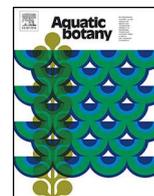




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Niche-breadth of freshwater macrophytes occurring in tropical southern African rivers predicts species global latitudinal range



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ABSTRACT

The study tested the hypothesis that measurement, using multivariate Principal Components Analysis (PCA), of the niche-breadth of river macrophyte species in southern tropical Africa, may predict their larger-scale biogeographical range. Two measures of niche-breadth were calculated for 44 riverine macrophyte species, from 20 families commonly occurring in Zambia, using an approach based on PCA ordination with 16 bio-physico-chemical input variables. These included altitude, stream order, stream flow, pH, conductivity and soluble reactive phosphate concentration (SRP). In the absence of additional chemical water quality data for Zambian rivers, invertebrate-based measures of general water quality were also used. These were benthic macroinvertebrate Average Score per Taxon (ASPT), and individual abundance of nine macroinvertebrate families with differing water quality tolerance, indicated by their Sensitivity Weightings within the Zambian Invertebrate Scoring System (ZISS). Macrophyte large-scale latitudinal range was derived from world geospatial records held by online databases, and additional records held by the authors. The two niche-breadth metrics divided the species into narrow-niche and intermediate/broad-niche categories, showing significant variation (from one or both of correlation and ANOVA test outcomes) in altitude, stream flow, conductivity, SRP, pH and ASPT, but not stream order. Macrophyte alpha-diversity (as a measure of number of individual niches co-existing per habitat) showed no significant relationship with individual species niche-breadth. Narrow-niche species included a higher proportion of Afrotropical endemics than did species with broader niche size. There were significant predictive relationships between macrophyte niche-breadth and latitudinal range of the target species at global and Afrotropical scales, but not for the Neotropics.

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1. Introduction

Species niche is conceived as a multidimensional space encompassing the total range of biotic and abiotic variables (both natural and anthropogenic-related), plus species-interactions, together affecting the survival of, and unique to, individual species. The concept was first described by Hutchinson (1957), who brought together earlier attempts at formulating the idea by Grinnell (1917) and Elton (1927, 1933). The concept of species niche continues to evolve (e.g., Collwell and Rangel, 2009), but the approach has recently been successfully applied as a basis for prediction of species geographical range (Soberón, 2007; Soberón and Nakamura, 2009; Slatyer et al., 2013).

The niche-breadth of a species is a shorthand measure of the size of the real multidimensional hypervolume forming the total niche occupied by the species. It can be quantified in terms of the suite of essential resources required by the species, such as nutrients and light in the case of plants. Other variables which can help quantify species niche are environmental factors, such as temperature regime; and biotic factors, notably competition and predation from other species (though these are more important as predictors of realised, or “actual”, niche rather than fundamental, or “theoretical” niche), which collectively impinge upon the survival, growth and reproductive success of the species (Feinsinger et al., 1981; Rørslett, 1987a,b). Axes of the niche space of a species may be measured: (1) directly, in terms of required resources and influential abiotic factors, both natural and anthropogenic; or (2) indirectly, by measuring values for surrogate factors associated with the species' occurrence (in the case of aquatic plants, for example, the occurrence and abundance of associated invertebrate bioindicator organisms indicating various water quality conditions).

For freshwater macrophytes (defined as “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” of freshwater systems: Chambers et al., 2008), data for variables such as those mentioned above can collectively provide an indication of the range of prevailing bio-physico-chemical conditions, and hence niche size, in habitats successfully occupied by the plant species. Species which occupy lengthy ranges along niche-axes associated with such measures, and with correspondingly wide niche-breadth, are usually considered to be generalist strategists (Grime 1979; Murphy et al., 1990), with broad geographical range (Slatyer et al., 2013; Cirtwill et al., 2015). The converse is likely to hold for species which exhibit only short niche-axis lengths, with specialised survival strategies, and only limited geographical range.

A wide spectrum of approaches has been used to measure niche-breadth. Some can be applied to all organisms, whilst others (e.g., food-web based studies) are appropriate for animals, but much less so, or not at all, for plants. Some studies have used individual niche-axis traits to quantify species niche-breadth (e.g., Luna and Moreno, 2010; Boulangeat et al., 2012). Other approaches aim to determine species niche-breadth in terms of the proportion of populations found in, or using, the individual states of given resources (e.g., Carrillo-Angeles et al. (2016), who utilised a resource-state niche-breadth index developed by Hurlbert (1978), in a study of the cactus genus *Astrophytum*). At the other end of the spectrum is the approach of Cirtwill et al. (2015) who used a biotic measure of niche-breadth based on average generality, vulnerability and links per species across a set of 196 empirical food webs, in their study of relationships between latitude and biotic niche-breadth in different ecosystems. In a recent meta-data analysis, Slatyer et al. (2013) identified a number of niche-breadth measures for plant and animal species, 15 of which they categorised as “habitat” measures (e.g., number of different habitat-types occupied); six as “diet” measures (e.g., number of different food-types used); and five as

“tolerance measures” (e.g., elevational range). These authors also suggested that some of these measures are good predictors of geographical range-size. They concluded that there is general evidence of a “positive relationship between niche-breadth and range-size that is maintained across niche-breadth measurements, taxonomic groups and spatial scales”.

Recently, studies using multivariate and modelling procedures to provide a summary of overall ecological niche-breadth across the *n*-dimensional space representing an organism's niche have been undertaken, in both terrestrial and aquatic systems (McNyset, 2005; Domínguez-Domínguez et al., 2006; Novak et al., 2010a,b; Janžekovič and Novak, 2012). The multivariate ordination procedure Principal Components Analysis (PCA) has been widely applied for analysis of aquatic environmental data (e.g., Blanck et al., 2007; Catalan et al., 2009), particularly as a means of identifying patterns in sets of sampling sites in relation to environmental gradients (Lepš and Šmilauer, 2003). The variables used to construct PCA ordinations for plant community ecology purposes are usually those which help define the multidimensional niche of a species (particularly in the Eltonian sense: Soberón, 2007). Hence, it follows that PCA can provide a powerful tool (Novak et al., 2010a,b; Janžekovič and Novak, 2012) for the determination of species niche-breadth, especially for plants, which make direct use of Eltonian resources: an obvious example being uptake of nutrients from hydrosols and/or water by macrophytes.

