

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

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

3

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35

36 **Highlights**

- 37 • Two measures of niche-breadth were calculated for 44 Zambian macrophyte species
- 38 • Species were divided into narrow- and intermediate/broad-niche categories
- 39 • These showed significant variation in 6 bio-physico-chemical variables
- 40 • Narrow-niche species included a high proportion of Afrotropical endemics
- 41 • Niche-breadth predicted species latitudinal range at global and Afrotropical scales
- 42

43 **ABSTRACT**

44 The study tested the hypothesis that measurement, using multivariate Principal Components
45 Analysis (PCA), of the niche-breadth of river macrophyte species in southern tropical Africa, may
46 predict their larger-scale biogeographical range. Two measures of niche-breadth were calculated for
47 44 riverine macrophyte species, from 20 families commonly occurring in Zambia, using an approach
48 based on PCA ordination with 16 bio-physico-chemical input variables. These included altitude,
49 stream order, stream flow, pH, conductivity and soluble reactive phosphate concentration (SRP). In
50 the absence of additional chemical water quality data for Zambian rivers, invertebrate-based
51 measures of general water quality were also used. These were benthic macroinvertebrate Average
52 Score per Taxon (ASPT), and individual abundance of nine macroinvertebrate families with differing
53 water quality tolerance, indicated by their Sensitivity Weightings within the Zambian Invertebrate
54 Scoring System (ZISS). Macrophyte large-scale latitudinal range was derived from world
55 geositional records held by online databases, and additional records held by the authors. The two
56 niche-breadth metrics divided the species into narrow-niche and intermediate/broad-niche
57 categories, showing significant variation (from one or both of correlation and ANOVA test outcomes)
58 in altitude, stream flow, conductivity, SRP, pH and ASPT, but not stream order. Macrophyte alpha-
59 diversity (as a measure of number of individual niches co-existing per habitat) showed no significant
60 relationship with individual species niche-breadth. Narrow-niche species included a higher
61 proportion of Afrotropical endemics than did species with broader niche size. There were significant
62 predictive relationships between macrophyte niche-breadth and latitudinal range of the target
63 species at global and Afrotropical scales, but not for the Neotropics.

64

65 **Key words:** Africa, aquatic plants, benthic macroinvertebrates, freshwater ecology, latitudinal
66 distribution, niche analysis, rivers

67

68 **1. Introduction**

69 Species niche is conceived as a multidimensional space encompassing the total range of biotic
70 and abiotic variables (both natural and anthropogenic-related), plus species-interactions, together
71 affecting the survival of, and unique to, individual species. The concept was first described by
72 Hutchinson (1957), who brought together earlier attempts at formulating the idea by Grinnell (1917)
73 and Elton (1927, 1933). The concept of species niche continues to evolve (e.g., Collwell and Rangel,
74 2009), but the approach has recently been successfully applied as a basis for prediction of species
75 geographical range (Soberón, 2007; Soberón and Nakamura, 2009; Slatyer et al., 2013).

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

89 For freshwater macrophytes (defined as “aquatic photosynthetic organisms, large enough to see
90 with the naked eye, that actively grow permanently or periodically submerged below, floating on, or
91 growing up through the water surface” of freshwater systems: Chambers et al., 2008), data for
92 variables such as those mentioned above can collectively provide an indication of the range of
93 prevailing bio-physico-chemical conditions, and hence niche size, in habitats successfully occupied by

94 the plant species. Species which occupy lengthy ranges along niche-axes associated with such
95 measures, and with correspondingly wide niche-breadth, are usually considered to be generalist
96 strategists (Grime 1979; Murphy et al., 1990), with broad geographical range (Slatyer et al., 2013;
97 Cirtwill et al., 2015). The converse is likely to hold for species which exhibit only short niche-axis
98 lengths, with specialised survival strategies, and only limited geographical range.

