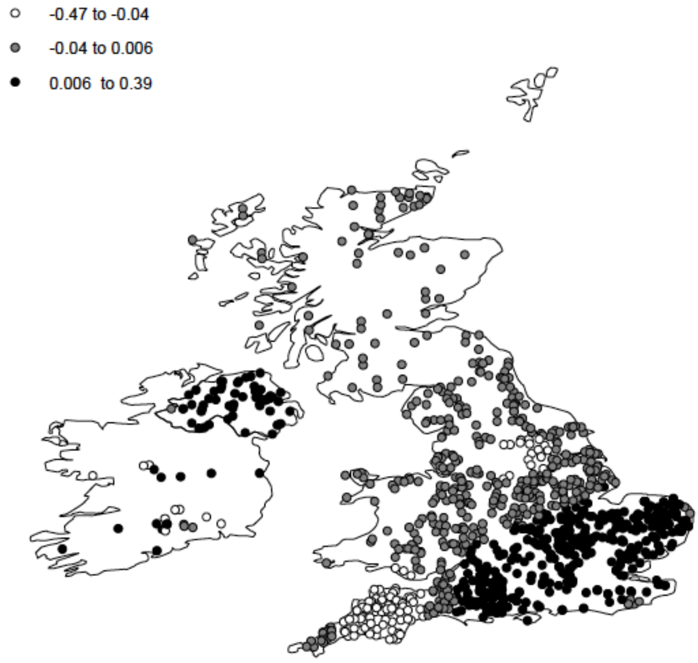
(c)

ALT m above sea level

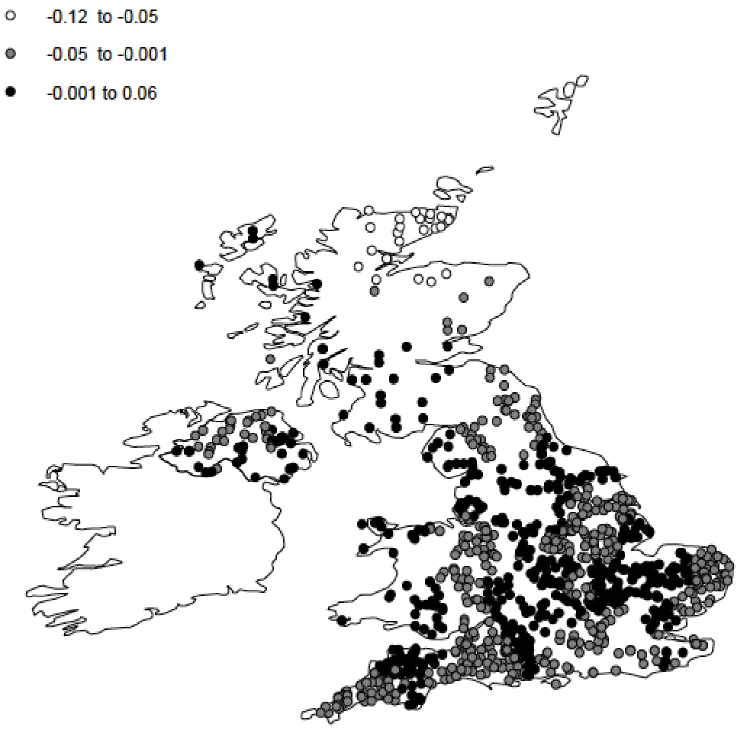


(d)

