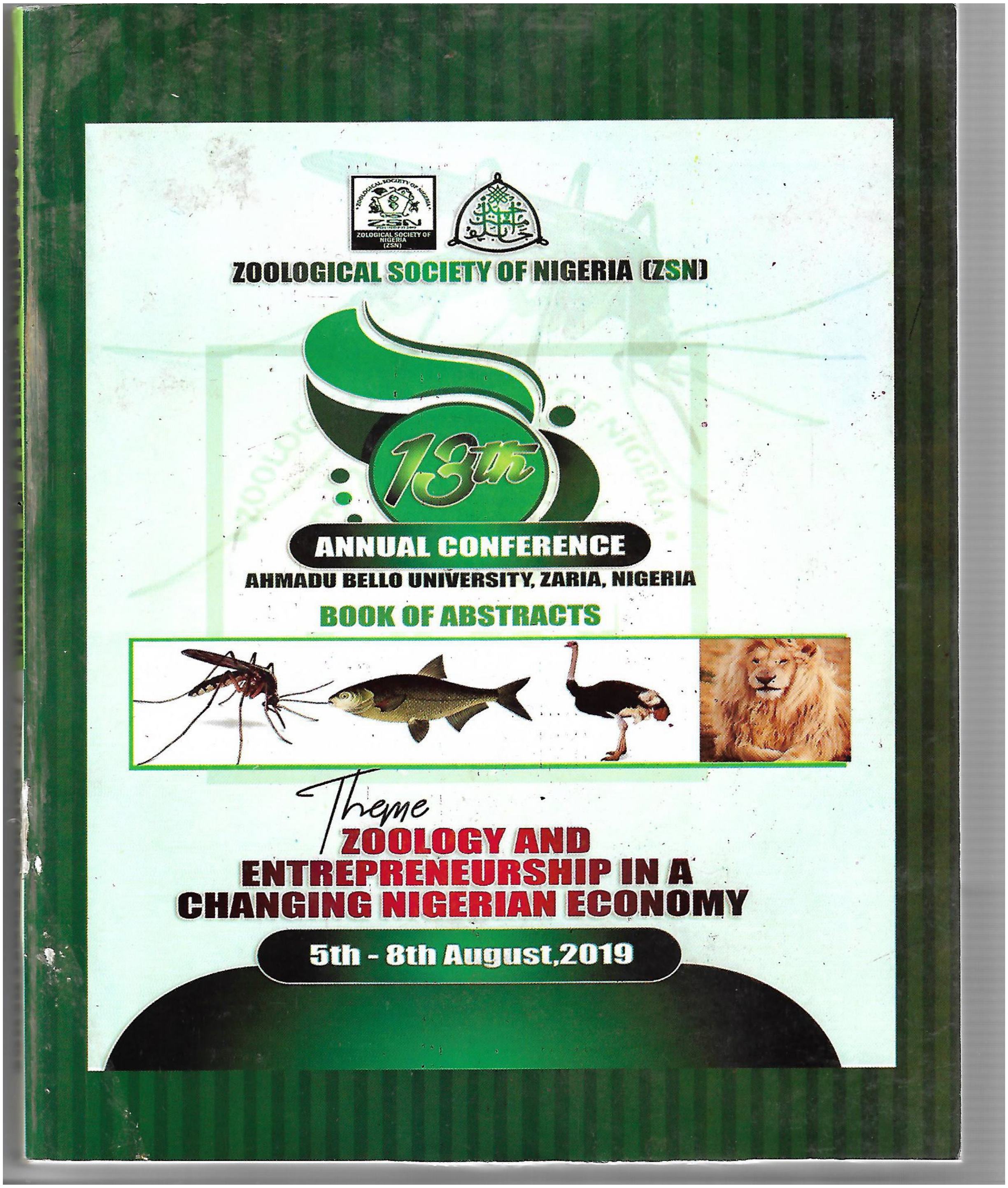

ZOOLOGICAL SOCIETY OF NIGERIA (ZSN)

13th

ANNUAL CONFERENCE

AHMADU BELLO UNIVERSITY, ZARIA, NIGERIA

BOOK OF ABSTRACTS

Theme

ZOOLOGY AND ENTREPRENEURSHIP IN A CHANGING NIGERIAN ECONOMY

5th - 8th August,2019

ZSN/160/2019

FRESHWATER BIODIVERSITY–ENVIRONMENT RELATIONSHIPS: QUANTIFYING AND DECOMPOSING THE COMPONENTS OF BETA DIVERSITY IN TROPICAL STREAM MACROINVERTEBRATES COMMUNITIES

Unique N. Keke, Francis O. Arimoro and Ayanwale, A. V.

