

Exploring stream communities in a tropical biodiversity hotspot: biodiversity, regional occupancy, niche characteristics and environmental correlates

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Abstract Exploring and describing biodiversity and the mechanisms structuring it is fundamental to advancing ecology. This is particularly pertinent in understudied biogeographical regions, such as the Afrotropics, that are characterised by strong seasonal climatic shifts. We investigated the characteristics of stream biodiversity in the Niger Delta region of Nigeria, a tropical biodiversity hotspot, by examining patterns in 20 stream invertebrate communities across both the wet and dry seasons. For this, we took a multi-faceted approach accounting for the three levels of biodiversity (α , β and γ), including partitioning the nestedness and turnover components of β diversity, regional occupancy-abundance patterns, niche characteristics, and the environmental drivers of community structure. α diversity was low in these streams, with strong turnover between sites leading to high β diversity contributing to regional biodiversity, but there was little variation in communities between seasons. The proportion of sites occupied by taxa declined with increasing niche position, and decreasing niche breadth. Occupancy was predicted well by a combination of these two factors (niche position and breadth), but not mean local abundance, as the abundance-occupancy link was an upper-limit unimodal relationship. On

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average, community structure was linked more strongly to environmental variables in the wet season. Our findings demonstrate the clear role of spatial, but not temporal, turnover in assemblages, which likely reflects the environmental heterogeneity of this region. This is further supported by the fact that regional occupancy was mostly related to niche characteristics, particularly niche position. We emphasise the importance of continued basic and applied ecological work in this important biogeographic region to enable better protection of its biodiversity.

Keywords Occupancy-abundance · Occupancy-frequency · Niche breadth · Niche position · Nigeria · Lotic · Benthic invertebrates

Introduction

Freshwater biodiversity is under ongoing pressure from processes such as land use change, eutrophication and invasive species (Dudgeon et al. 2006; Vörösmarty et al. 2010). To enable better predictions and protection, we must continue to explore patterns and processes shaping biodiversity. Tropical streams, in particular, are highly threatened ecosystems through a broad suite of stressors (Sodhi et al. 2004; Dudgeon 2008; Strayer and Dudgeon 2010). However, research into the ecology of tropical stream invertebrate communities has been strongly biased to a few geographic regions (Boyero et al. 2009). We also lack understanding of the factors structuring biodiversity in tropical regions, with a considerable need to fill these gaps (Heino 2009). For instance, while work has been expanding rapidly in recent years in tropical and neotropical systems (e.g. Costa and Melo 2008; Ligeiro et al. 2010; Landeiro et al. 2012; Al-Shami et al. 2013), little is still known about β diversity and its drivers compared to our understanding of temperate systems.

β diversity is an important consideration as it provides a direct link between local- and regional-scale biodiversity (Whittaker 1960; Anderson et al. 2011). Another important aspect of regional biodiversity is the linkage between regional occupancy and local abundance (Hanski et al. 1993; Gaston et al. 2000). The study of occupancy has been ongoing, with much of the work focusing on relationships between local abundance, occupancy and niche characteristics (Brown 1984; Passy 2012). Occupancy and abundance of species can be strongly affected by their niche breadth (NB) and niche position (NP) (Gaston et al. 2000; Tales et al. 2004; Heino and Grönroos 2014). Brown (1984) hypothesised that generalist species with tolerance of a variety of conditions and resources (broad niches), would have both a more widespread distribution and higher local abundance than specialists. Niche position may also be important in explaining occupancy and abundance (Hanski et al. 1993; Venier and Fahrig 1996), where species with marginal niches are less widely distributed as well as being locally less abundant compared to those with non-marginal niches (high habitat availability). However, few studies have examined the importance of NB and NP for occupancy patterns concurrently (but see Heino and Grönroos 2014).

Given the clear seasonality of tropical monsoonal regions, regional occupancy and biodiversity patterns in stream systems should be strongly affected by changes in conditions between the wet and dry seasons, as demonstrated in tropical Asian streams (Leung and Dudgeon 2011; Leung et al. 2012). Tropical rivers are highly dynamic systems, with the strong seasonality playing a key role in structuring riverine food webs (Winemiller and

Jepsen 1998), even at high altitudes (Ríos-Touma et al. 2011). For instance, seasonality may have two effects on species richness, depending on the characteristics of specific organisms and on the scale at which ecological and evolutionary processes happen. On the one hand, seasonality could increase regional species diversity if species specialise and occupy different temporal niches (i.e. temporal turnover) (Chesson and Huntly 1997). Clear differences in seasonal life history shifts are expected to be prevalent in tropical stream systems (Jacobsen et al. 2008). Such seasonal ‘time-sharing’ has been demonstrated in desert stream insect communities in response to flow variation (Bogan and Lytle 2007). On the other hand, depending on life-cycle length, seasonality could lead to low species diversity because species must evolve broad niches to survive in highly seasonal habitats, which may make the community more readily saturated (Tello and Stevens 2010).

Strong differences in rainfall patterns between wet and dry seasons will alter the environmental conditions in tropical streams, in turn affecting the niches available for biota to inhabit. Stream invertebrates are structured by a wide range of environmental factors ranging from water chemistry, depth and discharge, temperature, pH, substrate, stream size, and disturbance (Vinson and Hawkins 1998; Heino 2009), as well as multiple stressors (Leps et al. 2015). In addition, these environmental factors can interact with dispersal leading to an interplay between spatial and environmental structuring in meta-communities (Heino et al. 2012; Landeiro et al. 2012; Tonkin et al. 2015a). However, little is known about the environmental factors structuring macroinvertebrate communities in the northern Afrotropical region (but see e.g. Kasangaki et al. 2008; Masese et al. 2014), an important but threatened area of global biodiversity.