99 A wide spectrum of approaches has been used to measure niche-breadth. Some can be applied to
100 all organisms, whilst others (e.g., food-web based studies) are appropriate for animals, but much less
101 so, or not at all, for plants. Some studies have used individual niche-axis traits to quantify species
102 niche-breadth (e.g., Luna and Moreno, 2010; Boulangeat et al., 2012). Other approaches aim to
103 determine species niche-breadth in terms of the proportion of populations found in, or using, the
104 individual states of given resources (e.g., Carrillo-Angeles et al. (2016), who utilised a resource-state
105 niche-breadth index developed by Hurlbert (1978), in a study of the cactus genus *Astrophytum*). At
106 the other end of the spectrum is the approach of Cirtwill et al. (2015) who used a biotic measure of
107 niche-breadth based on average generality, vulnerability and links per species across a set of 196
108 empirical food webs, in their study of relationships between latitude and biotic niche-breadth in
109 different ecosystems. In a recent meta-data analysis, Slatyer et al. (2013) identified a number of
110 niche-breadth measures for plant and animal species, 15 of which they categorised as “habitat”
111 measures (e.g., number of different habitat-types occupied); six as “diet” measures (e.g., number of
112 different food-types used); and five as “tolerance measures” (e.g., elevational range). These authors
113 also suggested that some of these measures are good predictors of geographical range-size. They
114 concluded that there is general evidence of a “positive relationship between niche-breadth and
115 range-size that is maintained across niche-breadth measurements, taxonomic groups and spatial
116 scales”.

117 Recently, studies using multivariate and modelling procedures to provide a summary of overall
118 ecological niche-breadth across the n -dimensional space representing an organism’s niche have
119 been undertaken, in both terrestrial and aquatic systems (McNyset, 2005; Domínguez-Domínguez et

120 al., 2006; Novak et al., 2010a,b; Janžekovič and Novak, 2012). The multivariate ordination procedure
121 Principal Components Analysis (PCA) has been widely applied for analysis of aquatic environmental
122 data (e.g., Blanck et al., 2007; Catalan et al., 2009), particularly as a means of identifying patterns in
123 sets of sampling sites in relation to environmental gradients (Lepš and Šmilauer, 2003). The variables
124 used to construct PCA ordinations for plant community ecology purposes are usually those which
125 help define the multidimensional niche of a species (particularly in the Eltonian sense: Soberón,
126 2007). Hence, it follows that PCA can provide a powerful tool (Novak et al., 2010a,b; Janžekovič and
127 Novak, 2012) for the determination of species niche-breadth, especially for plants, which make
128 direct use of Eltonian resources: an obvious example being uptake of nutrients from hydrosols
129 and/or water by macrophytes.

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

137

138 **2. Materials and methods**

139 *2.1. Field sampling and laboratory analyses*

140 The starting point was a dataset produced by the first-ever national-scale survey of Zambian river
141 plant occurrence, during 2006-2013, comprising 271 samples from sites throughout Zambia in rivers
142 and associated high-connectivity riverine floodplain waterbodies (permanent riverine lagoons;
143 backwaters/ oxbows; and seasonal standing waterbodies such as dambos). As well as macrophytes,
144 this survey recorded benthic macroinvertebrates and water physico-chemistry at each site. Survey
145 methods, site locations and results are reported in detail by Kennedy et al. (2015: and

146 supplementary online files associated with that paper); Kennedy et al. (2016); Lowe et al. (2013b);
147 and Tapia Grimaldo et al. (2016), with relevant methods summarised briefly below. From the
148 dataset, 176 samples (mostly from rivers: 90% of samples; but with a small number of samples from
149 associated static-water sites in riverine floodplains, comprising lagoons: 7%; dambos: 2%; and
150 backwaters/ oxbows: 1%) were selected for use in the niche-breadth analysis exercise. These
151 samples comprised those, within the full dataset, which supported at least one of 44 common
152 macrophyte species from 20 families (listed in Table 1, which also provides authorities for species
153 names mentioned in text), each occurring in at least 7 samples within the dataset (considered to be
154 the minimum sample size per species needed statistically to provide meaningful results). The species
155 (or, in a few cases, infraspecies, e.g. *Nymphaea nouchali* var. *caerulea*) included nine submerged, six
156 floating, and 29 emergent plant species, following the macrophyte life-form definitions of Chambers
157 et al. (2008). These numbers roughly reflect the overall proportions (22% submerged, 8% floating,
158 70% emergent species) of these macrophyte life-forms found to occur in the flora of Zambian river
159 systems by Kennedy et al. (2015).

