



Weak relationships among macroinvertebrates beta diversity (β), river status, and environmental correlates in a tropical biodiversity hotspot

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ABSTRACT

Freshwater biodiversity is rapidly declining due to accelerated human-induced disturbances. Increased human-induced environmental disturbances are believed not to only decrease species numbers, but to also diminish beta diversity, for instance, by the local extinction of native species and wide-spread introduction of non-native species – a process widely known as biotic homogenization. Here, we investigated whether anthropogenic impacts reduce beta diversity. We also assessed the relative roles of environmental and spatial factors in driving beta diversity. We examined relationships among macroinvertebrates beta diversity, stream status classes (reference and impacted classes), and environmental predictors in streams in Northern Nigeria. We used PERMDISP and distance-based redundancy analysis followed by variation partitioning to evaluate how beta diversity of macroinvertebrates differed between the reference and impacted sites, and what mechanisms were responsible for their responses. While beta diversity between reference and impacted sites was similar for all distance matrices, there were significant differences in composition related to turnover between the reference and impacted sites using the distance matrices. Species sorting prevailed in structuring macroinvertebrates communities in our system, while spatial variables were not relevant. Our result of beta diversity of macroinvertebrates and their responses to disturbances support the hypothesis that disturbances do not necessarily lead to biotic homogenization. We recommend that tropical streams restoration ecologists need to emphasize the study of varying condition classes in their attempt to develop effective restoration strategies based on their environmental heterogeneity.

1. Introduction

Overwhelming increase of concerns regarding the impacts of anthropogenic influence on ecosystems has made the evaluation and investigations of biodiversity a progressively compelling matter in contemporary times (Meynard et al., 2011; Agra et al., 2020; Cid et al., 2020). The measurement of diversity has been carried out by looking at properties going from local (alpha) to regional (gamma) scales (Whittaker, 1960, 1975). Within-habitat diversity is frequently regarded as α -diversity, while between-habitat diversity represents beta diversity (Pound et al., 2019). Alpha diversity denotes the species number of a local system; beta diversity indicates variations in species composition between local ecosystems (Leprieur et al., 2012; Soininen et al., 2016). Furthermore, while α -diversity expresses the importance of abiotic and biotic components of local system, beta diversity mirrors species

response to environmental heterogeneity and dispersal along ecological gradients (Anderson et al., 2011; Shoemaker et al., 2020). As a result, beta diversity measurement is particularly interesting since it reveals the connectivity between α (local) and γ (regional) diversities (Socolar et al., 2016). Recently, perspectives which partition beta diversity into its components of turnover and nestedness (Baselga, 2010) are increasingly becoming influential in examining postulations regarding ecological dynamics at regional and continental scales. Therefore, in the attempt to conserve and restore the biodiversity of a given region in the face of continued natural and human-induced degradations, assessments of the biodiversity status of that region are important (Heino et al., 2015a, 2015b, 2015c, 2015d). Beta diversity can reflect changes in biodiversity better than alpha diversity, because beta diversity indicates long-time community shifts in dominance and identity (Hillebrand et al., 2018). Hence, biodiversity monitoring approaches should prioritize the

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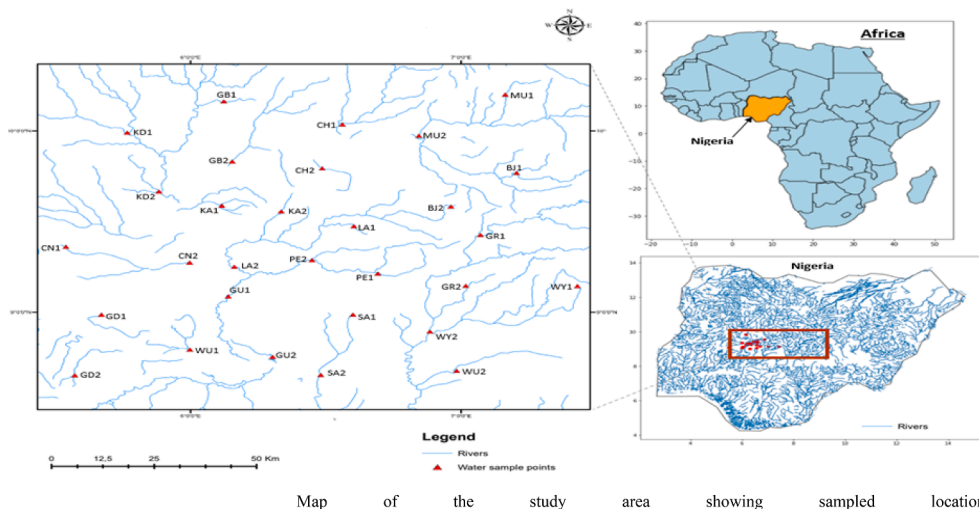


Fig. 1. Map of the study area showing sampled locations.

measurements of more relevant beta diversity indices over alpha diversity that provides insufficient information on biodiversity trends (Hillebrand et al. 2018).

While the association between alpha diversity (species richness) and disturbance magnitude is dependent on whether or not the source of the disturbance is natural or human-induced (Gutiérrez-Cánovas et al., 2013; McGarvey, 2014; Piano et al., 2019), several published evidences have suggested that alpha diversity is inversely associated with disturbance magnitude (Pound et al., 2019; Keke et al., 2020). The aforementioned richness gradients are eventually expressed into variations in community composition that generate beta diversity (species composition differences among localities). Beta diversity has been proven to be distinctly influenced by environmental heterogeneity and disturbances (Astorga et al., 2014; Alahuhta et al., 2017). While heterogeneity has been extensively revealed to magnify beta diversity by the provision of diverse niches, disturbance is usually anticipated to diminish beta diversity - a process known as biotic homogenization - by sieving sensitive taxa from the regional pool (Gutiérrez-Cánovas et al., 2013; Hawkins et al., 2015; Liborio & Tanaka 2016a). For certain instances, anthropogenic disturbance has impacted incidentally on beta diversity through the reduction of habitat heterogeneity, habitat loss and reduction of niche size (Siqueira et al. 2015). The prediction that environmental perturbation should necessarily lead to diminished beta diversity (biotic homogenization) is not always the regular outcome. For example, a few studies have shown that beta diversity increased with increased human disturbances (e.g. Hawkins et al., 2015; Fugère et al., 2016; Liborio & Tanaka, 2016b; Mykrä et al., 2017). It is now evidently clear that studies aimed at evaluating this prediction have produced diverse outcomes and therefore call for additional insights (Gutiérrez-Cánovas et al., 2013).