The Niger Delta forms an integrated mosaic of highly diverse aquatic, semi-terrestrial (mangrove and freshwater swamps) and terrestrial habitats, which support considerable terrestrial and aquatic biodiversity (Adekola and Mitchell 2011). The delta is highly heterogeneous at both local and regional scales, and is an area of international ecological importance being considered a biodiversity hotspot with several IUCN ‘Red List’ species (Ebeku 2004; Luiselli 2009). Despite its importance, an evaluation of regional patterns of the benthic invertebrate fauna in the Niger Delta is still lacking with most research having been conducted at local scales (Arimoro and Ikomi 2008; Arimoro 2009). Understanding regional patterns of stream biodiversity in the Niger Delta is important not only because it will foster a better understanding of ecological and evolutionary processes driving species richness, but also because it will allow the establishment of better conservation planning strategies.

In our study, we investigated the characteristics of stream biodiversity in the Niger Delta region of Nigeria. For this, we took a multi-faceted approach accounting for the three levels of biodiversity (α , β and γ), including partitioning the nestedness and turnover components of β diversity, regional occupancy-abundance patterns, niche characteristics, and the environmental drivers of community structure. Given that this is a first exploratory look at biodiversity of streams in this region, we set up the following three hypotheses to test on general biodiversity patterns and their seasonal changes. H₁: Based on the region being a biodiversity hotspot and situated in the tropics (refer to the latitudinal diversity gradient, Willig et al. 2003), α diversity will be high and β diversity will be promoted more through site-to-site turnover than nestedness. H₂: Based on previous tropical stream research (e.g. Leung and Dudgeon 2011) and the more suitable conditions in the dry season, such as reduced turbidity, richness, abundance, and diversity will be higher in the dry season. H₃: The clear differences in rainfall between wet and dry seasons will produce unique communities between the two seasons (i.e. seasonal ‘time-sharing’, Bogan and Lytle 2007). Understanding these seasonal shifts in communities is important for setting up

biomonitoring programmes as sample timing can have strong implications on biomonitoring results when clear within-year temporal turnover is apparent (Linke et al. 1999).

Understanding species' occupancy patterns within the landscape is important for a variety of reasons. From an applied standpoint alone, abundance-occupancy relationships can be important for conservation, harvesting, biological invasions and inventorying (Gaston et al. 2000). The understanding of these relationships can be further enhanced by incorporating the niche characteristics of organisms. Therefore, we tested the following three hypotheses relating to occupancy, abundance and niche characteristics of these understudied, but highly important Nigerian streams. H₄: Based on the large body of theory on occupancy, abundance and niche patterns, occupancy and abundance will be a positive function of niche breadth (NB) (Passy 2012; Slatyer et al. 2013) and a negative function of niche position (NP) (Gregory and Gaston 2000; Tales et al. 2004; Heino and Grönroos 2014). H₅: Being one of the most enduring patterns in macroecology (Gaston and Blackburn 2000), the relationship between occupancy and abundance will be positive, but we examined occupancy as a function of abundance rather than the typical abundance-occupancy relationship (Siqueira et al. 2009; Heino and Grönroos 2014). H₆: NP will be more important in structuring occupancy, compared to NB and local abundance (Heino and Grönroos 2014). While we explored which environmental variables linked best with community structure, we did not form any specific hypotheses.

Materials and methods

Study area

Twenty lowland rivers in southern Nigeria were included in this study, situated between 5°27' and 6°50' North, and 5°35' and 6°41' East. These are located in the western Niger Delta, particularly in the Delta and Edo States (Supplementary Material Fig. S1, Supplementary Material Table S1). The study area comprises the characteristic tropical climate of two distinct seasons; the dry season (November–April) and the wet season (May–October). The mean annual temperature is ca. 28 °C while the mean annual relative humidity is 85 %. The land use in most of the catchments consists of rainforest and a mosaic of cropland and natural vegetation. Aquatic vegetation at most sites consists of submerged and floating macrophytes (*Ceratophyllum submersum*, *Nymphae lotus*, *Azolla africana*, *Utricularia* spp.) and emergent macrophytes (*Pycreus lanceolatus*, *Cyrtosperma senegalense*, *Scirpus jacobii* and *Vossia cuspidata*) with a dominance of trees such as Indian bamboo (*Bambusia* spp.), palm tree (*Elaeis guineensis*), *Pandanus* spp., and *Mitragyna ciliata*.

Sampling of macroinvertebrates

Sites were sampled between 2008 and 2012. Each site was sampled twice within a period of between three and six months representing one from each of the wet and dry season. Kick samples of macroinvertebrates were collected with a D-frame net (500- μ m mesh) within an approximately 25-m wadeable portion of the river. Four 3-min samples were taken on each sampling visit to include all different substrata and flow zones. The four samples were then pooled in the field, representing a single sample for each station and preserved in 70 % ethanol. In the laboratory, samples were washed in a 500- μ m mesh

sieve and macroinvertebrates were sorted, enumerated and identified to the lowest possible taxonomic level using a stereoscopic microscope ($\times 10$ magnification). Macroinvertebrate specimens were identified using available regional keys (Day et al. 2003; Moor et al. 2003), keys from elsewhere (Merritt and Cummins 1996), and the help of regional specialists (see acknowledgements). This combined approach resulted in mainly genus or species level identifications (very few commonly-difficult-to-identify groups, such as Orthocladiinae, were left at higher taxonomic levels). These identification levels are comparable to those employed in most countries across the globe (e.g., Germany, US, Australia, etc.). Voucher specimens were deposited at Albany Museum, Grahamstown, South Africa.

Environmental variables

We calculated a suite of environmental variables ranging from local-scale, measured in situ, through to catchment land use and bioclimatic data. Local habitat characteristics were measured over a 100-m reach at each site and in both seasons. Depth was measured in the sample area using a calibrated rod. Flow velocity was measured over 10 m in the mid channel on three occasions by timing a float. Canopy cover was estimated visually as a percentage along the sampling reach. Substratum composition in each 100-m sampling reach was estimated visually as percentage of silt, loam, mud, clay and sand. At each stream the following physical and chemical variables were measured: dissolved oxygen (YSI 55 dissolved oxygen meter), temperature, pH, conductivity, total dissolved solids (TDS) (portable Hanna HI 991300/1), and turbidity (portable turbidity meter HI 93102). Water samples were taken for analysis of nitrates and phosphates, measured spectrophotometrically after reduction with appropriate solutions (APHA 1995). Biochemical oxygen demand (BOD₅) was determined in the laboratory using APHA (1995) methods.