In this study we aimed to: (i) derive niche-breadth for a set of common Zambian river macrophyte species; (ii) characterise groups of species of differing niche-breadth in terms of biological and environmental parameters measured at sites supporting the target species; (iii) determine the total latitudinal range of the target species at three global/regional scales; and (iv) use the outcomes of the exercise to examine the hypothesis that niche-breadth of river macrophyte species, occurring within a closely-defined geographical area in tropical Africa, may predict the larger-scale biogeographical range of these species.

2. Materials and methods

2.1. Field sampling and laboratory analyses

The starting point was a dataset produced by the first-ever national-scale survey of Zambian river plant occurrence, during 2006–2013, comprising 271 samples from sites throughout Zambia in rivers and associated high-connectivity riverine floodplain waterbodies (permanent riverine lagoons; backwaters/oxbows; and seasonal standing waterbodies such as dambos). As well as macrophytes, this survey recorded benthic macroinvertebrates and water physico-chemistry at each site. Survey methods, site locations and results are reported in detail by Kennedy et al. (2015); and supplementary online files associated with that paper; Kennedy et al. (2016); Lowe et al. (2013b); and Tapia Grimaldo et al. (2016), with relevant methods summarised briefly below. From the dataset, 176 samples (mostly from rivers: 90% of samples; but with a small number of samples from associated static-water sites in riverine floodplains, comprising lagoons: 7%; dambos: 2%; and backwaters/oxbows: 1%) were selected for use in the niche-breadth analysis exercise. These samples comprised those, within the full dataset, which supported at least one of 44 common macrophyte species from 20 families (listed in Table 1, which also provides authorities for species names mentioned in text), each occurring in at least 7 samples within the dataset (considered to be the minimum sample size per species needed statistically to provide meaningful results). The species (or, in a few cases, infraspecies, e.g. *Nymphaea nouchali* var. *caerulea*) included nine submerged, six floating, and 29 emergent plant species, following the macrophyte

Table 1

Species in each of three niche-breadth categories, as measured by the NB/100 metric. Family given in brackets.

Niche-breadth category (NB/100)	Intermediate (6.000–12.000)	Broad (>12.000)
Narrow (<6.000)		
<i>Aeschynomene fluitans</i> Peter (Fabaceae)	<i>Azolla filiculoides</i> Lam. (Azollaceae)	<i>Alternanthera sessilis</i> (L.) R. Br. ex DC. (Amaranthaceae)
^a <i>Aponogeton desertorum</i> Zeyh. ex Spreng (Aponogetonaceae)	<i>Ceratophyllum demersum</i> L. (Ceratophyllaceae)	<i>Commelina diffusa</i> Burm.f. (Commelinaceae)
<i>Fuirena umbellata</i> Rottb. (Cyperaceae)	<i>Cyperus alopecuroides</i> Rottb. (Cyperaceae)	<i>Eleocharis dulcis</i> (Burm.f.) Trin. ex Hensch (Cyperaceae)
^a <i>Hydrostachys polymorpha</i> Klotzsch (Hydrostachyaceae)	<i>Cyperus difformis</i> L. (Cyperaceae)	^a <i>Floscopa glomerata</i> (Willd. ex Schult. and Schult.f.) Hassk. (Commelinaceae)
^a <i>Ledermanniella tenax</i> (C.H. Wright) C. Cusset (Podostomaceae)	<i>Cyperus digitatus</i> Roxb. (Cyperaceae)	<i>Ludwigia adscendens</i> (L.) H. Hara (Onagraceae)
^a <i>Ottelia ulvifolia</i> (Planch.) Walp. (Hydrocharitaceae)	<i>Cyperus involucratu</i> Rottb. (Cyperaceae) (= <i>Cyperus imbricatus</i> Retz.)	^a <i>Nymphaea nouchali</i> var. <i>caerulea</i> (Savigny) Verdc. (Nymphaeaceae)
^a <i>Ottelia verdickii</i> Gürke ex De Wild. (Hydrocharitaceae)	<i>Cyperus longus</i> L. (= <i>Cyperus rotundus</i> L.) (Cyperaceae)	<i>Panicum repens</i> L. (Poaceae)
<i>Pennisetum glaucoclaudum</i> Stapf and C.E. Hubb. ex Stent and J.M. Rattray (= <i>Pennisetum macrourum</i> Trin.) (Poaceae)	<i>Eichhornia crassipes</i> (Mart.) Solms (Pontederiaceae)	^a <i>Panicum subalbidum</i> Kunth (Poaceae)
<i>Persicaria meisneriana</i> (Cham. and Schldtl.) M. Gómez (Polygonaceae)	^a <i>Lagarosiphon ilicifolius</i> Oberm. (Hydrocharitaceae)	<i>Persicaria attenuata</i> (R. Br.) Soják (Polygonaceae)
<i>Thelypteris confluens</i> (Thunb.) C.V. Morton (Thelypteridaceae)	<i>Leersia hexandra</i> Sw. (Poaceae)	^a <i>Phragmites mauritanus</i> Kunth. (Poaceae)
^a <i>Thelypteris interrupta</i> (Willd.) K. Iwats. (= <i>Cyclosorus interruptus</i> (Willd.) H. Itô) (Thelypteridaceae)	^a <i>Ludwigia senegalensis</i> (DC.) Troch. (Onagraceae)	
<i>Tristicha trifaria</i> (Bory ex Willd.) Spreng. (Podostomaceae)	<i>Najas horrida</i> A.Braun ex Magnus (Najadaceae)	
<i>Vallisneria spiralis</i> L. (Hydrocharitaceae)	<i>Nymphaea lotus</i> L. (Nymphaeaceae)	
	^a <i>Nymphoides indica</i> subsp. <i>occidentalis</i> (L.) Kuntze, A. Raynal (Menyanthaceae)	
	<i>Panicum parvifolium</i> Lam. (Poaceae)	
	<i>Persicaria decipiens</i> (R.Br.) K.L. Wilson (Polygonaceae)	
	^a <i>Persicaria senegalensis</i> (Meisn.) Soják (Polygonaceae)	
	<i>Potamogeton schweinfurthii</i> A. Benn. (Potamogetonaceae)	
	<i>Pycneus mundii</i> Nees (Cyperaceae)	
	<i>Salvinia molesta</i> D.S. Mitch. (Salviniaceae)	
	<i>Typha domingensis</i> Pers. (Typhaceae)	

