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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 geopositional 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 hydrosoils 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