Most studies in the tropic have shown that anthropogenic impacts alter macroinvertebrates biodiversity-environment relationships (Baumgartner and Robinson, 2017; Agra et al., 2020; Arimoro and Keke, 2021). Although species sorting and dispersal are generally the two most important factors that structure every metacommunity (Lindström & Langenheder 2012), most studies across the globe have shown that stream metacommunity is structured mostly by species sorting (Cottenie, 2005; Heino et al., 2015c). The concept of species sorting highlights the significance of the local environment, and changes along local explanatory variables cause the species to exist at environmentally suitable sites (Heino et al. 2015c). However, the predominance of species sorting over dispersal limitation in explaining variation in community composition is mostly valid for freshwater bodies situated within small drainage basins (Landeiroetal., 2012; Götheetal., 2013; Grönrosetal., 2013), while the prevalence of dispersal limitation is usually observed across larger drainage basins and spatial extents (Heino, 2011;

Astorgaetal., 2012), covering over 2000 km long geographical gradient (Bennett et al., 2010). In the Neotropical stream metacommunities, Siqueira et al. (2012) had earlier reported that macroinvertebrates beta diversity was driven mostly by species sorting, while Saito et al. (2015) showed that dispersal limitations were stronger drivers of macroinvertebrates beta diversity. Therefore, beta diversity and its components result from the interplay between environmental heterogeneity and dispersal limitation (Gianuca et al. 2017).

Streams in the tropics are often degraded ecosystems through a wide range of stressors (Dudgeon 2008; Strayer and Dudgeon, 2010; Arimoro et al. 2016; Keke et al., 2017; Arimoro et al., 2021). Biodiversity studies of tropical freshwater invertebrate communities have been biased to limited geographic regions (Boyer et al. 2009). There is also a paucity of understanding of the factors that seem to prevail in biodiversity structuring in tropical regions with a considerable need to fill these gaps (Tonkin et al. 2016; Arimoro and Keke, 2017). For example, while there is rapid expansion of ecological studies in recent years in tropical and neotropical systems (e.g. Ligeiro et al., 2009; Landeiro et al., 2012; Al-Shami et al., 2013), there is still little knowledge about beta diversity and its environmental correlates compared to the knowledge about beta diversity in temperate ecosystems (Tonkin et al. 2016). Therefore, for better conservation and protection of the biodiversity of a region, we must continually try to unravel the effects of these human and natural disturbances on beta diversity and overall environmental quality.

However, there is a global paucity of published information about how beta diversity changes in response to both natural and human-induced disturbances (Pound et al. 2019), especially in the tropics - as we are unaware of such tropical investigations on beta diversity. This is generally worrisome given that beta diversity is a fundamental contributor to regional diversity and a veritable tool for testing hypotheses of mechanisms that configure variations in aquatic biotic communities (Tonkin et al. 2016). In the light of the foregoing, our objective was to determine whether anthropogenic impacts reduce beta diversity. We therefore assembled comprehensive datasets comprising 30 sites representing two condition or status classes (reference and impacted) of streams in the Northern region of Nigeria. First, we analyzed variations in beta diversity with the prediction that beta diversity would be driven by its turnover component irrespective of the particular stream status, being a tropical stream with high biodiversity accounts (Boyer et al. 2011). Second, we tested for differences in beta diversity and community composition between reference and impacted sites, with the prediction that beta diversity will be promoted at reference sites. Third, we evaluated the contribution of environmental and spatial factors to beta diversity.

2. Methods

The data sets comprised river systems in Northern Nigeria (9°N to 10°N and 6°E to 7°E; Fig. 1). The study area comprises the characteristic tropical climate of two distinct seasons: the dry season (November–March) and the wet season (April–October). The land use in most of the catchments consists of a mosaic of natural vegetation, although some forms of forestry practices were visible in the catchments of some of the streams. Subsistence crop farming is among the major agricultural activities of this region. Also, fishing, bathing, laundry and washing of vehicles constitute most of the obvious human impacts for most easily assessable stretches of the rivers.

2.1. Sampling approach of the study sites

Thirty (30) sites were sampled during the study period based on contrasting degrees of impacts. The environmental variables assessment for each site was performed simultaneously with macroinvertebrates sampling. Each site was sampled four times within a period of two years (2016 and 2017), covering the wet and dry seasons of each year.