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

171 Environmental data collected at each sampling location during the field surveys, and used in this
172 study, included geospatial coordinates and altitude, using a Garmin Etrex hand-held GPS. A
173 subjective assessment of flow class (flow categories and approximate corresponding flow velocity
174 intervals follow Lang and Murphy, 2012) was made using a four-point scale: 0 = static: no visible flow
175 (0 m s^{-1}); 1 = slow flow or “pool” (approximately $<0.2 \text{ m s}^{-1}$); 2 = moderate flow or “glide”:
176 approximately $0.2 - 0.4 \text{ m s}^{-1}$; 3 = fast flow: “riffle” or white-water showing (approximately $> 0.4 \text{ m}$
177 s^{-1}). In addition pH and conductivity ($\mu\text{S cm}^{-1}$) were measured in situ, using a multi-function Schott
178 Handylab 264 meter. Stream order was taken from a GIS-generated regional stream network derived
179 from an ArcGIS digital elevation model (for details see Lowe et al., 2013a). Water samples were
180 collected, and stored in 10 mL glass sample vials for subsequent laboratory determination of soluble
181 reactive phosphate (SRP) following standard methods (MAFF, 1986; APHA, 1998). Full details of
182 phosphate analyses are provided in Kennedy et al. (2016).

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

195

196 *2.2. Data synthesis and statistical methods*

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

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

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

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

237 Correlation analysis was used to assess the significance of relationships between the two niche-
238 breadth metrics and mean values of seven bio-physico-chemical variables (SRP, altitude, stream
239 order, flow, pH, conductivity and ASPT), recorded for the samples in which each species occurred,
240 for the dataset of 44 species. Tests were run using untransformed or natural log transformed data,
241 as appropriate to the normality requirements of the datasets used. In addition analysis of variance
242 (ANOVA: with post hoc comparison of means by Tukey’s mean-separation testing, for significant
243 outcomes only), or Kruskal-Wallis tests (for datasets which were not normal, and could not be
244 normalised by transformation), were used to test for significant differences for each variable,
245 between sets of species of differing niche-breadth, identified using the NB/100 measure. ANOVA
246 was also used to test for differences in numbers of species records at Zambia and world scales (see
247 below), for sets of species assigned to each niche-breadth category.

248

249 *2.3. Total latitudinal range of species*

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

252 (1) the world as a whole (maximum possible latitudinal range for riverine plant species being
253 approximately from Tierra del Fuego (55°S) to northern Canada, Alaska, Scandinavia and northern
254 Siberia (approximately 75°N), giving a total potential world latitudinal range of 130°. A few
255 freshwater macrophyte species are additionally recorded from the Antarctic bioregion, mostly from
256 sub-Antarctic islands generally lacking river systems, but with very few exceptions (one such being
257 *Cyperus longus*, which has been introduced to the sub-Antarctic island of Tristan da Cunha) these
258 species do not occur in Zambia, and so the Antarctic bioregion is not further considered here
259 (Chambers et al., 2008);

260 (2) the Afrotropical bioregion, ranging from Cape Agulhas (35°S) in South Africa to northern
261 Mauritania, Mali, Niger, Chad and Sudan, approximately following the Tropic of Cancer (c.23°N),
262 giving a maximum possible latitudinal range in this bioregion of 58°; and

263 (3) the Neotropical bioregion, ranging from Tierra del Fuego (55°S) to the northern part of Sinaloa
264 State in Mexico at approximately 26°N, giving a maximum possible latitudinal range for this
265 bioregion of 81°.

266 TLR for each species was calculated as its recorded latitudinal range, for native/ naturalised
267 geositional records only (see below), in the Southern Hemisphere, plus any additional recorded
268 latitudinal range in the Northern Hemisphere. This exercise required identification, for each target
269 species, of its geositional record closest to the Equator, and that furthest from the Equator, in the
270 Southern and (where applicable) Northern Hemispheres. All the target macrophyte species occupied
271 a latitudinal band around the planet south of the Equator, and many also occupied a second
272 latitudinal band north of the Equator. In total 30 species (identified in Table S1 of Appendix 1,
273 attached to the online version of this paper) had a latitudinal range which includes native or