Applied Hydrobiology Unit, Department of Animal Biological, Federal University of Technology, Minna, Nigeria

ABSTRACT

There is considerable understanding of biodiversity–environment interactions in terms of species composition and richness, while other categories of biodiversity components, especially beta-diversity, have been scarcely considered and attended to in the tropics, and no attention at all in Nigeria. Effects of environmental and spatial factors on beta-diversity were assessed in a tropical biodiversity hotspot. Fifteen near-pristine/reference streams were surveyed for benthic macroinvertebrates in the northern part of Nigeria and beta-diversity was calculated based on combined multiple sites. Variations in each component of beta diversity were examined by obtaining dissimilarity matrices based on species abundance data and presence-absence data to quantify the contributions of each component of beta diversity to total beta diversity. Variation partitioning approach was employed in decomposing variations in community composition of macroinvertebrates along sets of categorical/predictor variables. Macroinvertebrates communities revealed that analysis involving both abundance and presence-absence were characterized by relative high degree of beta diversity. Turnover component of biodiversity accounted for high levels of total beta diversity, while the effect nestedness component (Simpson) was negligible. Variation partitioning revealed a relatively large pure fractions for environmental variable for Bray-Curtis, total, and turnover components as their pure fraction values were 14 %, 14 %, and 10 % respectively. However, small pure fractions were associated with geographical variables for Bray-Curtis, total, and turnover components with values of 3 %, 4 %, and 3 %, respectively. Similarly, the shared effects of environmental variables and geographical coordinates for Bray-Curtis, total, and turnover components were negligible as they all were associated with 0 % shared effects. No variable was related with nestedness-related community composition. dbRDA plot based on Bray-Curtis and total beta diversity revealed strong variation in species structure was related to environmental conditions. These findings suggest that, while species sorting is an important driver of ecological community in a small spatial scale metacommunity, the spatial factors and processes may also assume significance in structuring variations, but such variations are negligible and could be attributed to co-variance with other unexplained factors.

Keywords: Beta-diversity, variation partitioning, predictor variables, species sorting, macroinvertebrates, Nigeria

Freshwater Biodiversity–environment relationships: Quantifying and decomposing the components of beta diversity in tropical stream macroinvertebrates communities

Unique N. Keke, Francis O. Arimoro, and Ayanwale, A. V

Applied Hydrobiology Unit, Department of Animal Biological, Federal University of Technology, Minna, Nigeria

Abstract

There is considerable understanding of biodiversity–environment interactions in terms of species composition and richness, while other categories of biodiversity components, especially beta-diversity, have been scarcely considered and attended to in the tropics, and no attention at all in Nigeria. We examined effects of environmental and spatial factors on beta-diversity in a tropical biodiversity hotspot. We surveyed 15 near-pristine/reference streams for benthic macroinvertebrates in the northern part of Nigeria. Beta-diversity was calculated based on multiple sites of the near-pristine/reference stations combined (15 streams). We examined variation in each component of beta diversity by obtaining dissimilarity matrices based on species abundance data and presence-absence data to quantify the contributions of each component of beta diversity to total beta diversity. We employed variation partitioning approach in decomposing variations in community composition of macroinvertebrates along sets of categorical/predictor variables. Macroinvertebrates communities revealed that analysis involving both abundance and presence-absence were characterized by relative high degree of beta diversity. Turnover component of biodiversity accounted for high levels of total beta diversity, while the effect nestedness component (Simpson) was negligible. Variation partitioning revealed a relatively large pure fractions for environmental variable for Bray-Curtis, total, and turnover components as their pure fraction values were 14 %, 14 %, and 10 % respectively. However, small pure fractions were associated with geographical variables for Bray-Curtis, total, and turnover components with values of 3 %, 4 %, and 3 %, respectively. Similarly, the shared effects of environmental variables and geographical coordinates for Bray-Curtis, total, and turnover components were negligible as they all were associated with 0 % shared effects. No variable was related with nestedness-related community composition. dbRDA plot based on Bray-Curtis and total beta diversity revealed strong variation in species structure was related to environmental conditions. Our finding suggests that while species sorting is an important driver of ecological community in a small spatial scale metacommunity, the spatial factors and processes may also assume significance in structuring variations, but such variations are negligible and could be attributed to co-variance with other unexplained factors.

Keywords: Beta-diversity, variation partitioning, predictor variables, species sorting, macroinvertebrates, Nigeria

Correspondence: uniquekkn@gmail.com; n.keke@futminna.edu.ng.