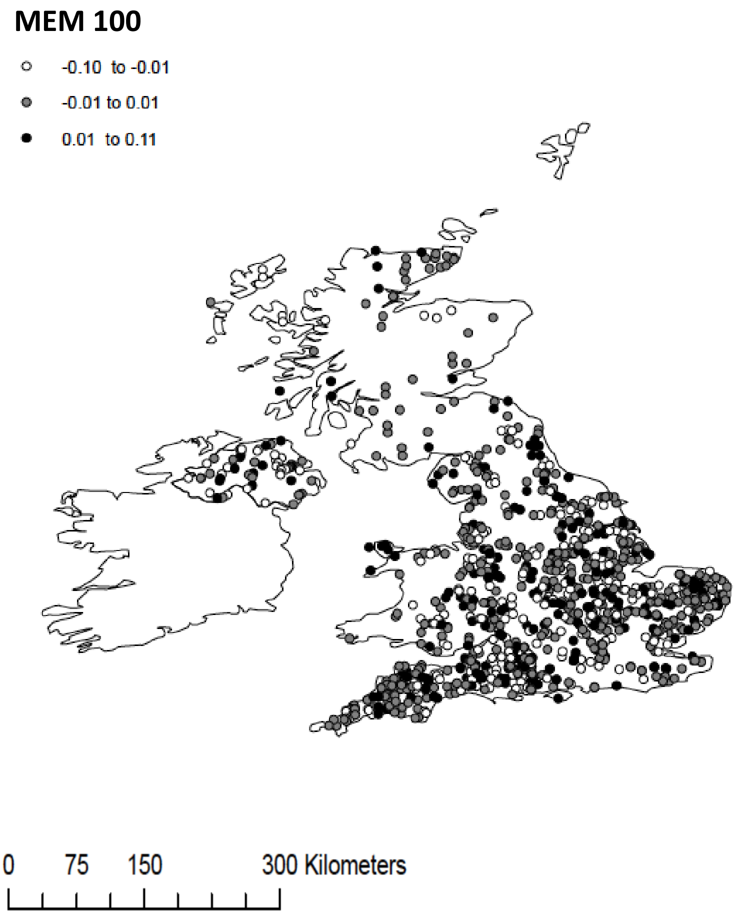
MEM 4


-0.47 to -0.04
-0.04 to 0.006
0.006 to 0.39

MEM 20