274 naturalised records within 1° North or South of the Equator. For example, *Eichhornia crassipes* has a
275 native record from Lago San Pablo, Ecuador at 0.217°N: www.gbif.org/species/2765940). For these
276 species a single TLR range band was considered to exist, from northernmost to southernmost limit of
277 the species' distribution on the planet's surface. For the others TLR was calculated as the sum of the
278 latitudinal width (°) of the Southern and Northern Hemisphere bands (including records located >1°
279 South or North of the Equator) for occurrence of each species. Geopositional records for each
280 species were acquired from a wide range of sources, including global-scale online databases such as
281 the Global Biodiversity Information Facility (GBIF: www.gbif.org/species), the CJB African Plants
282 Database (www.ville-ge.ch/musinfo/bd/cjb/africa/index.php?langue=an), and eMonocot ([www.e-](http://www.e-monocot.org)
283 [monocot.org](http://www.e-monocot.org)). Although these databases all have known weaknesses in terms of coverage, their
284 datasets proved to be substantial for many of the target species. For example the number of world-
285 scale records with full geocoordinates held by GBIF for the 44 target species ranged (as of November
286 2015) from a minimum of 23 (for *Ledermanniella tenax*) to a maximum of 39204 (for *Ceratophyllum*
287 *demersum*). As noted above, however, of interest for the purposes of this study were only the
288 northern and southern extreme records, within the two hemispheres (as appropriate), regardless of
289 the number of geographically-intermediate points present within an individual species dataset. The
290 TLR information from global databases was supplemented by data held by the authors for a few
291 plants which showed limited latitudinal ranges in Africa from global database records. For example,
292 our own data for Zambian and Egyptian river macrophyte records (Springuel and Murphy, 1990,
293 1991; Ali et al., 1995; Kennedy et al., 2015) extended the latitudinal range of records held by GBIF
294 and other database sources, for a number of species (e.g., *Najas horrida*).

295 A question which had to be addressed in compiling TLR data was the issue of introduced species
296 and other non-native records, and whether these should be included in the analysis. It was decided
297 to use only records from within the native and naturalised range of the target species to calculate
298 TLR, on the grounds that such records best represent the long-standing established range of the
299 species (though, obviously, still influenced by human interference, in the case of naturalized

300 species). In practice it was usually relatively straightforward to determine records (by reference to
301 the literature) towards the extreme northerly and southerly ranges (within either or both
302 hemispheres, as appropriate) which were clearly non-native or non-naturalised occurrences of each
303 species. Extreme examples included:

304 (i) *Vallisneria spiralis*, which has recently been introduced to geothermally-warmed waterbodies
305 in Arctic and sub-Arctic Iceland (Wasowicz et al., 2014);

306 (ii) the invasive species *Salvinia molesta*, the taxonomy of which remains debatable (Moran and
307 Smith, 1999), but which is now generally accepted as having only a small native latitudinal range
308 (approx. 9°), entirely located in southern Brazil (Forno and Harley, 1979; Forno, 1983), compared to
309 a world TLR for all records (including introduced and invasive occurrences) calculated by us to be in
310 excess of 87°; and

311 (iii) extreme (usually northerly Northern Hemisphere) records for a number of the target species,
312 mainly held by GBIF, which proved on closer inspection to be inappropriate for use in this study . As
313 an example, records for *Nymphaea lotus* were found in the GBIF database for plants growing in
314 Botanical Gardens in Stockholm and Missouri, as well as a palaeobotanical record for this species,
315 mapped for Poland.

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

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

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

327

328 **3. Results**

329 *3.1. Niche-breadth of Zambian freshwater macrophytes*

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

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

349 Six of the species (46%) in the narrow-niche category are Afrotropical endemics, but only four
350 intermediate-niche species (19%) have this status, although, in addition, *N. horrida* is confined to the

351 African continent (with additional records, outwith the Afrotropical region, from Algeria and Egypt).
352 In the broad-niche category four species (40%) are almost certainly Afrotropical endemics.

353 ANOVA analysis of number of records of each species in each niche-breadth category showed no
354 significant difference between categories ($p > 0.05$) for mean number of records per species at world
355 scale, but a significantly ($p < 0.001$) higher number of Zambian records per species for plants in the
356 broad-niche category compared to the other two (see Table S1 of Appendix 1).