2.2. Environmental variables

Environmental variables ranging from physical and chemical variables, riparian and physical-in-stream variables were measured. Depth was measured using a calibrated stick. Flow velocity was measured according to Gordon et al. (1994) method. Canopy cover was estimated visually as percentage along the sampling reach. The integrity (% riparian zone without obvious human impact) and tree species composition of the riparian zone were assessed in a 50-m section along both banks directly upstream of the sampling site. Shading by overhanging vegetation was measured as percent cover at 20 locations in evenly spaced cross-channel transects, including percentage macrophytes, and woods/logs (Ward 1992). Moss cover and substratum particle size were assessed in 10 randomly spaced 50 cm × 50 cm quadrats. The following classification of particle sizes was used (modified Wentworth scale): (0) organic matter; (1) sand (diameter 0.25 mm–2 mm); (2) fine gravel (2 mm–6 mm); (3) coarse gravel (6 mm–16 mm); (4) small pebble (16 mm–32 mm); (5) large pebble (32 mm–64 mm); (6) small cobble (62 mm–128 mm); (7) large cobble (128 mm–256 mm); (8) small boulder (256 mm–400 mm); and (9) large boulder and bedrock (>400 mm). The proportion of each size class was estimated for each quadrat and these estimates were subsequently averaged to give the mean substratum particle size for a site. At each site, 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 and they were measured spectrophotometrically after reduction with appropriate solutions (APHA 1995). Biochemical oxygen demand (BOD₅) was determined in the laboratory using APHA (1995) methods. Longitudes and latitudes were determined in the field using GPS navigator.

2.3. Macroinvertebrate sampling and processing

Macroinvertebrate samples were collected from each site alongside the environmental variables. Macroinvertebrates were sampled using a D-frame net of 500 µm mesh size according to Jeffries and Mills (1990). Samples were collected for four minutes per sampling site on each sampling occasion from sand, silt, mud, stone and vegetation per sampling site per sampling event. Samples collected from all representing biotopes per sampling event per site were pooled into one composite sample to ensure that all microhabitats are adequately sampled. The samples were preserved in 10% formaldehyde solution and transported to the laboratory for sorting, identification and enumeration. In the

Table 1

Summary of Environmental Variables Sampled for reference and impacted sites.

	Reference	Impacted
Temp (°C)	26.21 ± 0.65	26.17 ± 1.43
Depth (cm)	0.69 ± 22.74	1.00 ± 19.31
Flow (m s ⁻¹)	0.57 ± 0.45	0.30 ± 0.22
Conductivity (µS cm ⁻¹)	12.08 ± 58.35	41.27 ± 102.18
DO (mg L ⁻¹)	6.20 ± 0.59	4.38 ± 1.46
BOD (mg L ⁻¹)	2.61 ± 76.11	3.85 ± 48.52
pH	6.3 ± 0.30	6.4 ± 0.16
Nitrates (mg L ⁻¹)	0.30 ± 0.51	1.27 ± 1.39
Phosphate (mg L ⁻¹)	0.44 ± 0.88	1.48 ± 1.55

Data are the mean ± standard deviation

laboratory, samples were washed through a 250-µm mesh sieve, sorted and counted using a dissecting microscope. Sorted macroinvertebrates were identified to the lowest taxonomic level possible according to regional keys available (Day et al., 2002; De Moor et al., 2003) as well as keys from elsewhere (Merritt and Cummins, 1996). References were also made to the taxonomic lists of species known to be present in Nigeria and the region (e.g. Arimoro and James, 2008; Arimoro et al., 2012). This resulted in majorly species or genus level metrics.

3. Data analysis

All analyses were conducted in the R environment (R Core Team, 2017)

Designation of impact categories and selection of reference and impacted sites

To assess the disturbance status of the study sites, we used Principal Component Analysis on environmental variables indicative of human influence (Table 1; Fig. 2). The exact designation was achieved by extracting the coordinates of the river sites on the first axis of the PCA, and then, inter-site distances were calculated by the subtraction of the lowest scoring site from the highest scoring site (Murphy et al., 2013; Odume et al., 2016; Edegbene et al., 2019, 2020). The scores of the successive sites were also subtracted from the highest scoring sites. Thereafter, the inter-site distances were converted to per cent distances, and a percentile distribution was used to delineate the sites into reference (RS) and impacted (IS) categories with percentile distribution of 100–81th, and < 81–0th, respectively (Table 2). This procedure resulted in 14 reference sites and 16 impacted sites. The first PCA axis was used in categorizing the sampled sites into ecological status/categories because it explained 38% variation of the ordination plot which is higher than 22% variation explained by Axis 2 of the PCA ordination plot performed (Murphy et al. 2013). The remaining six PCA axes accounted for 40% variation. Similar approach has recently been used by Edegbene et al. (2019) and Edegbene et al. (2020) to classify river sites into impact categories by obtaining the environmental variables distances along the first axis of PCA. Also, Murphy et al. (2013) and Odume et al. (2016) had earlier employed the same method in calculating species distances along the first axis of canonical correspondence analysis (CCA). The PCA ordination was calculated in the R package vegan (Oksanen et al. 2017).

3.1. Analysis of the contributions of the components of Beta-diversity

We calculated beta diversity between the references and impacted sites. We used distance-based redundancy analysis (dbRDA; Legendre and Anderson, 1999) to examine variations in each component of beta diversity. In our initial analyses (result not shown), we considered the temporal effects by analysing the data seasonally and temporally, but the results showed that temporality had no effect on our analyses. Consequently, we based all analyses on the four temporal samples as replicates for each site.

Beta diversity was quantified by four components (Bray-Curtis, Sørensen, turnover, and nestedness). Bray-Curtis index is based on