^a Afrotropical endemic species.

life-form definitions of Chambers et al. (2008). These numbers roughly reflect the overall proportions (22% submerged, 8% floating, 70% emergent species) of these macrophyte life-forms found to occur in the flora of Zambian river systems by Kennedy et al. (2015).

Macrophyte surveys (detailed in full by Kennedy et al., 2015) at each site followed the guidelines of the international standard EN 14184 (European Committee for Standardization, 2003), including emergent vegetation due to its importance in Zambian rivers (Dallas et al., 2010). Samples were retained as herbarium-sheet specimens for subsequent confirmation of identification, primarily utilising Cook (1996, 2004) and Kennedy and Murphy (2012). Taxonomic literature (primarily Flora Zambesiaca: Exell and Wild, 1960 et seq.) was also used to assist identification, as were local sources of information for the region (e.g., Jacobsen and Jacobsen, 1973; Chabwela and Siwale, 1986; Gerber et al., 2004). Nomenclature followed Flora Zambesiaca (Exell and Wild, 1960 et seq.), cross-checked against The Plant List (Royal Botanic Gardens, Kew and Missouri Botanical Garden (2013); www.theplantlist.org). For the final macrophytes dataset, species alpha-diversity (S: number of plant species present per sample) was recorded as the count of species occurring in each sample.

Environmental data collected at each sampling location during the field surveys, and used in this study, included geospatial coordinates and altitude, using a Garmin Etrex hand-held GPS. A subjective assessment of flow class (flow categories and approximate corresponding flow velocity intervals follow Lang and Murphy, 2012) was made using a four-point scale: 0 = static: no visible flow (0 m s⁻¹); 1 = slow flow or “pool”

(approximately < 0.2 m s⁻¹); 2 = moderate flow or “glide”: approximately 0.2–0.4 m s⁻¹; 3 = fast flow: “riffle” or white-water showing (approximately > 0.4 m s⁻¹). In addition pH and conductivity (μS cm⁻¹) were measured in situ, using a multi-function Schott Handylab 264 meter. Stream order was taken from a GIS-generated regional stream network derived from an ArcGIS digital elevation model (for details see Lowe et al., 2013a). Water samples were collected, and stored in 10 mL glass sample vials for subsequent laboratory determination of soluble reactive phosphate (SRP) following standard methods (MAFF, 1986; APHA, 1998). Full details of phosphate analyses are provided in Kennedy et al. (2016).

Benthic macroinvertebrates were mostly sampled using the ZISS (Zambian Invertebrate Scoring System) kick-net sampling protocol (Lowe et al., 2013b) to collect macroinvertebrates from up to three biotopes, as present at individual sites: gravel, sand and mud (GSM); aquatic vegetation (V); and stones and rock (S). Data from all biotopes present per sample were pooled and identified to family level, as required by the ZISS protocol (for a few organisms (e.g. Turbellaria) the protocol requires identification only to supra-family level). Abundance was scored on a five-point scale: 1 = 1 individual present in the sample; 2 = 2–10; 3 = 11–100; 4 = 101–1000; 5 = >1000 animals present in the sample. At some sites where kick-net sampling was considered to be too hazardous (owing to deep or fast-flowing water, or an unacceptably high risk from dangerous animals, notably crocodile and hippopotamus) dredge-net sampling was undertaken, and data from these samples were recalibrated (Moore and Murphy, 2015) to permit comparative use with data from kick-sampled sites. Both kick- and dredge-nets had 1 mm mesh size.

2.2. Data synthesis and statistical methods

The macroinvertebrate data were used in the macrophyte niche-analysis exercise as follows. Nine macroinvertebrate families, commonly found in Zambian rivers and associated floodplain water bodies supporting the target aquatic plant species, were selected as indicators of water quality. Abundance values for each family per sample were then used as PCA input variables. The families were chosen on the grounds of reasonably wide occurrence in the dataset, but with differing ZISS Sensitivity Weighting Scores (Lowe et al., 2013b), values of which indicate tolerance of poor quality water (for low-scoring taxa), to occurrence only in clean, unpolluted water conditions (high-scoring taxa). The nine were Atyidae (Order: Decapoda; ZISS Sensitivity Weighting Score: 8), Dytiscidae (Coleoptera; 5), Simuliidae (Diptera; 5), Gerridae (Hemiptera; 5), Coenagrionidae (Odonata; 4), Libellulidae (Odonata; 4), Corixidae (Hemiptera; 3), Chironomidae (Diptera; 2) and Culicidae (Diptera; 1). The sum of Sensitivity Weighting Scores for all taxa present in a sample (not solely the nine selected for individual use) was used to calculate the total ZISS score, from which Average Score Per Taxon (ASPT: Walley and Hawkes, 1997) was calculated, as total ZISS score divided by number of ZISS taxa present. ASPT was then used as a tenth biological metric of overall bioassessed water quality as a PCA input. Where sites were sampled for invertebrates on more than one occasion during a single Southern Hemisphere summer season (e.g., 2012–2013, and for a few sites in other years too), average values for invertebrate metrics were calculated from all available data for the season concerned.

Principal Components Analysis (PCA) using CANOCO (ter Braak and Šmilauer, 1998) constructed an ordination of the 176 samples, with input variables comprising six physico-chemical variables (altitude, stream flow class, stream order, pH, conductivity and SRP) plus the 10 invertebrate measures described above. PCA procedures require input datasets to follow a normal distribution, so Ryan-Joiner tests were used to assess the normality of each input variable. The outcome required natural log (ln) transformation to be applied to SRP and conductivity, but not to the remaining variables.