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

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

372 The issue of whether a greater number of narrow-niche species (compared with intermediate or
373 broad-niche species) might be able to co-exist in a given habitat (here, a stretch of river or
374 associated water body, of pre-defined length) was addressed by using ANOVA to compare mean
375 macrophyte alpha diversity per sample (S: number of species present per sample), using data for the
376 full set of macrophyte taxa recorded at each site, available online as a supplementary file to Kennedy

377 et al., 2015) for sample sets supporting narrow-niche versus intermediate-niche versus broad-niche
 378 species. The result showed no significant difference ($p > 0.05$) between niche-breadth groups, with
 379 the mean value of S , for the sample-set in which each species occurred, being closely similar for each
 380 group, at 12 – 13 species per sample. This outcome hence provides no evidence to suggest that
 381 niche-breadth of species present within the assemblage existing in Zambian river system sites
 382 influences the number of species which can co-exist at a given site.

383

384 3.2. Relationships between macrophyte species niche-breadth and latitudinal range

385 The values for TLR_{world} based on native/naturalised records for the 44 target species, ranged from
 386 a minimum of 6.3° (4.8% of maximum possible TLR_{world}) for *Ottelia verdickii*, endemic to southern
 387 Africa, to a maximum of 108.7° (83.6%) for the cosmopolitan *C. demersum*. Corresponding TLR_{afr}
 388 values for 40 native/naturalised species (i.e., excluding non-native *S. molesta*, *L. hexandra*, *E.*
 389 *crassipes* and *A. filiculoides*) were from 6.3° (10.8% of maximum possible TLR_{afr}), again for *O.*
 390 *verdickii*, to 54.1° (93.3%) for *Floscopa glomerata*. For TLR_{neo} the range for the 19 Neotropical
 391 native/naturalised species also present in Zambia (whether or not having native/naturalised or non-
 392 native status there) was from 3.8° (4.7% of maximum possible TLR_{neo}) for *Ludwigia adscendens*, to
 393 62.3° (76.9%) for *A. filiculoides*, native to the Nearctic, and considered to be naturalized in the
 394 Neotropics.

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

399 Table 4 shows the best-fit linear regression and correlation outcomes for the linear modelling
 400 exercise to predict latitudinal range from niche-breadth variables. Significant outcomes were found,
 401 for both niche-breadth metrics, for TLR_{world} and TLR_{afr} , but not for TLR_{neo} . Fig. 2 shows an example of
 402 the scatter plot and trendline for one of the outcomes ($\ln NB/100$ versus $\ln TLR_{world}$). The results

403 indicated that a significant but weak positive predictive relationship (explaining at best some 30% of
404 the variation) exists between macrophyte niche-breadth measured in Zambian river systems, and
405 total latitudinal range of these species at global and Afrotropical scales. However, no such
406 relationship existed between niche-breadth and Neotropical latitudinal range, for those species
407 which occurred both in Zambia and native/naturalised in the Neotropics.

408

409 **4. Discussion**

410 There exists a large, and long-standing, published body of data for river macrophytes dealing with
411 species range and relationships with spatial and environmental factors, in both tropical and
412 temperate conditions, against which at least some of the detail of our findings for the ecology of
413 Zambian riverine macrophyte species can be compared (e.g., Butcher, 1933; Ferreira and Moreira,
414 1999; Baattrup-Pedersen et al., 2006; Lang and Murphy, 2012; Varandas Martins et al., 2013;
415 Chappuis et al., 2012; Kennedy et al., 2015; Tapia Grimaldo et al., 2016). However, only a few studies
416 have hitherto examined niche-breadth in aquatic macrophytes, and all but one (Fu et al., 2015: on
417 riverine wetland plants) have dealt solely with temperate lentic waterbodies. Examples include
418 Rørslett (1987a,b, 1988, 1991; Rørslett and Agami, 1987) on Scandinavian lake macrophytes; Pip
419 (1988) working with standing waterbodies in central North America; Fu et al. (2014), who examined
420 niche-differentiation along a depth gradient in a Chinese lake; and Pulido et al. (2015) on
421 macrophytes of softwater lakes in the Pyrenees. To the best of our knowledge, no study has hitherto
422 attempted to quantify species niche-breadth for tropical lotic macrophyte species, and then use this
423 information to predict geographical range size of these plants. In consequence, there is no
424 information available in the literature against which we can directly compare our results, and there
425 is clearly a need for further work in this respect, both in tropical and temperate freshwater systems,
426 building from the baseline provided by our study.