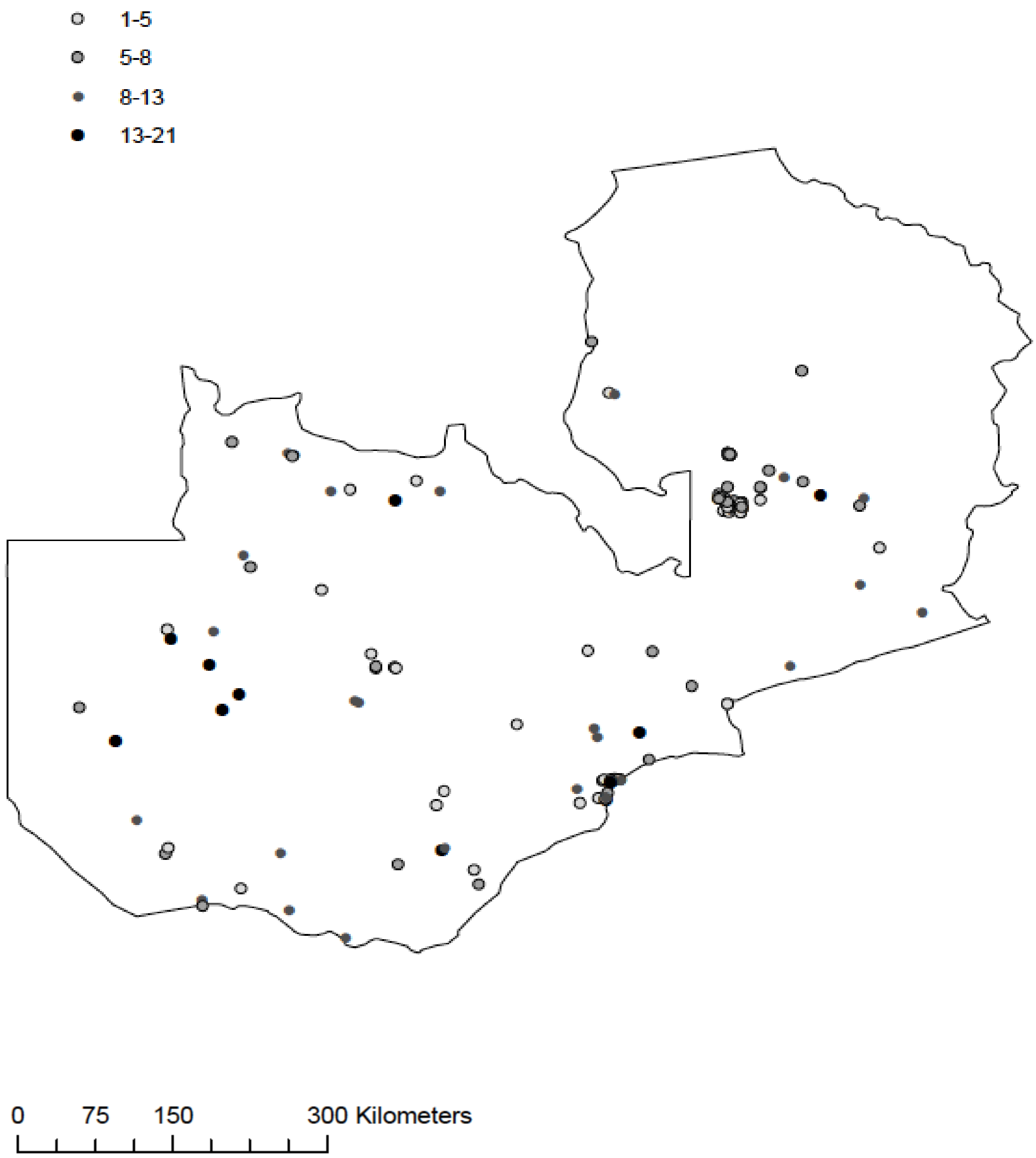

-0.12 to -0.05
-0.05 to -0.001
-0.001 to 0.06

(a)

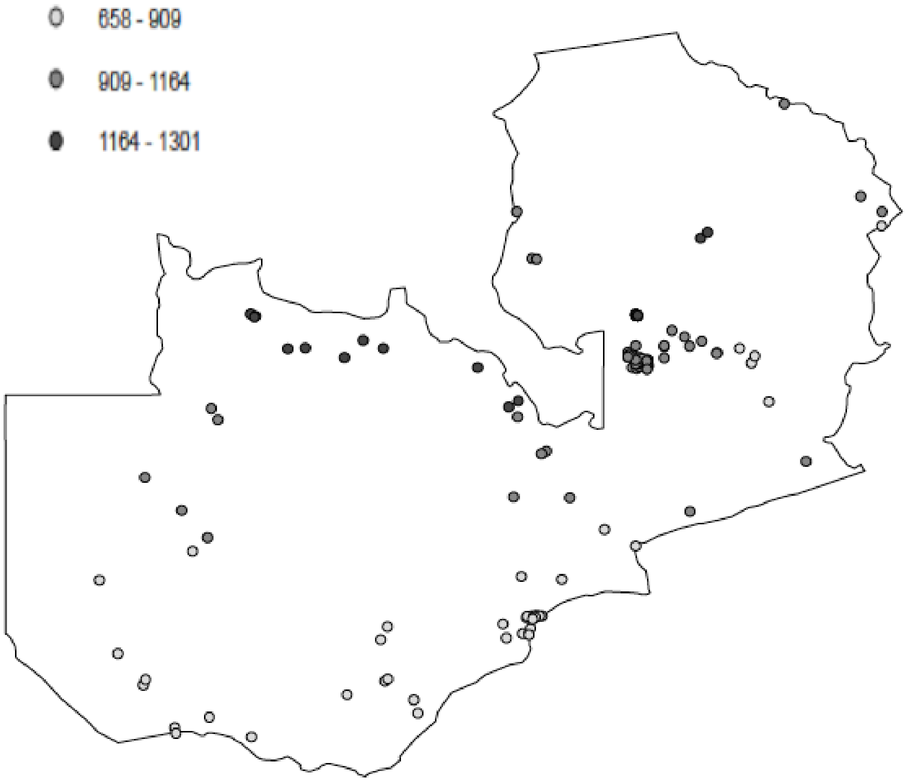


(b)