Calculation of niche-breadth for each of the 44 target macrophyte species followed the approach laid out by Janžekovič and Novak (2012). This first required the occurrence of each species in samples to be plotted on the first two principal axes (PCA 1, PCA 2) of the sample ordination. Maximum and minimum axis-scores given in the program output for each species were then used to find its range on each axis. Niche-breadth per species (NB: the units of which are “axis-score²”) was calculated as the product of the two range values for axis-scores on PCA 1 and PCA 2. For ease of subsequent interpretation NB scores were divided by 100 to give the final metric (termed NB/100).

A criticism of niche-breadth measurement is that commonness may influence the values recorded for the metric, because widespread species can be expected to occur more commonly in sample sets than species having narrower distributions, and are hence more likely to be encountered across a wider range of their niche, thereby potentially increasing the calculated size of their niche-breadth (Brown, 1984; Hanski, 1993). Following the recommendations of these authors, we corrected for this by calculating an additional measure of niche-breadth which takes account of the number of samples (n) supporting each species (n range: 7–130). NB was divided by n to produce this second metric for niche-breadth, termed NB/ n .

Correlation analysis was used to assess the significance of relationships between the two niche-breadth metrics and mean values of seven bio-physico-chemical variables (SRP, altitude, stream order, flow, pH, conductivity and ASPT), recorded for the samples in which each species occurred, for the dataset of 44 species. Tests were run using untransformed or natural log transformed data, as

appropriate to the normality requirements of the datasets used. In addition analysis of variance (ANOVA: with post hoc comparison of means by Tukey’s mean-separation testing, for significant outcomes only), or Kruskal-Wallis tests (for datasets which were not normal, and could not be normalised by transformation), were used to test for significant differences for each variable, between sets of species of differing niche-breadth, identified using the NB/100 measure. ANOVA was also used to test for differences in numbers of species records at Zambia and world scales (see below), for sets of species assigned to each niche-breadth category.

2.3. Total latitudinal range of species

The total latitudinal range (TLR) of each macrophyte target species was calculated at three global scales:

- (1) the world as a whole: maximum possible latitudinal range for riverine plant species being approximately from Tierra del Fuego (55°S) to northern Canada, Alaska, Scandinavia and northern Siberia (approximately 75°N), giving a total potential world latitudinal range of 130°. A few freshwater macrophyte species are additionally recorded from the Antarctic bioregion, mostly from sub-Antarctic islands generally lacking river systems, but with very few exceptions (one such being *Cyperus longus*, which has been introduced to the sub-Antarctic island of Tristan da Cunha) these species do not occur in Zambia, and so the Antarctic bioregion is not further considered here (Chambers et al., 2008);
- (2) the Afrotropical bioregion, ranging from Cape Agulhas (35°S) in South Africa to northern Mauritania, Mali, Niger, Chad and Sudan, approximately following the Tropic of Cancer (c.23°N), giving a maximum possible latitudinal range in this bioregion of 58°; and
- (3) the Neotropical bioregion, ranging from Tierra del Fuego (55°S) to the northern part of Sinaloa State in Mexico at approximately 26°N, giving a maximum possible latitudinal range for this bioregion of 81°.

TLR for each species was calculated as its recorded latitudinal range, for native/naturalised geospatial records only (see below), in the Southern Hemisphere, plus any additional recorded latitudinal range in the Northern Hemisphere. This exercise required identification, for each target species, of its geospatial record closest to the Equator, and that furthest from the Equator, in the Southern and (where applicable) Northern Hemispheres. All the target macrophyte species occupied a latitudinal band around the planet south of the Equator, and many also occupied a second latitudinal band north of the Equator. In total 30 species (identified in Table S1 of Appendix A, attached to the online version of this paper) had a latitudinal range which includes native or naturalised records within 1° North or South of the Equator. For example, *Eichhornia crassipes* has a native record from Lago San Pablo, Ecuador at 0.217°N: (www.gbif.org/species/2765940). For these species a single TLR range band was considered to exist, from northernmost to southernmost limit of the species’ distribution on the planet’s surface. For the others TLR was calculated as the sum of the latitudinal width (°) of the Southern and Northern Hemisphere bands (including records located > 1° South or North of the Equator) for occurrence of each species. Geospatial records for each species were acquired from a wide range of sources, including global-scale online databases such as the Global Biodiversity Information Facility (GBIF: www.gbif.org/species), the CJB African Plants Database (www.ville-ge.ch/musinfo/bd/cjb/africa/index.php?langue=an), and eMonocot (www.e-monocot.org). Although these databases all have known weaknesses in terms of coverage, their datasets proved to be sub-

stantial for many of the target species. For example the number of world-scale records with full geocoordinates held by GBIF for the 44 target species ranged (as of November 2015) from a minimum of 23 (for *Ledermannia tenax*) to a maximum of 39204 (for *Ceratophyllum demersum*). As noted above, however, of interest for the purposes of this study were only the northern and southern extreme records, within the two hemispheres (as appropriate), regardless of the number of geographically-intermediate points present within an individual species dataset. The TLR information from global databases was supplemented by data held by the authors for a few plants which showed limited latitudinal ranges in Africa from global database records. For example, our own data for Zambian and Egyptian river macrophyte records (Springuel and Murphy, 1990, 1991; Ali et al., 1995; Kennedy et al., 2015) extended the latitudinal range of records held by GBIF and other database sources, for a number of species (e.g., *Najas horrida*).