To calculate catchment slope, aspect and land use percentages we used catchments created with the ‘watershed’ tool in ArcMap 10.0 (ESRI Inc., Redlands, CA, U.S.A.), using the ‘flow direction’ layer from the HydroSHEDS database (<http://hydrosheds.cr.usgs.gov>; Lehner et al. 2006). Catchment slope and aspect were calculated using the 3D Analyst Tools in ArcMap 10.0. Bioclimatic variables taken from the Worldclim database (<http://www.worldclim.org>; Hijmans et al. 2005), as well as Global Aridity Index (AI) and Global Potential Evapo-Transpiration (PET) (CGIAR Consortium for Spatial Information; <http://www.csi.cgiar.org>; Zomer et al. 2008), were extracted for each site using the ‘sample’ tool of ArcMap 10.0.

Land cover data (Global Land Cover Database; <http://bioval.jrc.ec.europa.eu/products/glc2000/products.php>) was extracted from the entire upstream catchment of each site (Supplementary Material Table S2). The percentage of land cover was merged and calculated for common land cover types: broadleaf tree cover, flooded saline forest, shrub and mosaic forest (Table S2).

Statistical analysis

Biodiversity patterns

All analyses were performed using R version 3.02 (R Core Team 2015). First, to reduce the number of dimensions of the bioclimatic data, we used principal component analysis

(PCA) with the ‘prcomp’ function in the base *stats* package. This resulted in two dimensions adequately describing the data (eigenvalues: PC1 = 13.96; PC2 = 6.26), explaining 96 % of the cumulative variance in the bioclimatic data (proportion explained: PC1 = 0.665; PC2 = 0.963; Supplementary Materials Fig. S2). These two components were then used to represent climate in further analyses (named climate 1 and climate 2).

For all multivariate analyses, the raw invertebrate data was transformed to reduce heteroscedasticity. We used the method of Anderson et al. (2006), where values are $\log(x) + 1$ transformed for values greater than zero, but zeros remain as zeros. We did this with the ‘decostand’ function in the *vegan* R package (Oksanen et al. 2016).

To test H_1 (α diversity will be high and β diversity will be promoted more through site-to-site turnover than nestedness), we first calculated a suite of biodiversity metrics. These included mean local taxonomic richness, abundance, and the Shannon diversity index for each site in each season. The Shannon index was calculated using the ‘diversity’ function in *vegan*.

We then examined β diversity patterns for each of the two seasons using presence-absence data. We tested if β diversity was greater, less than or no different to chance expectation using a null model approach. We partitioned β diversity into nestedness and turnover components (β_{SNE} and β_{SIM} , respectively), as well as overall Sorensen β diversity (β_{SOR}), following the methods of Baselga (2010). To examine whether these partitions differed from chance, we compared with null matrices, using 10,000 permutations. We used the R1 (fixed-incidence proportional) method to constrain the null matrix. Simulations were run using the *oecosimu* function and the *nestedbetasor* function partitioned β diversity, both using *vegan*. We examined whether values differed from chance (10,000 permutations) using the standardised z-score. We also employed the methods of Jost (2007) to partition diversity into the independent α and β diversity components for each season. We used the ‘multipart’ function in *vegan* to do this and ran 10,000 simulations to compare values against a null model, as in the previously mentioned approach.

To test H_2 (richness, abundance, and diversity will be higher in the dry season), we tested for differences in richness, abundance and Shannon diversity between seasons using Mann–Whitney–Wilcoxon tests, with the function ‘wilcox.test’ due to non-normality after checking for normality using Shapiro-Wilks test and inspecting qqplots and residuals.

To test our third hypothesis (H_3 : rainfall between wet and dry seasons will produce unique communities between the two seasons) and examine community shifts between seasons, we examined community structure with non-metric multidimensional scaling (nMDS) ordinations using the ‘metaMDS’ function in *vegan*, using Bray-Curtis distances on log-transformed data. We tested for differences using PERMANOVA (Anderson 2001) with the ‘adonis’ function in *vegan* using 999 permutations. To further explore community differences, we tested for differences in multivariate homogeneity of group dispersions (a measure of β diversity; Anderson et al. 2006) between wet and dry seasons using PERMDISP2 (Anderson 2006) with the ‘betadisper’ function in *vegan*. To test these differences in dispersion, we used a permutation test with 999 permutations.

Niche characteristics and regional occupancy

The following steps all contribute to the testing of our third to sixth hypotheses (H_4 – H_6). First, to test for strong multicollinearity in environmental variables, Pearson’s correlation was performed using the ‘rcorr’ function in the *Hmisc* package (Harrell Jr 2015). As a result of strong redundancy between nitrates and phosphates ($r = 0.97$), we removed phosphates for the remainder of the analysis. Wood and slope also exhibited

multicollinearity with several other variables (i.e. $r = 0.75\text{--}0.8$), thus we removed them for the analysis. We had two classes of variables for analyses of these two different seasons: static, which were those that categorized the catchment, physical and climatic conditions of the sites; and seasonal, which were those that were sampled at each sampling visit such as chemical measurements (Supplementary Materials Table S2).