Introduction

The emphasis on the importance of biodiversity conservation and management strategies can never be overemphasized, following very serious decline in biodiversity globally. Hierarchically, two major classifications of biodiversity are rife: First, the one that recognizes three (3) levels of organization, namely, Intraspecific (that is genetic diversity or diversity at the generic level), Interspecific (that is species diversity or diversity at species level), and hyperspecific (referring to ecosystem diversity or diversity at the ecosystem level). Second, the other by Whittaker (1972) that recognizes three (3) types of biodiversity considered over spatial scales, namely, apha (α) diversity (that describes diversity within the same ecosystem or diversity within species), beta (β) diversity (that describes diversity between species or diversity or variation in species richness/number between ecosystems of same region), and gamma (γ) diversity (that refers to diversity of ecosystems or the total diversity of different ecosystems of a particular region).

Apha and gamma diversities are expressed in form of species numbers. Gamma diversity, on the other hand, is relative; and therefore, expressed as gamma/apha diversity quotient. Again, beta diversity is driven by its components of turnover (replacement of some species by others) and nestedness-resultant (species richness differences between sites or loss or gain of species) (Baselga, 2010; Legendre, 2014). In modern empirical and theoretical ecological studies, patterns in both Local (α -diversity) and regional (γ -diversity) species richness have been considered with specific reference to environmental heterogeneity. (Field *et al.*, 2009; Heino *et al.,* 2013). Opposite, the ecological studies on beta diversity (β-diversity) have been scarcely represented, especially within the last two (2) decades (Soininen *et al.*, 2007; Heino *et al.,* 2013) – though substantial advances and efforts have been put in methods of its characterization. (Koleff *et al.*, 2003, Tuomisto 2010, Anderson *et al.*, 2011).

It has become a fundamental target in community ecology, macroecology, and applied ecological research to understand how patterns in beta diversity are structured by disturbance-related mechanisms (Magurran, 2004; Velle *et al.*, 2014; Rolls *et al.,* 2016). Since the patterns of flooding and drying of rivers and streams differ in time and space (spatio-temporal dynamics), rivers and streams constitute veritable systems to study and relate how much disturbance-related mechanisms factor biodiversity on a landscape scale. (Townsend, Datry *et al*., 2016a). Therefore, rivers flow regime characteristics are classified according to several environmental predictors that showcase their multifaceted approach (Olden & Poff, 2003; Kennard *et al*., 2010), thus: the Perennial streams that refer to streams and rivers that are in continuous flow; and the Intermittent steams that describes streams and rivers that cease to flow at certain times or periodically. However, each of these types can further be divided according to their individual patterns of predictability, seasonality, and flow durations (Kennard *et al*., 2010; Rolls *et al.,* 2016). It is expected that differing environmental composition of niches should consequently lead to differences in species composition and beta-diversity accompanied with spatial variations in their environmental correlates (Heino and Mykra¨ 2008, Brown and Swan, 2010; Heino *et al.,* 2013). Interestingly, the research of decomposing the relationships between various components of beta-diversity and environmental heterogeneity has been scarce, especially in tropical stream ecology (Clarke *et al*., 2008). This is rather very surprising given their high heterogenous nature portrays the streams as ideal models and platforms to unravel the relationships between beta-diversity and environmental heterogeneity (Heino *et al.,* 2013).

Several accounts of stream survey have revealed that different organisms tend to respond differently to environmental variables ((Paavola *et al*., 2003; Heino *et al*., 2005; Grenouillet *et al*., 2008; Mykra¨ *et al*., 2008; Heino, 2011). For example, algae tend to be closely related with water acidity and nutrients composition (Griffith *et al*., 2002; Heino and Soininen, 2005) while bryophytes are closely related with substratum characteristics and stream stability (Fritz *et al*., 2009). Similarly, benthic macroinvertebrates are associated closely to stream acidity, shading, canopy cover, and stream size (Heino *et al*., 2003a; Sandin and Johnson, 2004). Albeit, there seems to be a weak and problematic link in establishing the influence of these very important environmental variables on the overall species composition and beta-diversity of benthic invertebrates. For instance: first, different studies conducted on the possible effects of decrease in pH resulted an unexpected outcome (Sandin, 2003; Petchey *et al*., 2004; Petrin *et al*., 2007). Second, Donohue *et al.* (2009) posited from their outcome in a 45-lake research that there was no significant relationships of whatever dimension between any of the considered diversity measures of benthic macroinvertebrates and either of phosphorus concentrations or and/or loads of nutrients. Third, there was a clear demonstration from a study by Johnson and Hering (2009) in 143 streams in Europe that there were no relationships between macrobenthos diversity and nutrient enrichment and/or habitat degradation. However, while it is evidenced that macroinvertebrates diversity tend to be significantly connected with some sorts of strong ecological descriptors, including stream productivity or even habitat heterogeneity, it is also possible for simple and even abiotic environmental variables to have very strong effects on different benthic invertebrates groups (Voelzl and McArthur, 2000). This assertion is strongly corroborated by a number of other studies that abound the world. For instance, Tixier and Guerold (2005) showed that freshwater acidification was the most environmental predictor of diversity of Plecoptera species. Again, Koperski (2010a) similarly demonstrated from his study that the taxonomic diversity of the major dominant groups of benthic macroinvertebrates is a function of their various responses to differing environmental variables. For example, while Odonata group responds to or is affected by stream width, the Ephemeroptera group responds to stream pollution, and; Gastropoda is affected by the nature of the substrate composition. Similarly, Moore and Palmer (2005) have demonstrated that the EPT