A question which had to be addressed in compiling TLR data was the issue of introduced species and other non-native records, and whether these should be included in the analysis. It was decided to use only records from within the native and naturalised range of the target species to calculate TLR, on the grounds that such records best represent the long-standing established range of the species (though, obviously, still influenced by human interference, in the case of naturalized species). In practice it was usually relatively straightforward to determine records (by reference to the literature) towards the extreme northerly and southerly ranges (within either or both hemispheres, as appropriate) which were clearly non-native or non-naturalised occurrences of each species. Extreme examples included:

- (i) *Vallisneria spiralis*, which has recently been introduced to geothermally-warmed waterbodies in Arctic and sub-Arctic Iceland (Wasowicz et al., 2014);
- (ii) the invasive species *Salvinia molesta*, the taxonomy of which remains debatable (Moran and Smith, 1999), but which is now generally accepted as having only a small native latitudinal range (approx. 9°), entirely located in southern Brazil (Forno and Harley, 1979; Forno, 1983), compared to a world TLR for all records (including introduced and invasive occurrences) calculated by us to be in excess of 87°; and
- (iii) extreme (usually northerly Northern Hemisphere) records for a number of the target species, mainly held by GBIF, which proved on closer inspection to be inappropriate for use in this study. As an example, records for *Nymphaea lotus* were found in the GBIF database for plants growing in Botanical Gardens in Stockholm and Missouri, as well as a palaeobotanical record for this species, mapped for Poland.

No such inappropriate records of occurrences of the target species were utilised in calculating TLR values for world (TLR_{world}), Afrotropical (TLR_{afr}) or Neotropical (TLR_{neo}) regions.

Linear regression and correlation procedures were used to determine relationships, and their significance, between niche-breadth measures (NB/100 and NB/n), and TLR_{world} (all 44 species); TLR_{afr} values (40 species native or naturalised in Africa); and TLR_{neo} for the 19 species which occurred both in Zambia and as native/naturalised species in the Neotropical region. Analyses were undertaken with untransformed and ln-transformed data, as appropriate, in order to find optimal outcomes for predicting species large-scale latitudinal range from their niche-breadth as measured in Zambian river systems.

ANOVA, regression, and correlation analyses were performed throughout the study using MINITAB version 15.1.0.

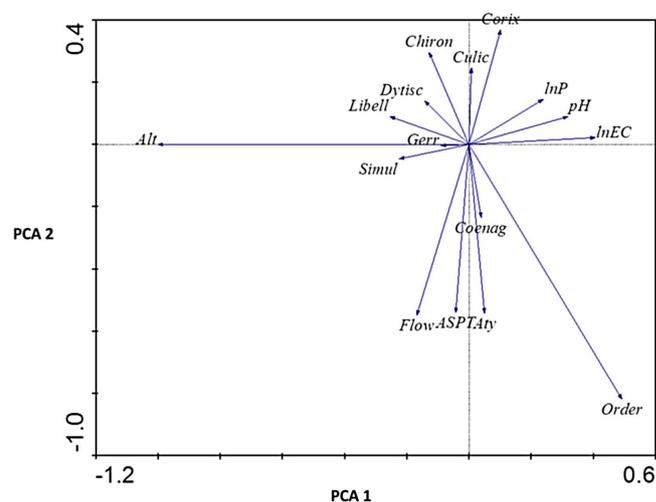


Fig. 1. PCA ordination diagram produced by analysis of a matrix of 176 samples x 16 environmental variables from Zambian rivers and high-connectivity riverine floodplain water bodies (sample locations are detailed in full in a Supplementary file associated with the on-line version of Kennedy et al. (2015)) showing vectors for 16 input variables. Eigenvalues: Axis 1 (horizontal: PCA 1): 0.900; Axis 2 (vertical: PCA 2): 0.080. Benthic invertebrate families: Atyidae (*Aty*), Chironomidae (*Chiron*), Coenagrionidae (*Coenag*), Corixidae (*Corix*), Culicidae (*Culic*), Dytiscidae (*Dytisc*), Gerridae (*Gerr*), Libellulidae (*Libell*), Simuliidae (*Simul*). ASPT: benthic invertebrate Average Score per Taxon; Alt: altitude; Order: stream order; Flow: stream flow class; InP: log normal SRP; InEC: log normal conductivity.

3. Results

3.1. Niche-breadth of Zambian freshwater macrophytes

PCA ordination (plotted on the first two ordination axes, which explained >90% of total variability) of bio-physico-chemical variables showed that stream order and altitude were major variables influencing the ordination outcome (Fig. 1). However flow, invertebrate ASPT, and Atyidae abundance (ZISS score 8: indicating high water quality) were also good predictors (as shown by length of vector arrows: Lepš and Šmilauer (2003)) of sample position within the ordination plot, together suggesting that clean, fast flowing stream samples tended to occupy the middle to lower part of the ordination plot. In contrast, poorer water conditions, indicated by low ASPT and high abundance of invertebrates tolerant of low water quality, notably Chironomidae (ZISS score 2), tend to occur towards the upper part of the plot, i.e. for samples with high positive PCA2 axis scores. Higher nutrient status, pH and conductivity characterised samples that occurred towards the right-hand side of the plot, with high positive PCA1 scores.

For ease of interpretation, species were arbitrarily divided into three groups each covering approximately one third of the total range of calculated NB/100 values. These were termed narrow-, intermediate- and broad-niche categories: see Table 1 and Supplementary information in Table S1 in Appendix A, attached to the online version of this paper, which lists for each species values of calculated niche-breadth metrics, TLR_{world}, number of records at world scale, and number of records for Zambia found by Kennedy et al. (2015). Using the NB/n metric produced some minor differences in the categorisation, though values for this metric also blurred the distinction between the intermediate and broad categories derived from NB/100 values.

Six of the species (46%) in the narrow-niche category are Afrotropical endemics, but only four intermediate-niche species (19%) have this status, although, in addition, *N. horrida* is confined to the African continent (with additional records, outwith the Afrotropical region, from Algeria and Egypt). In the broad-niche category four species (40%) are almost certainly Afrotropical endemics.

Table 2
Results of correlation analysis to assess the significance of relationships between NB/100 and NB/n niche-breadth measures for $n=44$ species and mean values of seven bio-physico-chemical variables ($\text{PO}_4\text{-P}$, altitude, stream order, flow, pH, conductivity (EC) and ASPT), recorded at sites supporting each species. Tests were run using untransformed and natural log (ln) transformed data, as appropriate, and significant optimal outcomes only are shown. No significant outcomes (for transformed or untransformed data) were found for NB/100 versus altitude, stream order, SRP or pH; nor for NB/n versus stream order, conductivity or SRP.