427 Analysis using two niche-breadth metrics for 44 macrophyte species occurring in Zambian river
428 systems showed a substantial range of niche-breadth. For convenience of subsequent analysis the

429 species were grouped into categories (narrow versus intermediate/broad-niches), which proved to
430 show significant variation (from the outcomes of one or both of correlation and ANOVA testing) in
431 altitude, stream flow, conductivity, SRP, pH and ASPT, but not stream order.

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

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

454 *subalbidum*, which is also an Afrotropical endemic, and further work is needed to examine this issue
455 in more detail.

456 The outcomes of the study tell a rather consistent story with regard to relationships between
457 niche-breadth and environmental factors for tropical riverine macrophyte species. In particular they
458 suggest that narrow niche-breadth is characteristic of plants which tend to occur in harsher riverine
459 conditions, where both environmental stress (e.g., limited nutrient availability) and environmental
460 disturbance (e.g., faster flow conditions with a high probability of spate events, potentially damaging
461 to vegetation, occurring during the rainy season) are likely to provide significant challenges to
462 macrophyte survival, growth and reproduction (though other factors may be more benign, such as
463 the generally good water quality found in sites showing such conditions). These conditions generally
464 typify upland stream habitats in Zambia which are, with the exception of a few intermediate-niche
465 and broad-niche species, such as *N. nouchali* var. *caerulea* (NB/100: 14.011) and *Eleocharis dulcis*
466 (16.037), primarily occupied by narrow-niche species, with specialist plants like *Hydrostachys*
467 *polymorpha* (1.407), *L. tenax* (3.349) and *Tristicha trifaria* (4.412) frequently present. Such species
468 are well-adapted to highly-disturbed fast-flowing, spatey (or even torrential) river conditions
469 (Kennedy et al., 2015).

470 The study provided evidence that broad-niche species occurring in Zambian river systems tend to
471 include relatively few Afrotropical endemic species; are much commoner; and are more widely
472 distributed in Zambia than species with narrow or intermediate niche-breadth. Conversely, narrow-
473 niche species had the highest proportion of Afrotropical endemic species and individually these
474 macrophyte species tended to occur at relatively few sites in Zambia.

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

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

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

496 Our calculation of niche-breadth for tropical river macrophyte species utilised information
497 gathered from sites within a strictly-limited latitudinal range. Zambia extends between the frontier
498 with Tanzania in the north, at Ndole Bay on Lake Tanganyika, at 8.23°S, to the southernmost point
499 on the frontier with Zimbabwe, on the Zambezi River, downstream of Livingstone, at 18.04°S, giving
500 a maximum latitudinal range for river systems in the country of 9.83° (for comparison, the maximum
501 latitudinal range of the UK is c. 11°, and California c. 9.5°). Nevertheless, the outcomes of the study
502 permitted prediction of total latitudinal range of the target species across much wider African and
503 global-scale ranges of latitude. This finding has clear potential as a basis for further investigations
504 aimed at understanding environmental controls on macrophyte distribution and diversity, at small to

505 large scales, building on studies such as the work of Rørslett (1991), Crow (1993), Hillebrand (2004),
506 Chambers et al. (2008), and O'Hare et al. (2012). It also has implications for our understanding of
507 how such plant - environment interactions may change in response to large-scale human impacts
508 upon river ecosystems. For example, recent work on macrophyte communities in hardwater rivers
509 ($>10 \text{ mg L}^{-1} \text{ CaCO}_3$ concentration) has shown that spatial, as well as environmental, variables help
510 explain macrophyte diversity at both global and regional scales (Tapia Grimaldo, 2013; Tapia
511 Grimaldo et al., 2016). Improved knowledge of the niche-characteristics and niche-breadth of
512 macrophyte species may improve our ability to predict how freshwater macrophytes will respond, at
513 large scales, to likely future challenges affecting their ecology.