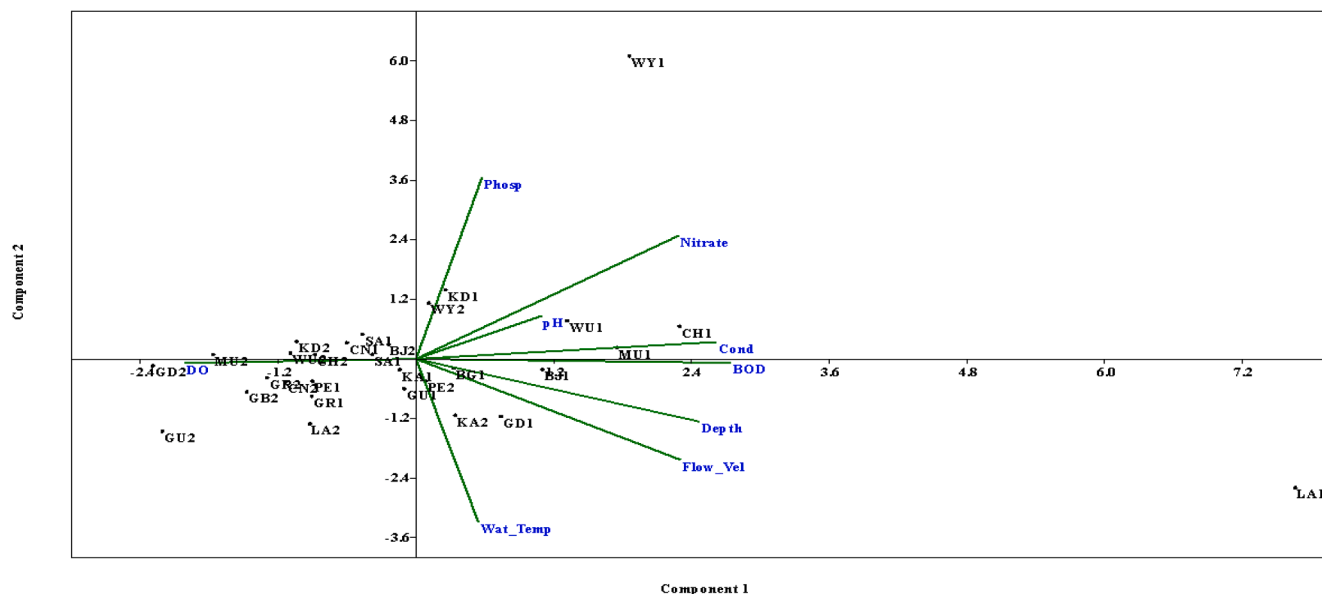


Fig. 2. PCA correlation function showing sites categorization of environmental variables (Variation explained: Axis 1 = 38%; Axis 2 = 22%). Abbreviations: Wat Temp (water temperature), Flow Vel (flow velocity), Cond (conductivity), DO (Dissolved oxygen), BOD (five-day biochemical oxygen demand), Phosp (phosphate). See Table 2 for site codes.

Table 2
River sites categorization into ecological status in the study area.

River sites	River sites codes	Sites coordinates on the first axis of the PCA	Distance of inter-sites	% Distance of inter-sites	Ecological categories/status of river sites
Baka-Jeba 1	BJ1	1.101	6.559	65.904	IS
Baka-Jeba 2	BJ2	-0.240	7.900	79.378	IS
Chanchaga 1	CN1	-0.602	8.261	83.009	RS
Chanchaga 2	CN2	-1.131	8.790	88.328	RS
Chike 1	CH1	2.296	5.363	53.890	IS
Chike 2	CH2	-0.880	8.540	85.810	RS
Gada 1	GD1	0.740	6.920	69.531	IS
Gada 2	GD2	-2.292	9.952	100	RS
Gbako 1	GB1	0.329	7.330	73.653	IS
Gbako 2	GB2	-1.474	9.133	91.778	RS
Grigada 1	GR1	-0.908	8.567	86.087	RS
Grigada 2	GR2	-1.296	8.955	89.982	RS
Gurara 1	GU1	-0.102	7.761	77.984	IS
Gurara 2	GU2	-2.209	9.869	99.162	RS
Kaduna 1	KD1	0.259	7.400	74.358	IS
Kaduna 2	KD2	-1.039	8.699	87.408	RS
Kataregi 1	KA1	-0.141	7.800	78.384	IS
Kataregi 2	KA2	0.341	7.318	73.537	IS
Landzun 1	LA1	7.66	0.000	0	IS
Landzun 2	LA2	-0.924	8.583	86.252	RS
Musa 1	MU1	1.752	5.907	59.359	IS
Musa 2	MU2	-1.767	9.426	94.713	RS
Penyan 1	PE1	-0.900	8.560	86.011	RS
Penyan 2	PE2	0.083	7.575	76.120	IS
Samu 1	SA1	-0.464	8.124	81.633	RS
Samu 2	SA2	-0.382	8.041	80.806	IS
Wushishi 1	WU1	1.316	6.343	63.740	IS
Wushishi 2	WU2	-1.093	8.753	87.955	RS
Wuya 1	WY1	1.860	5.799	58.273	IS
Wuya 2	WY2	0.110	7.549	75.850	IS

Note: River sites categorization: IS = impacted sites, RS = reference sites

abundance data (driven by differences in species abundance between sites), while Sørensen index is based on presence/absence data (driven by species composition between sites). However, turnover and nestedness components of beta diversity were computed for presence/absence data from Sørensen index. All these lead to the four distance matrices that were further used as response variable/data in dBRDAs. We first obtained dissimilarity matrices based on abundance and presence-absence data using the function “beta.pair” in the R package *betapart* (Baselga et al. 2017). The index used was a monotonic transformation of a Sørensen index, in which turnover (i.e. replacement of some species by others) and nestedness (i.e. number of species is subset of richer sites) can be separated (Baselga, 2010, 2012). This function produces three multiple-site dissimilarity matrices: (1) Sørensen dissimilarity that measures overall spatial turnover in species composition; (2) Simpson dissimilarity that measures turnover immune to species richness variation (i.e. replacement of some species by others), and; (3) nestedness resulting from species richness differences between sites (Baselga, 2010, 2012).