Niche-breadth metric	Bio-physico-chemical variable	R	R ² (%)	p
ln NB/100	ASPT	-0.303	9.2	<0.05
	ln flow	-0.3454	12.5	<0.05
	ln EC	0.349	12.2	<0.05
NB/n	ASPT	-0.483	23.3	<0.01
	altitude	-0.497	24.7	<0.01
	pH	0.433	18.7	<0.01
ln NB/n	flow	-0.476	22.7	<0.01

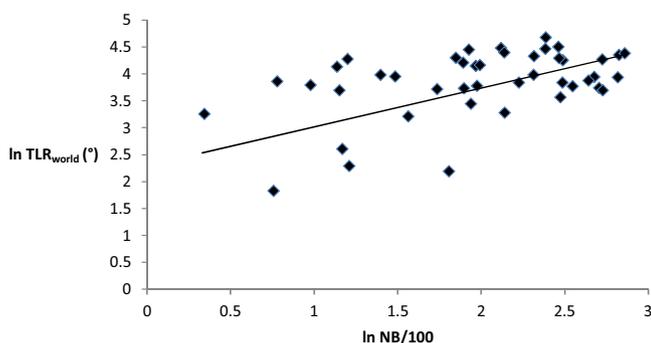


Fig. 2. Scatter plot and trendline showing relationship between log normal-transformed niche-breadth (ln NB/100) and world total latitudinal range (ln $\text{TLR}_{\text{world}}$) of native/naturalised Zambian river macrophyte species.

ANOVA analysis of number of records of each species in each niche-breadth category showed no significant difference between categories ($p > 0.05$) for mean number of records per species at world scale, but a significantly ($p < 0.001$) higher number of Zambian records per species for plants in the broad-niche category compared to the other two (see Table S1 of Appendix A).

Correlation analysis to assess the significance of relationships between the NB/100 and NB/n niche-breadth measures and mean values of seven bio-physico-chemical variables (SRP, altitude, stream order, flow, pH, conductivity and ASPT) showed that, with the exception of stream order and SRP, significant relationships were found between at least one of the niche-breadth metrics and these variables (Table 2). Niche-breadth was positively correlated with pH and conductivity, and negatively correlated with altitude, flow and ASPT. These results hence suggest that macrophyte species exhibiting broad niche-breadth tend to occur in Zambian riverine conditions with higher pH and conductivity, but at lower altitude, in slower flow, and in generally poorer-quality water (as indicated by invertebrate ASPT), compared with species of narrower niche-breadth.

Table 3
Comparison of means (\pm standard error: SE) of seven bio-physico-chemical variables, measured for sets of samples supporting the species comprising each of three niche-breadth groups determined by the NB/100 metric. One-way ANOVA with subsequent mean separation by Tukey's test (significant ANOVA outcomes only) for all variables except conductivity which could not be normalised (EC: Kruskal-Wallis test; n/a: F value not applicable). Means within a given variable sharing a superscript letter in common do not differ significantly.

	Species niche-breadth group (mean \pm SE)			F	p
	Narrow ($n=13$ spp)	Intermediate ($n=21$ spp)	Broad ($n=10$ spp)		
Altitude (m)	1171.8 ^a \pm 33.85	937.0 ^b \pm 42.96	1065.5 ^{ab} \pm 29.06	8.50	<0.001
Flow class	2.0 ^a \pm 0.16	1.4 ^b \pm 0.08	1.6 ^{ab} \pm 0.07	7.48	0.0017
Stream order	4.3 \pm 0.35	4.7 \pm 0.35	4.2 \pm 0.19	0.59	0.556
pH	7.44 \pm 0.09	7.67 \pm 0.06	7.60 \pm 0.05	2.87	0.067
EC ($\mu\text{S cm}^{-1}$)	73.3 \pm 8.7	139.4 \pm 13.0	115.9 \pm 12.6	n/a	0.004
SRP ($\mu\text{g L}^{-1}$)	9.9 ^b \pm 0.8	12.6 ^a \pm 0.8	11.6 ^{ab} \pm 0.6	3.32	0.046
ASPT	5.7 ^a \pm 0.16	5.1 ^b \pm 0.08	5.3 ^{ab} \pm 0.08	6.66	0.003

Inferential statistical testing to compare the means of bio-physico-chemical variables for species grouped by the three niche-breadth categories (measured in terms of NB/100) showed similar results to the correlation analysis exercise (Table 3), in terms of habitat preferences of narrow-niche versus broader-niche species. Stream order and pH showed no significant differences among niche-breadth categories, but the other five variables showed significant trends, generally supporting (with the exception of pH) the outcomes of the correlation exercise.

The issue of whether a greater number of narrow-niche species (compared with intermediate or broad-niche species) might be able to co-exist in a given habitat (here, a stretch of river or associated water body, of pre-defined length) was addressed by using ANOVA to compare mean macrophyte alpha diversity per sample (S : number of species present per sample), using data for the full set of macrophyte taxa recorded at each site, available online as a Supplementary file to Kennedy et al. (2015) for sample sets supporting narrow-niche versus intermediate-niche versus broad-niche species. The result showed no significant difference ($p > 0.05$) between niche-breadth groups, with the mean value of S , for the sample-set in which each species occurred, being closely similar for each group, at 12–13 species per sample. This outcome hence provides no evidence to suggest that niche-breadth of species present within the assemblage existing in Zambian river system sites influences the number of species which can co-exist at a given site.