We calculated niche characteristics (niche position: NP; and niche breadth: NB) using the outlying mean index (OMI) method of Doledec et al. (2000). The OMI method calculates the marginality of habitat distribution of species by calculating the distance from the mean habitat conditions occupied by a species and the mean conditions within a particular region. Thus, the OMI represents the NP of a species as the position of a species reflects its deviation from the “average” habitat conditions. Low OMI values for a species represent non-marginal niches or high habitat availability, and vice versa for high OMI values (i.e. marginal niches). The OMI method also calculates a metric of species tolerance, which measures the distributional range of a species along the (sampled) environmental gradient of the region. Tolerance, therefore, represents the NB of a species, with low values representing species with narrow NBs (i.e. occur across narrow environmental gradient), and high values representing broad NBs (Heino and Grönroos 2014).

We used the ‘niche’ function in *ade4* (Dray et al. 2015) to calculate NP (OMI) and NB (species tolerance). We calculated niches based on the full suite of environmental variables (Table S2) after removal of strongly multicollinear variables. We calculated the niche values based on the full set of 40 sites (20 wet and 20 dry season), rather than for each season individually as the low numbers of sites in each season would have created false niches for species that overlapped seasons.

First, we tested H_4 (occupancy and abundance will be a positive function of niche breadth (NB) and a negative function of niche position (NP)) and H_5 (the relationship between occupancy and abundance will be positive). To do this, we explored relationships between niche characteristics (NP and NB) and both mean local abundance (of occupied sites only) and regional occupancy (proportion of sites occupied). For these particular relationships, we tested for significance of relationships for both seasons combined (i.e. the full 40 wet and dry season samples rather than individually) as patterns for individual seasons matched those of the overall joint response. After checking for normality using Shapiro-Wilks test and inspecting qqplots and residuals, we logit-transformed occupancy, log-transformed NP and square root transformed NB. We then examined relationships using linear regression with the ‘lm’ function.

We then explored the factors explaining occupancy for each season individually. While the most commonly-applied approach for examining abundance-occupancy relationships is to consider abundance as the dependent variable, there is uncertainty as to the direction of causality (i.e. it may be that occupancy is a function of local abundance), if causality exists (see Gaston and Blackburn 2000 for discussion). Therefore, as in previous stream studies (Siqueira et al. 2009; Heino and Grönroos 2014), we examined occupancy as a function of local abundance. We explored the relationship between mean local abundance and occupancy with linear and quadratic regressions, and also using quadratic quantile regression with the ‘rq’ function in the *quantreg* package (Koenker 2015). We examined the upper-limit relationship using $\tau = 0.9$.

To test H_6 (NP will be more important in structuring occupancy, compared to NB and local abundance), we assessed the ability of NP, NB and mean local abundance to explain variation in regional occupancy. We did this using variance partitioning, based on partial linear regression. This method is able to estimate the pure and shared contributions of the three variables in explaining regional occupancy. We ran variance partitioning using the

‘varpart’ function in *vegan*. Finally, we visually examined the occupancy-frequency distributions for each season.

Community-environment relationships

To compare environmental linkages between different niche groups, we grouped taxa into two equal groups for both NP and NB (i.e. we split the full data set into two even groups for each niche measure).

To select the best subset of environmental variables explaining variation in both the dry and wet season macroinvertebrate community structure, we used the BVSTEP procedure of Clarke and Ainsworth (1993) using the ‘bvStep’ function in *sinkr* (Taylor 2015). We did this for all taxa combined and for the four niche groups (non-marginal NP, marginal NP, broad NB and narrow NB), individually. The BVSTEP routine searches for the highest correlation (Mantel test) between dissimilarities of two multivariate datasets. One dataset is fixed (i.e. community data) and the other is variable (i.e. environmental). BVSTEP is essentially the same as the BIO-ENV procedure of Clarke and Ainsworth (1993), but provides a less computationally demanding search of combinations, by taking a stepwise approach rather than searching for all possible combinations. Therefore, this method selects the best subset of environmental variables (Euclidean distances) correlating with community data. We used Spearman rank correlations to correlate the matrices and Bray-Curtis distances for the community dataset.

Results

Overall biodiversity patterns and seasonality

168 taxa were collected from these 20 rivers sampled in each of the wet and dry seasons. Taxonomic richness ranged between 12 and 52 taxa per site, with a mean of 26.7 ± 2.9 (S.E.) for the dry season, and between 7 and 61 taxa, with a mean of 22.2 ± 3.1 taxa for the wet season. However, richness did not differ significantly between the wet and dry seasons (Fig. 1a). Likewise overall abundance per site (Fig. 1b), Shannon diversity (Fig. 1c) and β diversity (measured as mean distance to group centroid; Fig. 1d) did not differ between seasons. Furthermore, while there was some clear variability, overall community structure did not differ consistently between seasons (Fig. 1e).

For both wet and dry seasons, stream communities were clearly structured by the turnover component of β diversity (β_{SIM}), when using a null model approach on presence-absence data (Fig. 2). Likewise, overall β diversity (β_{SOR}) was significantly higher than chance expectation (Fig. 2). The nestedness component (β_{SNE}) was significantly lower than expected for the wet season but not the dry season (Fig. 2). Multiplicative β diversity was significantly greater than null expectation for both seasons ($P < 0.0001$; Supplementary Material Table S3), and α diversity was significantly less than null ($P < 0.0001$; Table S3).