3.2. Selection of explanatory variable of beta diversity and community structure

We used dBRDA-based forward selection technique to select the final local environmental variables for the models of each biological dissimilarity matrix using the functions *capscale* and *ordIR2step* in the R package *vegan*. In the light of this, the local environmental variables selection was based on two stopping rules technique (Blanchet et al. 2008), whereas the status variable (one variable, two levels) and geographical variables (2 variables) were forced in all analyses (Brittain et al 2020). We did not perform forward selection with variable groups ‘status’ (one variable, two levels) or ‘geography’ (2 variables), so forward selection was only done with the environmental predictor (Brittain et al 2020).

3.3. Variation partitioning of selected predictor variable group

We specifically used dBRDA in variation partitioning to test for the contribution of local environmental, status, and geographical (spatial) factors on the beta diversity. After the final sets of variables for each predictor variable group were selected, variation partitioning in each

dissimilarity matrix was decomposed into X1 (environmental variables) and X2 (status/group variables) and X3 (geographical variables) as predictor variables following a partitioning approach that is widely used (Borcard et al., 1992; Legendre & Legendre, 2012; Heino & Alahuhta 2015). In all our analyses that involved dBRDA, we included the square root transformation of dissimilarities ($\text{sqrt.dist} = \text{TRUE}$) in the R script to euclidify biological dissimilarities (Legendre, 2014). We also used presence-absence data in our analysis to remove any bias that could be initiated by variations in collection regimen that might influence the abundance data (Brittain et al. 2020). Variation partitioning of species data (Y) among three sets of predictor variables results in pure environment fraction, pure status classes fraction, pure geographical fractions, as well as their shared effects and unexplained variance (U). Variation partitioning was run using the function ‘varpart’ in the R package vegan (Oksanen et al. 2013). Finally, the significance of the pure fractions was tested using the function ‘anova’ in the R package vegan. In all dBRDA-related analyses, a Lingoes correction for negative eigenvalues was added in the script (Oksanen et al. 2017). Values of adjusted R^2 were reported since they typically represent impartial estimation of explained variance (Peres-Neto et al., 2006). Our interpretations of effects of predictors were built on adjusted R^2 values rather than P-values, given our interest in effect sizes rather than just significance. Principal coordinates analysis (PCoA) was drawn to elucidate further differences in beta diversity between reference and impacted sites for the abundance and presence-absence dissimilarities (Rocha et al. 2017). We did not use more sophisticated spatial modelling approaches and associated variables such as Moran Eigenvector maps (MEM), PCNM, AEMs and others (Dray et al., 2012; Legendre & Legendre, 2012) given that such spatial methods are not likely perfect when the distances in space between sampled points are large (Declerck et al. 2011)

We used PERMDISP to examine differences in beta diversity (average distances of communities to group multivariate centroids) between the reference and impacted sites (Anderson et al. 2009). PERMDISP was run using the *betadisper* function in the R package vegan. PERMDISP is a useful statistical tool for testing the homogeneity of multivariate dispersions within factor groups based on deviations from the group centroid. Given that PERMDISP compares distances from observations to their group centroids using ANOVA F statistics, it is only useful in analyzing the influence of factors, and therefore not useful in analyzing the influence of continuous variables. Once all the groups are centered to a common location, group sample permutations are used to obtain the P-values resulting from residual permutation. This approach excludes possible location variations and enables the replacement of obtained residuals under the null hypothesis of homogeneity of dispersions, in contrast to location influence. By implications, PERMDISP tests if the reference sites communities differ from impacted sites communities in their variance. Furthermore, if any of the groups (reference and impacted groups in our study) has a significantly higher mean distance, it means that this group has more variable and heterogenous macro-invertebrates assemblages and therefore has greater beta diversity (Anderson et al. 2006).

Multivariate analysis of differences in community composition between the reference and impacted sites was conducted using Permutational Multivariate Analysis of Variance (PERMANOVA). PERMANOVA tests were run using the function *adonis* in the R package vegan (Oksanen et al., 2017). PERMANOVA is an analysis of variance using distance matrices among variation sources; it is a test of location of group centroids, not of dispersion. It is a robust tool for evaluating variation attributes of different experimental treatments (Legendre and Anderson, 1999). PERMANOVA tests if the communities differ between treatments and time (if the position of the centroids differ among the treatments). For instance, if the communities in reference sites do not differ from communities in impacted sites, then the position of the centroids will not also differ.