3.2. Relationships between macrophyte species niche-breadth and latitudinal range

The values for $\text{TLR}_{\text{world}}$ based on native/naturalised records for the 44 target species, ranged from a minimum of 6.3° (4.8% of maximum possible $\text{TLR}_{\text{world}}$) for *Ottelia verdickii*, endemic to southern Africa, to a maximum of 108.7° (83.6%) for the cosmopolitan *C. demersum*. Corresponding TLR_{afr} values for 40 native/naturalised species (i.e., excluding non-native *S. molesta*, *L. hexandra*, *E. crassipes* and *A. filiculoides*) were from 6.3° (10.8% of maximum possible TLR_{afr}), again for *O. verdickii*, to 54.1° (93.3%) for *Floscopa glomerata*. For TLR_{neo} the range for the 19 Neotropical

Table 4

Optimal outcomes of linear regression modelling ($y=c+mx$) of relationships between niche-breadth variables (NB/100 and NB/n) calculated for Zambian river macrophyte species and species total latitudinal range for the world (TLR_{world}: $n=44$ species), Afrotropical bioregion (TLR_{af}: $n=40$ species) and Neotropical bioregion (TLR_{neo}: $n=19$ species in common between Zambia and Neotropics). For key to significance outcome see caption to Table 3. Regression equations were not calculated for non-significant relationships.

x	y	c	m	R	R ² (%)	p
ln NB/100	lnTLR _{world}	2.931	0.463	0.473	22.4	<0.01
	lnTLR _{af}	2.857	0.380	0.562	31.6	<0.001
ln NB/n	lnTLR _{world}	2.380	0.400	0.330	10.9	<0.05
	lnTLR _{af}	2.284	0.364	0.430	18.5	<0.01
NB/100	TLR _{neo}	–	–	0.061	0.4	>0.05
NB/n	TLR _{neo}	–	–	0.047	0.2	>0.05

native/naturalised species also present in Zambia (whether or not having native/naturalised or non-native status there) was from 3.8° (4.7% of maximum possible TLR_{neo}) for *Ludwigia adscendens*, to 62.3° (76.9%) for *A. filiculoides*, native to the Nearctic, and considered to be naturalized in the Neotropics.

Most species showed both a southern and northern hemisphere distribution pattern, at world scale, but on the evidence found here, six species appear to be southern African endemics, occurring solely in Africa south of the Equator: *Aponogeton desertorum*, *Ottelia exserta*, *N. nouchali* var. *caerulea*, *Aeschynomene fuitans*, *Lagarosiphon ilicifolius* and *L. tenax*.

Table 4 shows the best-fit linear regression and correlation outcomes for the linear modelling exercise to predict latitudinal range from niche-breadth variables. Significant outcomes were found, for both niche-breadth metrics, for TLR_{world} and TLR_{af}, but not for TLR_{neo}. Fig. 2 shows an example of the scatter plot and trendline for one of the outcomes (ln NB/100 versus ln TLR_{world}). The results indicated that a significant but weak positive predictive relationship (explaining at best some 30% of the variation) exists between macrophyte niche-breadth measured in Zambian river systems, and total latitudinal range of these species at global and Afrotropical scales. However, no such relationship existed between niche-breadth and Neotropical latitudinal range, for those species which occurred both in Zambia and native/naturalised in the Neotropics.

4. Discussion

There exists a large, and long-standing, published body of data for river macrophytes dealing with species range and relationships with spatial and environmental factors, in both tropical and temperate conditions, against which at least some of the detail of our findings for the ecology of Zambian riverine macrophyte species can be compared (e.g., Butcher, 1933; Ferreira and Moreira, 1999; Baattrup-Pedersen et al., 2006; Lang and Murphy, 2012; Varandas Martins et al., 2013; Chappuis et al., 2012; Kennedy et al., 2015; Tapia Grimaldo et al., 2016). However, only a few studies have hitherto examined niche-breadth in aquatic macrophytes, and all but one (Fu et al., 2015: on riverine wetland plants) have dealt solely with temperate lentic waterbodies. Examples include Rørslett (Rørslett, 1987a,b, 1988, 1991; Rørslett and Agami, 1987) on Scandinavian lake macrophytes; Pip (1988) working with standing waterbodies in central North America; Fu et al. (2014), who examined niche-differentiation along a depth gradient in a Chinese lake; and Pulido et al. (2015) on macrophytes of softwater lakes in the Pyrenees. To the best of our knowledge, no study has hitherto attempted to quantify species niche-breadth for tropical lotic macrophyte species, and then use this information to predict geographical range size of these plants. In consequence, there is no information available in the literature against which we can directly compare our results, and there is clearly a need for further work in

this respect, both in tropical and temperate freshwater systems, building from the baseline provided by our study.

Analysis using two niche-breadth metrics for 44 macrophyte species occurring in Zambian river systems showed a substantial range of niche-breadth. For convenience of subsequent analysis the species were grouped into categories (narrow versus intermediate/broad-niches), which proved to show significant variation (from the outcomes of one or both of correlation and ANOVA testing) in altitude, stream flow, conductivity, SRP, pH and ASPT, but not stream order.

An obvious criticism of our results is that most of the biophysico-chemical data are based on single snapshot samples (though a small proportion (<10%) of samples did represent repeat-sampling from some individual sites: for more on this see Kennedy et al., 2015, 2016). This undoubtedly increases the noise in the dataset, and future work should endeavour to gain more data, across seasons and years, from Zambian rivers. Nevertheless, given the sampling limitations involved in surveying a remote, difficult-access area of the planet, with an exceptionally low availability (for most sites nothing at all) of previous relevant survey data, we consider it encouraging that significant outcomes were found from the study, suggesting that our data may provide a useful basis for future work.

The results for niche-breadth values produced by the two metrics used here gave broadly comparable outcomes in identifying narrow-niche macrophyte species. This is probably because species with small niches also all have small numbers of records in the Zambian dataset, and so show similar trends of low niche-breadth values for both metrics. With the commonest species, with occurrences of $n > 50$, notably *Phragmites mauritianus* and, to a lesser extent, *P. subalbidum*, it is, however, clear that the NB/n metric suggests narrower niche-breadth compared to the high values produced by calculation of NB/100 values for these plants. It is possible that adjusting for commonness better reflects the true niche-breadth of such species, although this appears to be of much less importance in species of narrower niche-breadth. Certainly, despite its widespread occurrence in Zambia, *P. mauritianus* is a plant of relatively limited world geographical range (an Afrotropical endemic, also introduced to Egypt, within the Palaearctic: www.e-monocot.org). It might be argued that the true niche-breadth of this species is more likely to be of only moderate size, rather than the high value suggested by NB/100. This argument could also be applied to *P. subalbidum*, which is also an Afrotropical endemic, and further work is needed to examine this issue in more detail.