Regional occupancy relationships

The proportion of sites occupied declined strongly with increasing niche position ($R^2 = 0.698$, $F_{1,166} = 384.26$, $P < 0.0001$; Fig. 3c), and increased with increasing niche

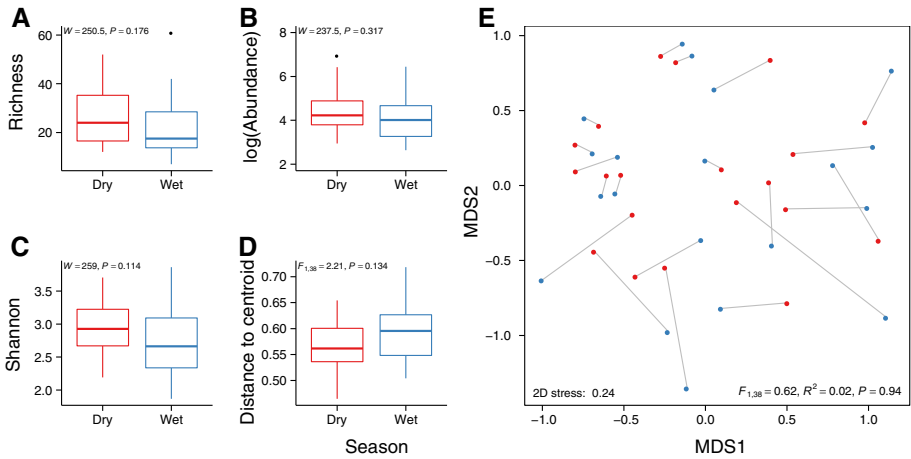


Fig. 1 Overview of biodiversity patterns of benthic invertebrate communities at 20 sites in the Niger Delta region, Nigeria, sampled in each of the dry and wet seasons. Differences in taxonomic richness (a), abundance (b), Shannon diversity index (c) and beta diversity (mean distance to group centroid; (d) between wet and dry seasons. e Difference in the full community structure (log-transformed abundance) between the seasons, based on a non-metric multidimensional scaling ordination

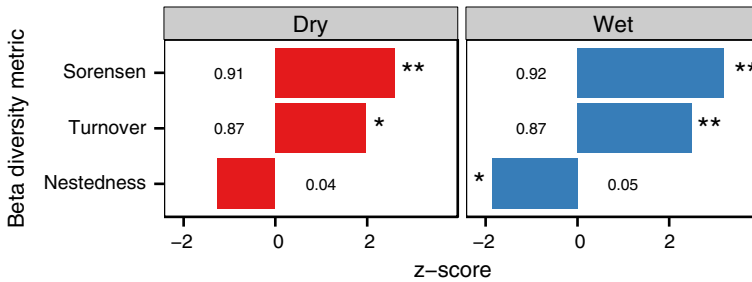


Fig. 2 Results of partitioning beta diversity into overall (Sorensen), and turnover and nestedness components for benthic macroinvertebrates sampled from 20 sites in the Niger Delta region, Nigeria, in each of the dry and wet seasons. Analyses are based on presence-absence data. Displayed with bars are z-scores resulting from comparison with 10,000 simulated null communities, using the R1 method to constrain the null matrix. A higher z-score represents higher value for that facet of beta diversity than expected by chance and vice versa. Raw Sorensen, turnover and nestedness metrics are displayed as text corresponding with each bar. Significance of z-scores are indicated with asterisks. ** $P < 0.01$, * $P < 0.05$

breadth ($R^2 = 0.38, F_{1,166} = 101.62, P < 0.0001$; Fig. 3d). In contrast, the mean local abundance of taxa was not related to either niche position ($R^2 = 0.016, F_{1,166} = 2.78, P = 0.098$; Fig. 3a) or niche breadth ($R^2 < 0.001, F_{1,166} = 0.01, P = 0.94$; Fig. 3b). Patterns between abundance, occupancy and niche characteristics for individual seasons were similar and matched those of the combined analysis, so we did not test these patterns directly (Fig. 3e–h).

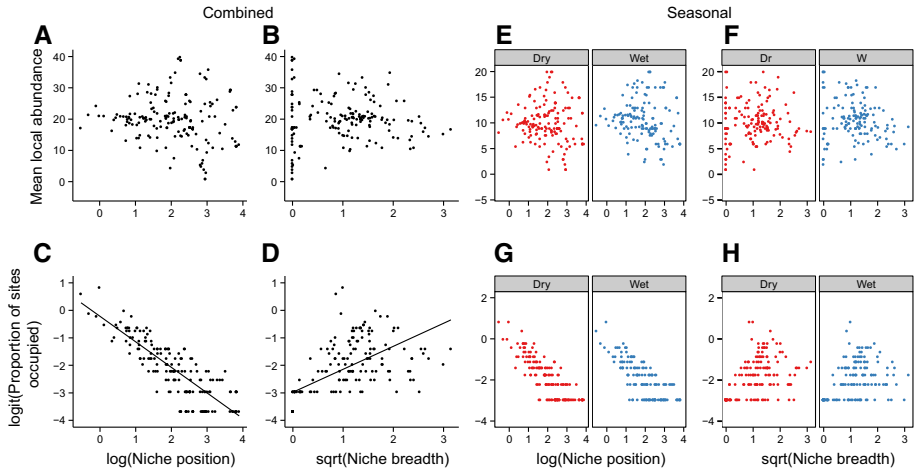


Fig. 3 Mean local abundance at occupied sites as a function of niche position (**a, e**) and niche breadth (**b, f**), and regional occupancy (proportion of sites occupied) as a function of niche position (**c, g**) and niche breadth (**d, h**) of 168 benthic invertebrate taxa collected from streams in the Niger Delta region in Nigeria. Niche metrics were derived from the outlying mean index (OMI) analysis

Regional occupancy exhibited an upper-limit unimodal relationship, with the proportion of sites occupied highest by taxa that were found at intermediate abundances when present at a site (Fig. 4a). Patterns were similar for the two seasons. There was no linear relationship between abundance and occupancy ($P > 0.05$), but the mean response was unimodal (wet: $R^2 = 0.194$, $F_{2,139} = 16.71$, $P < 0.0001$; dry: $R^2 = 0.152$, $F_{2,154} = 13.78$, $P < 0.0001$; Fig. 4a). Using variance partitioning based on linear regression showed that regional occupancy of taxa was able to be explained well (% variance explained: wet = 63 %; dry = 75 %) by NP, NB and MA (Fig. 4b). Occupancy was best explained by the NP of organisms (pure adj. $R^2 = 0.51$ and 0.50 [wet and dry, respectively]; full adj. $R^2 = 0.59$ and 0.70), with a strong shared effect of 0.20 (dry) and 0.11 (wet) with NB. This was the main influence of NB, with a low pure effect in explaining occupancy (pure adj. $R^2 = 0.03$ and 0.06 [wet and dry, respectively]; full adj. $R^2 = 0.13$ and 0.26), but mean local abundance contributed near zero in both seasons.