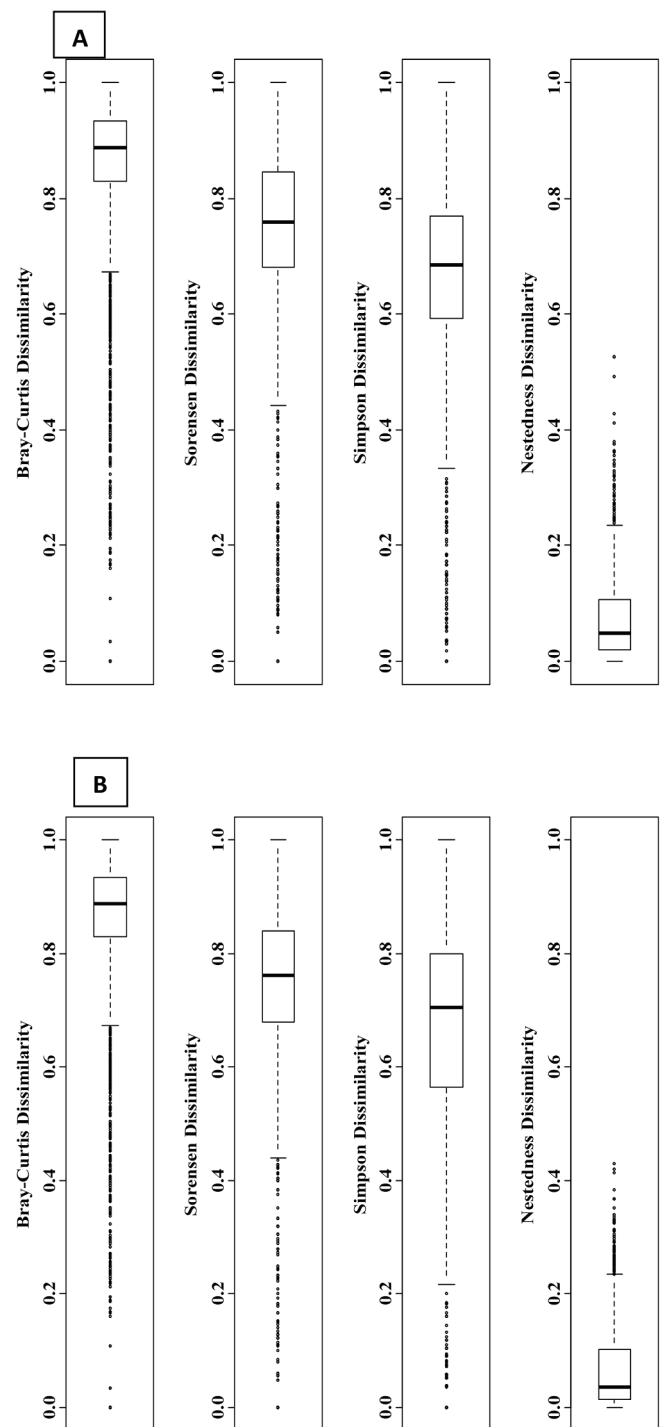


Fig. 3. Boxplots of variation in between-site pairwise dissimilarity matrices for abundance (Bray-Curtis) and presence-absence (based on the total beta diversity, turnover, and nestedness-resultant) for the reference (A) and impacted (B) sites.

4. Results

Though the impacted sites were more relatively abundant than the reference sites, the reference sites were largely comprised of the pollution-sensitive taxa (Ephemeroptera, Tricoptera, Coleoptera, and Odonata), while the impacted sites were largely composed of the pollution-tolerant taxa (Diptera, Oligochaeta, and Mollusca). The average number of species was higher for reference sites (51.2) than impacted sites (43.9).

Table 3Variation partitioning results of dissimilarities showing contributions of various response variables. Shown are adjusted R² values.

Distance matrix	Pure Fraction			Shared Fraction				Residual
	Env	Status	Coord	Env/Status	Env/Cord	Status/Cord	Env/Status/Cord	
Bray-Curtis	0.10	0.03	–	0.01	–	–	–	0.91
Sørensen	0.06	0.02	–	0.02	–	–	0.00	0.92
Simpson	0.04	0.01	–	–	0.00	–	0.00	0.95
Nestedness	0.01	0.00	–	–	0.00	–	0.00	1.00

Key: Env = environmental; Coord = coordinate

Table 4

Summary of PERMDISP Average distance to median in differences in Beta diversity between reference and impacted sites and PERMDISP tests of homogeneity of dispersions results based on mean distance to group centroid between reference and impacted sites.

Distance Matrix	Average distance to median		Sum of square	Mean square	F value	Pr (>F)
	Reference	Impacted				
Bray-Curtis	0.6061	0.5843	0.01413 (0.50499)	0.0141311 (0.0042796)	3.302	0.07173
Sørensen	0.5200	0.5188	00,004 (1.02662)	0.0000887 (0.0087002)	0.0000374	0.9478
Simpson	0.4705	0.4663	0.00052 (1.63866)	0.0005239 (0.0138870)	0.0377	0.8463
Nestedness	0.05954	0.05559	0.000468 (0.298888)	0.00046835 (0.00253295)	0.1849	0.6680

Values before parenthesis represent the groups while values in parenthesis represent values of residuals

For both reference and impacted sites, the total beta diversity (Sørensen) was driven by the turnover (Simpson) component of beta diversity, while the effects of nestedness-resultant were largely negligible (Fig. 3).

Plots of variation partitioning revealed that the model was very weak, as it explained only minor part of the variation in community structure (Table 3). However, most of the variations in community compositions were associated with the environmental variables as predictor in the model, followed by the status as predictor. The range of pure fractions of environmental variables, status variables, and geographical variables were 0.1% – 1%, 0% – 3%, and 0%, respectively. The geographical variables (longitudes and latitudes) had no (0%) contribution, and therefore, no pure fraction was associated with it. The highest shared effect among the predictor variables was observed between environmental variables and status variables (2%). In each case of shared effects of environmental and geographical variables, the value was 0%. This further typified how unimportant the geographical variables were in community composition and beta diversity of the present study. The lack of clarity in the gradient condition pattern was further buttressed by the irregular manner by which environmental variables were selected by the model. Nonetheless, the nutrients (phosphates and nitrates), moss, large pebbles, and conductivity were the variables most often selected in the model.

Beta diversity did not show any clear differences between reference and impacted sites as indicated by PERMDISP tests for all distance measures used as response (Table 4; Fig. 4). PERMANOVA for differences in community composition between reference and impacted sites revealed slight/average significant differences in composition related to turnover (i.e. the species are replaced between habitat type) between reference and impacted sites using the distance measures (Table 5; Fig. 4). Likewise, Sørensen nestedness did not reveal any significant differences in community composition between reference and impacted sites.