(Ephmeroptera, Plecoptera, and Trichoptera) species richness sensitivity to oxygen depletion has become a veritable use as an index of stream pollution, as well as indicators of land-use patterns and riparian cover characteristics.

In Nigeria, environmental perturbations and land use procedures are major threats to the biodiversity and integrity of its natural ecosystems. Despite being considered hotspots of riparian and stream biodiversity, headwater ecosystems have not been studied and conservation programs for both long and short time have not been earmarked. Our aim was to fill this gap by disentangling and decomposing the various components of beta-diversity among 15 streams metacommunity in the northern part of Nigeria. We also determined the factors that contribute mostly to community structure and beta-diversity.

Methods

We studied a total of 15 streams from Northern Nigeria. The range of the study area was from 9°N to 10°N and 6°E to 7°E (Figure 1), and it is characteristics of tropical climate of dry season (from November – March) and wet season (from April – October). Natural vegetation and mosaic of cropland mainly constitute the land use practices in the catchment. Albeit, forestry practices were also noted around the riparian and catchment areas of some of the streams. We ensured that we sampled the sites in the same season, and within a short period of time, so as to ensure collections portrayed both spatial and seasonal differences – considering differing timings of insect life cycles (Heino and Mykra, 2008).

Sampling of the study sites

The fifteen (15) sites were sampled for 24 months in 2016 and 2017, with regards to channel morphology and the chemistry of water. Each of these sites was sampled twice in a single year, and same process was repeated the following year. The assessment of the environmental variables and the sampling of macroinvertebrates were done simultaneously. To ensure that some sets of potentially interacting species were being surveyed, we endeavoured that surveys of benthic macroinvertebrates were conducted within a single period of time (see Leibold *et al*., 2004)

Environmental variables

Several environmental variables were sampled, including physical and chemical variables, riparian and physical-in-stream variables, and geographical and regional variables.

The characteristics of the local habitat

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. 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 were measured as percent cover at 20 locations in evenly spaced cross-channel transects, including percentage macropytes, 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 were 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 was subsequently averaged to give the mean substratum particle size for a site. 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. Longitudes, latitudes, altitudes, and land-use types are considered as geographical and regional variable, and they were determined in the field using GPS navigator.

Macroinvertebrate sampling and processing

At each station, using a 0.09-m^2 surber sampler with a 250-µm mesh, macroinvertebrates was collected from a 100-m stream reach comprised of three microhabitats, i.e. pools, riffles and runs, and all different substrata (vegetation, sand, gravel, etc) identified according to Jeffries and Mills (1990). To avoid bias due to spatial variations or patchiness, three random samples were collected from each of the three microhabitats by establishing a transect at each sampling reach with five equally spaced points from which a sampling point was selected using random numbers. This procedure was replicated three times for each microhabitat, making nine samples per reach and then the replicates pooled to form one composite sample per station per sampling event. Samples from the three microhabitats per sampling event per site was pooled into one composite sample to avoid artificial effects of pseudo-replication since the reason for the replicate samples from each microhabitat will be to ensure that all microhabitats are adequately sampled. The samples was preserved in 10 % formaldehyde solution and transported to the laboratory for sorting and identification. In the laboratory, samples was washed through a 250-µm mesh sieve, sorted and counted using a stereomicroscope. Sorted macroinvertebrates were identified to the lowest taxonomic level possible, mostly genus, according to Merritt and Cummins (1996), Day *et al*. (2002) and De Moor *et al*. (2003). Reference were also made to the taxonomic lists of species known to be present in Nigeria (e.g. Arimoro and James 2008; Arimoro *et al*., 2012).

Data Analysis

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

Beta-diversity analysis.