Occupancy-frequency distributions were clearly right skewed indicating that rare taxa dominated assemblages, with slightly more rare taxa in the wet season (Fig. 4c).

Community-environment linkages

On average, invertebrate community structure was linked more strongly to environmental variables in the wet rather than dry season (BVSTEP; Fig. 5). This was particularly evident when considering the full community, with the best BVSTEP model for the wet season (comprising nitrates, % cobbles, % catchment flooded saline forest cover and climate axis 1) having a ρ of 0.49 compared to that of the dry season ($\rho = 0.32$). The best dry season model comprised depth, % mud, % CPOM and % catchment shrub cover. Linkages between environmental variables and community structure were variable when considering the niche groups separately (Fig. 5). Non-marginal NP taxa were more strongly linked with environmental descriptors than those with marginal NPs for both wet and dry seasons.

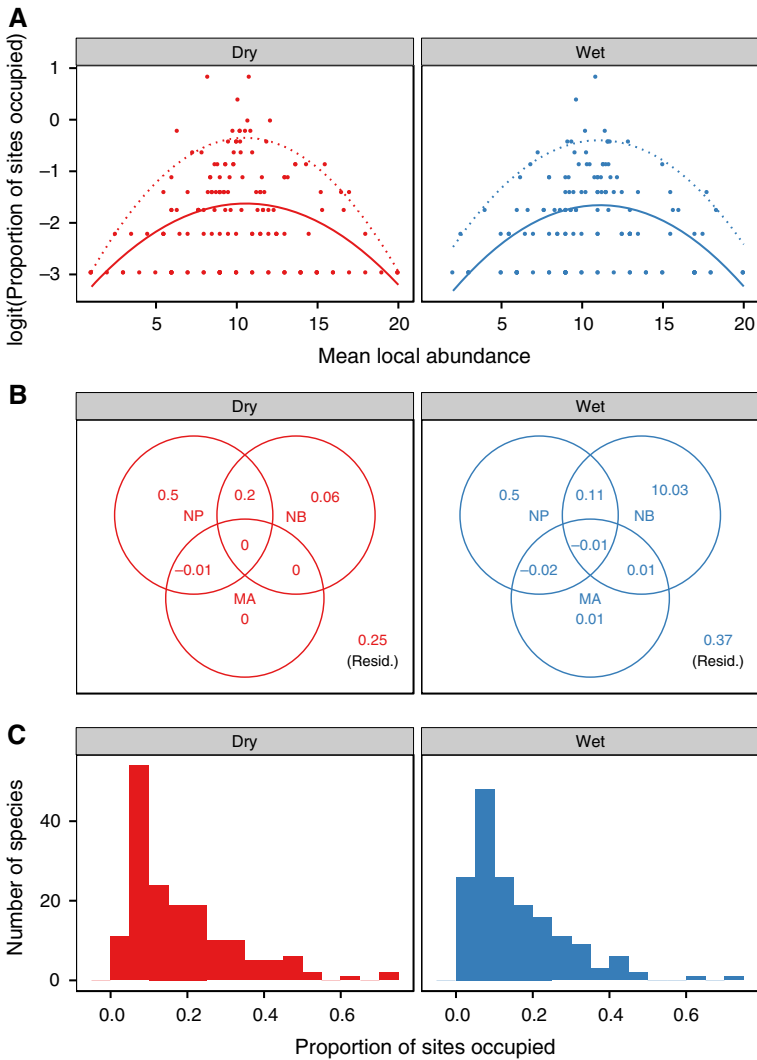


Fig. 4 Exploration of regional occupancy by season in relation to species characteristics in benthic invertebrate communities in the Niger Delta, Nigeria. **a** Regional occupancy as a function of mean local abundance at occupied sites. *Solid regression line* is the mean response (full results in main text). *Dotted regression line* is a quantile regression based on $\tau = 0.9$. Wet: $y = -0.77 - 0.39x - 5.92x^2$; Dry: $y = -0.76 + 0.05x - 7.72x^2$. **b** Results of variance partitioning predicting regional occupancy from niche position (NP), niche breadth (NB) and mean local abundance at occupied sites (MA). Values given represent the pure and shared fractions of variation (adjusted R^2) explained by the independent variables, as well as the remaining unexplained variance (Resid.). **c** Occupancy-frequency distributions examining the relationship between regional occupancy and the number of species

However, environmental variables were better linked with narrow than broad NB taxa in the wet season, but there was little difference in the dry season. Conductivity, % mud and % CPOM were commonly selected in the best models in the dry season, whereas nitrates, % catchment flooded saline forest and climate were often selected in the wet season.