5. Discussion

We surveyed the relationships among macroinvertebrates beta diversity (β), river status, and environmental correlates in Northern region of Nigeria. To our knowledge, this is the first multivariate analysis of ecological communities in Africa that surveyed beta diversity patterns considering two status classes (reference and impacted). Our study revealed weak relationships among macroinvertebrate beta diversity, stream status, and environmental conditions. Although beta diversity

between reference and impacted sites was similar in our study, there were significant differences in composition related to turnover between the reference and impacted sites. When subjected to similar type and severity of disturbance, the trends of variation in species composition are possibly dependent on variations in starting productivity and disturbance (Smart et al. 2006). This might plausibly be the reason why a consistent association between species composition and beta diversity decline (biotic homogenization) is not likely (Smart et al. 2006). As shown by the results of our constrained ordination technique and the prevalence of species turnover component of beta diversity, variations in our community structure were most strongly related to environmental factors, while the spatial factors were not important in macroinvertebrates community structuring. Hence, in agreement with our expectation, species sorting processes were likely the important drivers of community structure in our study, while spatial factors (dispersal) were not influential. This result agrees with world-wide patterns exhibited by insects, and also corroborates with previous studies that were limited to single or few drainage basins (Landeiro et al., 2012; AL-Shami et al., 2013; Göthe et al., 2013; Grönroos et al., 2013).

Although there was a high degree of unexplained variation, our inability to explain large amounts of variation is neither an obstacle nor a limitation, given that such low or critically lower accounts of explained variations are typical in recent surveys that employed similar modern analytical methods (constrained ordination analyses) based on adjusted R² (Beisner et al., 2006; Heino et al., 2012, 2013, 2015b; Landeiro et al., 2012; Göthe et al., 2013; Souffreau et al., 2015; Tonkin et al., 2016; Rocha et al., 2017; Brittain et al., 2020); and yet they never threatened the disclosures of important mechanisms of community structure. The potential mechanisms underlying high residual (unexplained) variation include stochastic processes, unmeasured environmental variables, inadequacy in modelling of spatial processes, and many more (Heino et al., 2015b; Rocha et al., 2017). While we measured a broad suite of environmental variables, we cannot overlook the possibility that stochastic processes and unmeasured environmental variables (such as land use) are likely to be important in our study, and would have strengthened our findings and generated much higher degree of explained variation than we observed. This may also likely explain why the variance explained by environment for our communities was lower than those reported in other studies

The concept of biotic homogenization is understood to mean that if there is higher human impact in the system, beta diversity should diminish. Our second prediction that beta diversity will be promoted more in the reference sites than impacted sites was rejected since it is not

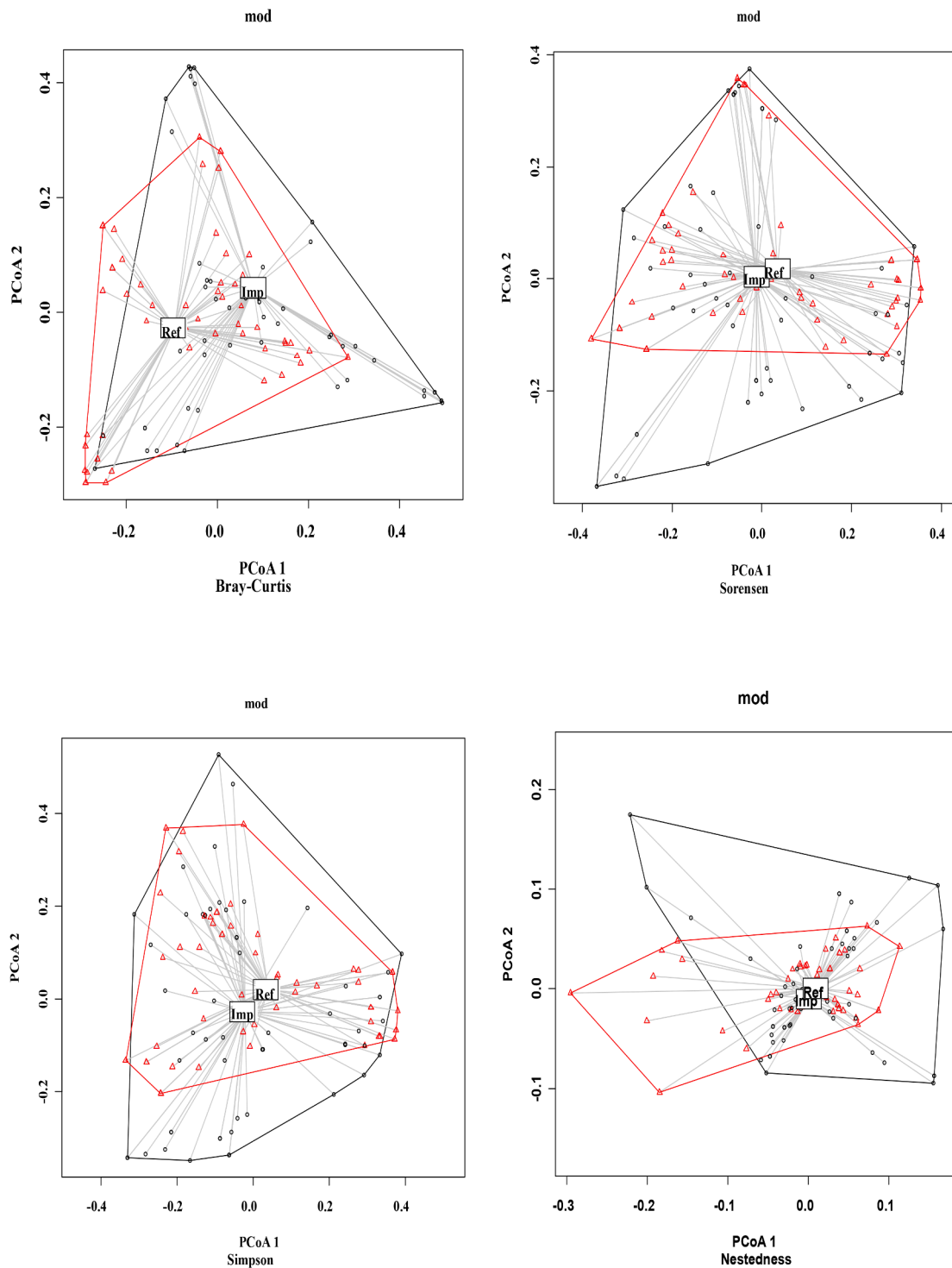


Fig. 4. Plots of variation in beta diversity between reference and impacted sites based on the different distance matrices. Red colour = reference sites; black colour = impacted sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in consonance with the findings of this study. This study, therefore, supports the hypothesis that human impacts and disturbances do not necessarily lead to biotic homogenization (Ekroos et al., 2010; Flohre et al., 2011; Karp et al., 2012). Environmental disturbances affect some species and favor other species, resulting to the tendency of certain taxa becoming more frequent while some other taxa become less frequent (Heino and Peckarsky, 2014; Hawkins et al., 2015), which may provide some explanation for the similarity between beta diversity of the reference and impacted sites of this study. The lack of consistent