The outcomes of the study tell a rather consistent story with regard to relationships between niche-breadth and environmental factors for tropical riverine macrophyte species. In particular they suggest that narrow niche-breadth is characteristic of plants which tend to occur in harsher riverine conditions, where both environmental stress (e.g., limited nutrient availability) and environmental disturbance (e.g., faster flow conditions with a high probability of spate events, potentially damaging to vegetation, occurring during the rainy season) are likely to provide significant challenges to macrophyte survival, growth and reproduction (though other factors may be more benign, such as the generally good water quality found in sites showing such conditions). These conditions generally typify upland stream habitats in Zambia which are, with the exception of a few intermediate-niche and broad-niche species, such as *N. nouchali* var. *caerulea* (NB/100: 14.011) and *Eleocharis dulcis* (16.037), primarily occupied by narrow-niche species, with specialist plants like *Hydrostachys polymorpha* (1.407), *L. tenax* (3.349) and *Tristicha trifaria* (4.412) frequently present. Such species are well-adapted to highly-disturbed fast-flowing, spatey (or even torrential) river conditions (Kennedy et al., 2015).

The study provided evidence that broad-niche species occurring in Zambian river systems tend to include relatively few Afrotrop-

ical endemic species; are much commoner; and are more widely distributed in Zambia than species with narrow or intermediate niche-breadth. Conversely, narrow-niche species had the highest proportion of Afrotropical endemic species and individually these macrophyte species tended to occur at relatively few sites in Zambia.

There was no evidence from this study that niche-breadth influenced the number of macrophyte species which can co-exist in a given habitat. The basic underlying issue of macrophyte diversity support functioning (and threats to it) in tropical river systems (e.g. Bando et al., 2015; Santos and Thomaz, 2007) is however clearly in urgent need of further research.

The results of the exercise to assess relationships between three large-scale measures of latitudinal range, and niche-breadth of the 44 target macrophyte species, assessed in Zambian river conditions, indicated a weak but significant predictive outcome for both world latitudinal range and Afrotropical latitudinal range. Our results complement the findings of Cirtwill et al. (2015), who used a very different measure of niche-breadth to our approach, but nevertheless found, for freshwater communities (but not for communities in other ecosystem types), strong effects of latitude on scaling relationships (between species richness and average generality, vulnerability and links per species across empirical food webs).

However, from our work, it proved impossible to predict Neotropical latitudinal range, for those macrophyte species which co-occurred in Zambia and the Neotropics, from niche-breadth data measured in Zambian rivers. A major reason for this is likely to be the general absence of narrow-niche species from the dataset common to the two regions, because in Zambia many of these are Afrotropical endemics, which are likely to be replaced in Neotropical riverine ecosystems by functionally-similar (though not necessarily taxonomically-similar) Neotropical endemics. The upshot is that the small-range, narrow-niche species which form the lower part of the relationship are inevitably missing from the TLR_{neo} – niche-breadth scatters, summarised in Table 4, making it impossible to find significant relationships.

Our calculation of niche-breadth for tropical river macrophyte species utilised information gathered from sites within a strictly-limited latitudinal range. Zambia extends between the frontier with Tanzania in the north, at Ndole Bay on Lake Tanganyika, at 8.23°S, to the southernmost point on the frontier with Zimbabwe, on the Zambezi River, downstream of Livingstone, at 18.04°S, giving a maximum latitudinal range for river systems in the country of 9.83° (for comparison, the maximum latitudinal range of the UK is c. 11°, and California c. 9.5°). Nevertheless, the outcomes of the study permitted prediction of total latitudinal range of the target species across much wider African and global-scale ranges of latitude. This finding has clear potential as a basis for further investigations aimed at understanding environmental controls on macrophyte distribution and diversity, at small to large scales, building on studies such as the work of Rørslett (1991), Crow (1993), Hillebrand (2004), Chambers et al. (2008), and O'Hare et al. (2012). It also has implications for our understanding of how such plant – environment interactions may change in response to large-scale human impacts upon river ecosystems. For example, recent work on macrophyte communities in hardwater rivers (>10 mg L⁻¹ CaCO₃ concentration) has shown that spatial, as well as environmental, variables help explain macrophyte diversity at both global and regional scales (Tapia Grimaldo, 2013; Tapia Grimaldo et al., 2016). Improved knowledge of the niche-characteristics and niche-breadth of macrophyte species may improve our ability to predict how freshwater macrophytes will respond, at large scales, to likely future challenges affecting their ecology.

5. Conclusions

PCA ordination of bio-physico-chemical data for a set of samples collected from Zambian river systems permitted determination of two metrics of niche-breadth for 44 common Zambian macrophyte species. Narrow-niche species showed significantly differing niche-characteristics from broader-niche species. Using correlation testing and ANOVA, significant outcomes (from one or both approaches) were found between at least one of the niche-breadth metrics derived by the study and six of seven bio-physico-chemical variables for which data were available, stream order being the only non-significant variable. Niche-breadth showed no direct relationship with macrophyte alpha-diversity.

The results suggested that broader-niche macrophyte species tended to occur in Zambian riverine conditions of higher trophic status, pH and conductivity, but at lower altitude, in slower flow conditions, and in generally poorer-quality water, compared with narrower-niche species. Narrow-niche species had significantly fewer occurrences in Zambian rivers than broader-niche species, and comprised a high proportion of Afrotropical endemics.

To conclude, the main finding of this study, that macrophyte niche-breadth (derived from a strictly geographically-limited dataset) is a significant predictor of larger-scale geographical range for tropical river macrophyte species, provides new evidence, for freshwater plants, which supports the general relationships for niche-breadth and range size suggested by Slatyer et al. (2013).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.aquabot.2016.09.003>.

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