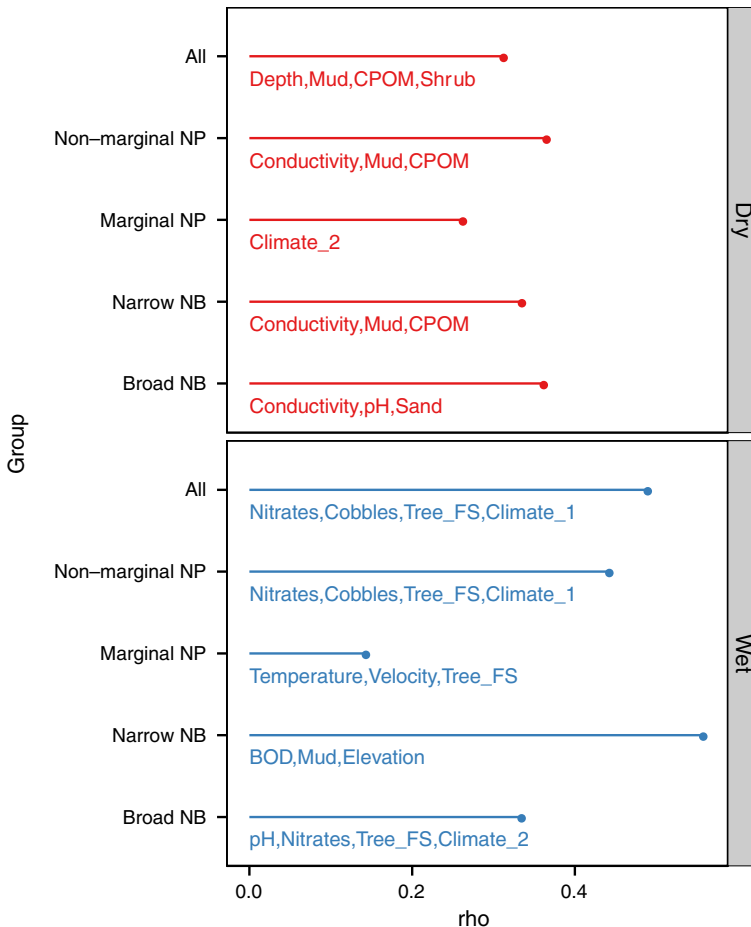


Fig. 5 The best subset of environmental variables selected using BVSTEP (stepwise BIO-ENV) correlating with log-transformed multivariate community structure of benthic invertebrates in 20 Niger Delta, Nigeria, streams in the dry and wet seasons. In addition to the full community, data was broken down into species with a central and marginal niche position (NP) and narrow and broad niche breadth (NB). Environmental data was normalised prior to analyses. The community data distance matrix was based on Bray-Curtis distances and environmental data on Euclidean. Climate_1 and Climate_2 = BIOCLIM PCA axes; CPOM = Coarse Particulate Organic Matter; Tree_FS = % catchment flooded saline forest. Full list of environmental variables and their units can be found in Table S2.

Discussion

Overall biodiversity patterns and seasonality

Contrary to our first hypothesis (H_1), mean local taxonomic richness was low in these streams, but in support of H_1 strong turnover between sites was evident (and no evidence of nestedness) contributing to high regional biodiversity. While strong turnover was expected, the low α diversity is surprising, given this region is known as a biodiversity hotspot and the well-known increase in biodiversity towards the equator (Willig et al. 2003), as well as

the known differences between tropical and temperate streams (Boulton et al. 2008). However, Vinson and Hawkins (2003) did not find a clear latitudinal gradient in mayflies, stoneflies and caddisflies, but in fact found highest genus richness at mid-latitudes in the new world. While based on EPT (taxa with variable temperature preferences), several other studies have found conflicting results for tropical-temperate richness comparisons (see Heino 2009 for review). Nevertheless, while we found low α diversity in these streams, β diversity was high.

This finding of low α but high β diversity and strong turnover in these streams likely reflects a large amount of variation in environmental conditions between streams. Habitat heterogeneity is a key factor regulating regional variation in β diversity (Anderson et al. 2006; Heino et al. 2015a). There were no clear gradients in environmental conditions across the streams in this study, but generally varied conditions for all variables, with multiple principal components required to explain the variation in environmental conditions (Supplementary Material Fig. S3). This was reflected in the multiple variables selected to explain community structure. Nevertheless, strong turnover between sites may be a function of dispersal limitation between streams, rather than niche control (Heino et al. 2015b). Our study crossed major catchment boundaries and covered a relatively large spatial extent (Fig. S1), thus dispersal limitation could be an important factor structuring these communities. This is confounded by the clear variations often found between catchments in stream studies. Such context dependency in metacommunity structuring is a now well-recognised issue in stream metacommunity studies (Heino et al. 2012; Tonkin et al. 2016). In tropical Malaysian streams, Al-Shami et al. (2013) found within-stream β diversity was influenced by a combination of environmental factors and their membership to a particular catchment. Moreover, Costa and Melo (2008) found a stronger role of environmental conditions than spatial structuring for stream invertebrate communities in Brazilian streams, as did Landeiro et al. (2012) in Amazonian caddisflies.

Contrary to H_2 (higher predicted biodiversity in dry season) and H_3 (temporal turnover in community structure between seasons), there was little difference in biodiversity patterns between the two seasons, when considering all approaches employed. This is surprising given the clear difference in rainfall between seasons. However, while there was no significant difference in community structure between the two seasons (rejecting H_3), there was clear variability in individual stream communities (e.g. Umaluku, Oleri and Anwai streams), suggesting regional variation overrode within-stream temporal variation. Masese et al. (2014) found that season influenced structural and functional organization of macroinvertebrates by accentuating differences in water quality and habitat characteristics. It is important to remember that the streams in our study were sampled over more than one wet-dry season (although individual streams were always sampled within one year). Thus, year-to-year variation in climatic conditions may have reduced the ability to detect differences at the regional scale.

Regional occupancy patterns

β diversity patterns were reflected in the occupancy-frequency distributions, which exhibited similar distributions in the wet and dry seasons. Metapopulation dynamics, with dispersal dynamics connecting high local abundances (Hanski 1998), is thought to lead to the bimodal occupancy-frequency distributions relationship (McGeoch and Gaston 2002; Verberk et al. 2010), but we found clearly right-skewed occupancy-frequency distributions representing a predominance of satellite species, rather than core species regularly occurring across the distribution. Two factors make metapopulation dynamics unlikely in

our study: (1) the region crossed major catchment boundaries and covered a relatively large spatial extent (Fig. S1). (2) The large variability in dispersal mode of aquatic invertebrates and their ability to disperse between catchments (Thompson and Townsend 2006; Canedo-Arguelles et al. 2015).