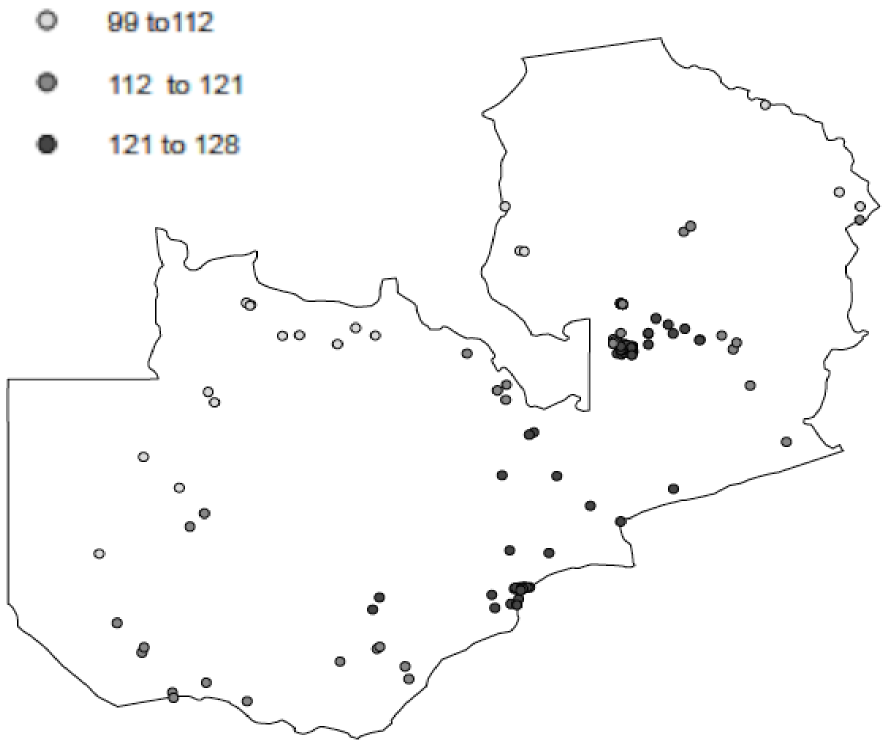
Macrophyte species richness per 100m (S)



AP mm

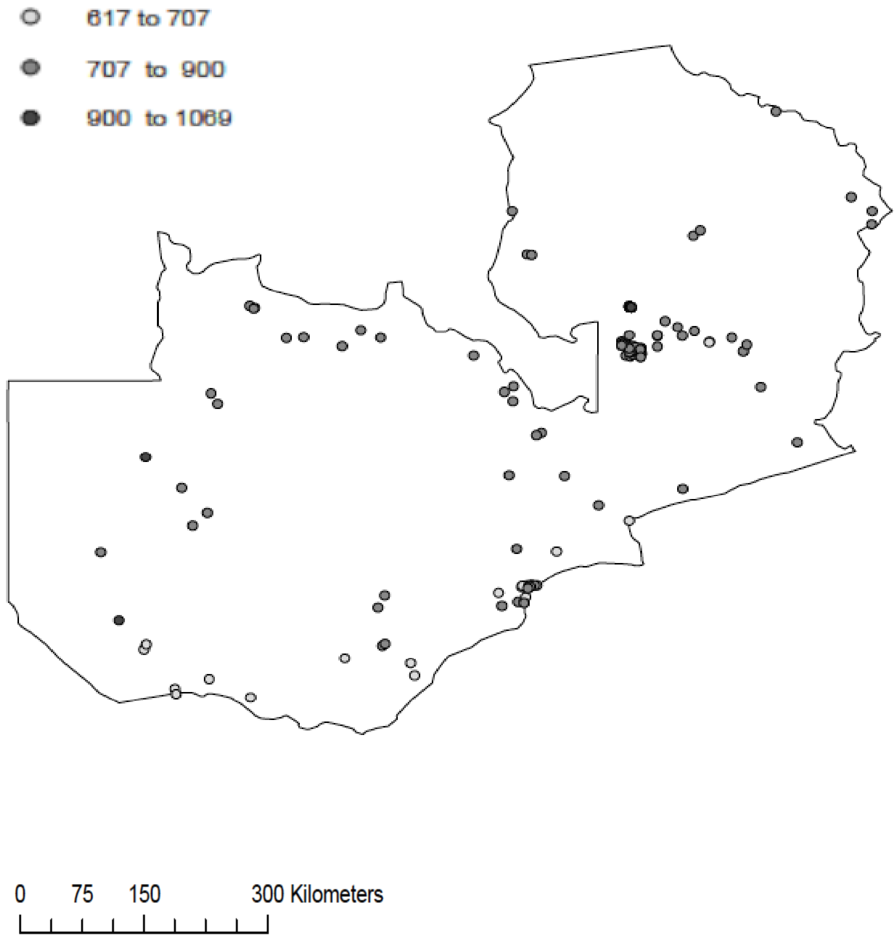


PS (coefficient of variation)



(a)

EVAP mm



(b)