coupling between beta diversity and community composition changes (between the reference and impacted sites), where sites close in space (same river) but showing changes in community composition, further supports the fact that species sorting could be prevalent in our study. Heino et al. (2015b) analyzed a dataset of 95 stream insect communities from 31 drainage basins distributed around the world. The outcome from their findings deviated from the general biodiversity patterns as they found weak relationship between beta diversity and environmental predictors. In light of their results, they called for further consideration

Table 5

Permutational Multivariate Analysis of variance (PERMANOVA) result showing differences in community composition between reference and impacted sites using distance matrices.

Distance Matrix	Sum of square	Mean square	F model	R2	Pr (>F)
Bray-Curtis	1.837 (42.976)	1.837 (0.364)	5.0447	0.041 (0.959)	0.001**
Sorensen	1.321 (33.276)	1.3212 (0.2820)	4.685	0.0382 (0.96181)	0.001**
Simpson	1.2089 (27.8234)	1.20891 (0.23579)	5.1271	0.04164 (0.95836)	0.001**
Nestedness	-0.03216 (0.65305)	-0.32147 (0.005534)	-5.8105	-0.05179 (1.05179)	0.999

Values before parenthesis represent the groups while values in parenthesis represent values of residuals.

of how predictions are inferred on beta diversity and environmental correlates. The result of Hawkins et al. (2015) revealed that environmental disturbance increased beta diversity across the Mid-Atlantic highlands region of the USA and Finland, citing different attributes of environmental filtering and other unexplained conditions as possible reasons. Furthermore, the results of Fugère et al. (2016) showed that beta diversity was higher in the agricultural streams than the forested streams of tropical Africa. Al-Shami et al. (2013) associated reduced beta diversity to anthropogenic pollution (low water pH) in tropical streams of Peninsular Malaysia. Similarly, the findings of Liborio and Tanaka (2016) in rivers in Sao Paulo, Brazil, showed that beta diversity was higher in forested streams than disturbed streams. The outcome of Canovas et al. (2013) in streams of Iberian Peninsula supported the hypothesis that natural and human-induced degradations produce entirely contrasting patterns on beta diversity – and that the contrasting patterns are as a result of varying mechanisms. Our present study revealed weak relationships among beta diversity, stream status, and environmental correlates. The implication of the results of the aforementioned studies on beta diversity and environmental predictors is that beta diversity is not likely controlled by a single factor, and that these differing factors have different effects on beta diversity. Such results in the tropics may be due to elevated demographic stochasticity or neutral processes that govern community structure in the tropics in comparison to temperate communities (Zhang et al. 2015; Liborio and Tanaka 2016a). The significance of these findings stresses how highly unpredictable stream community structure is.

Anthropogenic activities are usually associated with alterations in many water quality variables (Keke et al., 2020), such as thermal changes and toxic agents (Hawkins et al. 2015). Unfortunately, these parameters are rarely measured or overly overlooked in several studies (Hawkins et al. 2015), including our present study. Other important ecological descriptors, including primary production, predation, and proximity and degree of substratum dislodgement have also been classified as important drivers of community structure and beta diversity in single-case-studies (Townsend et al. 2000). Since measuring such site-level predictors allows for strict comparisons across datasets (Heino et al. 2015a), we cannot guarantee that the presence of unmeasured pollutants and/or unmeasured ecological predictors did not affect beta diversity in our study. The poor explanatory power in our study as well as most other studies across the world that employed similar technique could be suggesting that researchers should endeavour to measure more of some of these important ecological and pollution indicators in the field. Additionally, since beta diversity can either be increased or decreased by disturbance-induced mortality -depending on individual taxa vulnerability to disturbance - regardless of alterations in habitat heterogeneity (Hawkins et al. 2015), we cannot also preclude the importance of environmental disturbance more severe than what we recorded on beta diversity. We, therefore, advocate that in examining the mechanisms regulating changes in waterways and landscape and

how they affect beta diversity, a holistic evaluation of the types of stressors that occur in a stream and the effect these stressors impact on the individual organism is uppermost.

Understanding the patterns of biodiversity, especially with reference to effects of both natural and anthropogenic disturbances on biodiversity is uttermost in biodiversity management, conservation, and restoration. To synthesize the major findings of our study, we conclude that this study adds to the growing literature worldwide that environmental disturbances do not necessarily lead to biotic homogenization. In addition, we also broaden the perspective that species sorting (by local environmental factors) is the prevalent factor in metacommunity structure. It is fundamental for environmental conservationists and restoration ecologists to take advantage of the usefulness of evaluating homogeneity (PERMDISP) and location effects (PERMANOVA) in unravelling the effects of anthropogenic impacts on beta diversity, by considering varying degrees of disturbances, in their attempt to develop more efficient restoration techniques.

CRedit authorship contribution statement

Unique N. Keke: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Francis O. Arimoro:** Supervision, Writing - original draft. **Adesola V. Ayanwale:** Supervision, Writing - review & editing. **Oghenekaro N. Odume:** Writing - review & editing. **Augustine O Edegbene:** Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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