Niche breadth (NB) (i.e. tolerance, Brown 1984; Slatyer et al. 2013) and niche position (NP) (i.e. habitat availability, Venier and Fahrig 1996) are well understood as key factors that drive occupancy. We found these characteristics much more important than local abundance in explaining variation in occupancy. Likewise, niche characteristics could not predict local abundance, which may reflect the fact that abundance is more stochastic and more prone to error than occupancy (Heino and Grönroos 2014). Partitioning the variation in regional occupancy between NP, NB and local abundance revealed NP as the most important structuring variable for occupancy, as per expectation (H_6). As hypothesised (H_4), occupancy decreased strongly with increasing NP and increased with increasing NB in these Nigerian streams, but the amount of variation explained was almost double for NP. Passy (2012) suggested that NB should play a more central role in explaining occupancy and abundance than NP, whereas Gaston and Blackburn (2000) indicated NP to be more important than NB in controlling range size. Nonetheless, previous stream studies focusing on occupancy found conflicting results, with Siqueira et al. (2009) finding NB to be a better predictor of local abundance and occupancy in Brazilian streams, whereas Heino and Grönroos (2014) found a weak increase in occupancy with NB.

While we focused on patterns across two seasons where the mean abundance of taxa that were seasonally specific would be reduced, we found no clear difference between the seasonal-based and the combined approach. Observed occupancy patterns are dependent on the spatial extent of the study, particularly in river systems, where catchment boundaries divide regional distributions. Within single catchments, NB tends to be more important than NP in structuring occupancy (e.g. Heino 2005). This probably reflects the fact that fewer non-marginal niches are found within catchments than when considering multiple catchments at large spatial extents. Studies on stream invertebrates within single catchments have provided support for both the metapopulation dynamics and NB hypotheses (Heino 2005; Heatherly et al. 2007; Siqueira et al. 2009).

Contrary to our fifth hypothesis (H_5), occupancy was highest for taxa found at intermediate local abundances, but this was an upper-limit relationship, with considerable variation below the line. This is not a common finding, with positive abundance-occupancy relationships being one of the most robust macroecological patterns (Gaston and Blackburn 2000; Gaston et al. 2000); i.e. species occupying more sites tend to be more locally abundant. Such a positive relationship has been found in streams for diatoms (Soininen and Heino 2005), bryophytes (Heino and Virtanen 2006) and invertebrates (Heino and Grönroos 2014). Our findings may reflect the low number of study sites compared to macroecological assessments. The spatial extent of the study region and the range of environmental variables sampled and examined are known to influence the inferences that are able to be drawn (Mykrä et al. 2007; Heino 2011). Abundance-occupancy relationships, while positive, often exhibit considerable variability in stream systems with low levels of variation explained. This was reflected in our approach, with the association being a clearly upper-limit scenario. This weak association may reflect clearly different species-environment relationships or spatial structuring of conditions (Verberk et al. 2010; Heino and Grönroos 2014).

Community-environment linkages

Communities were better linked with environmental variables in the wet season than dry, but the important variables varied. Likely in reflection of available conditions, non-marginal niche groups were better linked with environmental variables than marginal niches, but differences between narrow and broad NB groups were inconsistent between seasons. A species is likely to be widely distributed within a region if it has a central NP and an abundance of available habitat within that particular region, particularly across large ranges such as catchment boundaries (e.g. Tales et al. 2004). Specialists (narrow NB) should be more limited by their required local environmental conditions, whereas generalists (broad niche) have been suggested to be more influenced by metapopulation dynamics (Verberk et al. 2010).

Tropical streams exhibit substantial variability in their structure, function and factors shaping communities (Boyero et al. 2011; Boyero et al. 2015), thus we did not form hypotheses about which environmental variables would be important in this relatively understudied northern Afrotropical region. The most often selected variables were those relating to substrate size, CPOM coverage, climatic conditions, and water quality (i.e. conductivity and nitrates). The lack of clear gradient in conditions in these streams was reflected in the varied set of variables that were linked with the biota. In the Afrotropical region, the environmental factors structuring macroinvertebrate communities are poorly known. A recent study by Arimoro et al. (2012) identified canopy cover and macrophytes as important predictors of stream macroinvertebrate richness and composition at the local scale in Nigerian streams. Likewise, Masese et al. (2014) reported an overriding influence of canopy cover and litter biomass on macroinvertebrate distribution in Kenyan highland streams. This importance of canopy matches findings of studies in temperate streams (e.g. Fuller et al. 2008; Tonkin 2014). Temperature remains constant during the year in tropical streams and is thus not a major factor structuring tropical benthic communities (Hynes 1970). This was reflected in our results, with temperature only selected once in the BVSTEP procedure (marginal NP, wet season). Nevertheless, Kasangaki et al. (2008) found water temperature, pH and transparency were the most important predictors of benthic invertebrate communities in Ugandan streams. They found that land use strongly influenced stream communities in this Afrotropical region. Land-use stress can influence stream communities through a variety of means, including altering co-occurrence patterns (Larsen and Ormerod 2014) and linkages with riparian organisms (Tonkin et al. 2015b). However, while certain variables selected in our study may reflect land use stressors (e.g. conductivity, nitrates, sediment/substrate), we cannot directly attribute these variables to land use influences. Moreover, percentage flooded saline forest was the only catchment land use variable linked with the invertebrate community in our study.

Conclusions

Our findings suggest that regional biodiversity in this region is promoted through clear spatial turnover in assemblages, with rare taxa dominating, particularly in the wet season. Yet, despite the clear seasonal shifts in climatic conditions, temporal variation did not appear to be a key mechanism structuring biodiversity. Our findings demonstrate the clear role of spatial, but not temporal, turnover in assemblages, which likely reflects the strong environmental heterogeneity of this region, as demonstrated by the variable selection of

environmental variables linked with community structure. This is further supported by the fact that regional occupancy was mostly related to niche characteristics, particularly niche position. We have opened the door to more in-depth research into regional biodiversity patterns of this unique hotspot of biodiversity. We emphasise the importance of continued basic and applied ecological work in this important biogeographic region to enable better protection of its biodiversity.

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