514

515 **5. Conclusions**

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

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

529 To conclude, the main finding of this study, that macrophyte niche-breadth (derived from a
530 strictly geographically-limited dataset) is a significant predictor of larger-scale geographical range for

531 tropical calcareous river macrophyte species, provides new evidence, for freshwater plants, which
532 supports the general relationships for niche-breadth and range size suggested by Slatyer et al.
533 (2013).

534

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555

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740 **SUPPORTING INFORMATION**

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742 Additional Supporting Information may be found in the online version of this article:

743 Appendix 1. World and Zambian records, niche-breadth and world total latitudinal range (TLR_{world} °)

744 of Zambian riverine macrophyte species.

745 Table 1. Species in each of three niche-breadth categories, as measured by the NB/100 metric.
 746 Family given in brackets. *: Afrotropical endemic species.

Niche-breadth category (NB/100)		
Narrow (< 6.000)	Intermediate (6.000 – 12.000)	Broad (>12.000)
<i>Aeschynomene fluitans</i> Peter (Fabaceae)	<i>Azolla filiculoides</i> Lam. (Azollaceae)	<i>Alternanthera sessilis</i> (L.) R. Br. ex DC. (Amaranthaceae)
* <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)
* <i>Hydrostachys polymorpha</i> Klotzsch (Hydrostachyaceae)	<i>Cyperus difformis</i> L. (Cyperaceae)	* <i>Floscopa glomerata</i> (Willd. ex Schult. and Schult.f.) Hassk. (Commelinaceae)
* <i>Ledermanniella tenax</i> (C.H. Wright) C. Cusset (Podostomaceae)	<i>Cyperus digitatus</i> Roxb. (Cyperaceae)	<i>Ludwigia adscendens</i> (L.) H. Hara (Onagraceae)
* <i>Ottelia ulvifolia</i> (Planch.) Walp. (Hydrocharitaceae)	<i>Cyperus involucratus</i> Rottb. (Cyperaceae) (= <i>Cyperus imbricatus</i> Retz.)	* <i>Nymphaea nouchali</i> var. <i>caerulea</i> (Savigny) Verdc. (Nymphaeaceae)
* <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)	* <i>Panicum subalbidum</i> Kunth (Poaceae)
<i>Persicaria meisneriana</i> (Cham. and Schltld.) M. Gómez (Polygonaceae)	* <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)	* <i>Phragmites mauritanus</i> Kunth. (Poaceae)
* <i>Thelypteris interrupta</i> (Willd.) K. Iwats. (= <i>Cyclosorus interruptus</i> (Willd.) H. Itô) (Thelypteridaceae)	* <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)	
	* <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)	
	* <i>Persicaria senegalensis</i> (Meisn.) Soják	

(Polygonaceae)
Potamogeton schweinfurthii A.
Benn.
(Potamogetonaceae)
Pycnus mundii Nees
(Cyperaceae)
Salvinia molesta D.S. Mitch.
(Salviniaceae)
Typha domingensis Pers.
(Typhaceae)

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748

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

756

Niche-breadth metric	Bio-physico-chemical variable	<i>R</i>	<i>R</i>² (%)	<i>p</i>
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

757

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

	Species niche-breadth group (mean \pm SE)			<i>F</i>	<i>p</i>
	Narrow (<i>n</i> = 13 spp)	Intermediate (<i>n</i> = 21 spp)	Broad (<i>n</i> = 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

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765

766 Table 4. Optimal outcomes of linear regression modelling ($y = c + mx$) of relationships between
 767 niche-breadth variables (NB/100 and NB/n) calculated for Zambian river macrophyte species and
 768 species total latitudinal range for the world (TLR_{world}: $n = 44$ species), Afrotropical bioregion (TLR_{afr}: n
 769 = 40 species) and Neotropical bioregion (TLR_{neo}: $n = 19$ species in common between Zambia and
 770 Neotropics). For key to significance outcome see caption to Table 3. Regression equations were not
 771 calculated for non-significant relationships.

772

<i>x</i>	<i>y</i>	<i>c</i>	<i>m</i>	<i>R</i>	<i>R</i>² (%)	<i>p</i>
ln NB/100	lnTLR _{world}	2.931	0.463	0.473	22.4	<0.01
	lnTLR _{afr}	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 _{afr}	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

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775 **Figure legends**

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

785

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