Beta-diversity was calculated based on multiple sites of the reference stations combined (15 streams). The emphasis is on reference/headwater streams, because their biodiversity remains generally poorly-known, yet they are sensitive to and severely threatened by landscape alteration and instream habitat changes. Specifically, distance-based redundancy analysis (dbRDA; Legendre and Anderson, 1999) was used to examine variation in each component of beta diversity. We first obtained dissimilarity matrices based on species presence-absence data using the function “beta.pair” in the R package *betapart* (Baselga *et al.,* 2017). The index that we used is 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 in subset of richer sites) can be separated (Baselga, 2010, 2012). This function produces three multiple-site dissimilarity matrices: (1) Sorenson dissimilarity that measures overall spatial turnover in species composition; (2) Simpson dissimilarity that measure turnover immune to species richness variation (i.e. replacement of some species by others), and: (3) nestedness resulting from species richness differences between sites (i.e. number of species in subset of richer sites) (Baselga, 2010, 2012). We also obtained dissimilarity matices based on species abundance data using the function "beta.pair" in the R package *betapart* (Baselga *et al.,* 2017). Beta-diversity calculations may help revealing the degree of differentiation of species composition within and across the streams. Each of the resulting three dissimilarity matrices was used as response variable/data in dbRDAs.

Selection of explanatory variables.

The final sets of local environmental (phosphorus, nitrates, pH, Conductivity, Cobbles, sand, canopy cover, etc) and geographical variables (latitude and longitude) were selected for the constrained ordination (dbRDA) models, using a forward selection method with two stopping rules (Blanchet *et al.,* 2008b). This method first tests for the significance of the global model (i.e. a model comprised of all environmental and all geographical variables), and only if the global model is significant we proceed with forward selection. The forward selection was stopped when the critical P-value was reached ($P = 0.05$) or when the adjusted R2 value of a reduced model exceeded that of the global model. Forward selection was run using the function 'ordiR2step' in the package vegan in the R environment (Oksanen et al., 2017). Each variable group was analysed separately, using forward selection as explained above. However, following the fact that the number of environmental variables sampled (n=20) were far bigger than the number of streams sampled (n=15), all the environmental variables were subjected to pair-wise correlation matrix. This allowed one of the pairs of variables with correlation > 0.7 to be excluded from the environmental variables that were used to run the final analyses as explanatory variables.

Variation partitioning.

Variation in a site-by-species matrix variation in macroinvertebrates community structure across the study sites were analysed (Legendre *et al.*, 2005; Anderson *et al.*, 2011). After the final sets of variables for each predictor variable group were selected, variation partitioning in each dissimilarity matrix using X1 (environmental variables) and X2 (geographical variables) as predictor variables following a partitioning approach that is widely used (Borcard *et al.*, 1992; Legendre & Legendre, 2012; Heino & Alahuhta, 2015). Variation partitioning of species data (Y) among two sets of predictor variables results in pure environment, 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). Adjusted R2 values were reported in all analyses because they are unbiased estimates of explained variation (Peres-Neto *et al*., 2006). R2 values rather than P-values, as we were interested in effect sizes rather than significance alone. However, we also reported P-values. Finally, the significance of the pure fractions were tested using the function “anova” in the R package vegan. In all dbRDAs, a Lingoes correction for negative eigenvalues was added in the script (Oksanen *et al.,* 2017).

Community–environment relationships across the overall metacommunity were evaluated using distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999). This constrained ordination method is an extension of the original RDA based on

Euclidean distances (Legendre and Legendre, 1998) and can use any type of distance matrix as the response. They showed that RDA could be used as a form of ANOVA which was applicable to community composition data if they were transformed in some appropriate way, which went through the calculation of a dissimilarity matrix of the user's choice. This approach remains fully valid and useful for all dissimilarity measures that cannot be obtained by a data transformation followed by the calculation of the Euclidean distance. Results obtained were compared with the distance coefficients described above as the basis of the response matrices.

Taxon dbRDA ordination plots and taxon accumulation curves were drawn to ensure further understanding of the metrics. Taxon accumulation curves were based on the method "exact" in the function "specaccum" from the R package vegan (Oksanen *et al.,* 2017).

Results

The macroinvertebrates communities showed relatively high levels of beta diversity. The distance to centroids considered revealed that the total beta diversity (Sorenson) is driven by the turnover component (Simpson) while the nestedness components (Simpson) was almost negligible **(Figure 2).**

For Bray-Curtis: Conductivity ($P < 0.002$), pH ($P < 0.002$), nitrates ($P < 0.004$), flow velocity ($P < 0.012$), depth ($P < 0.002$), moss ($P < 0.008$), CPOM ($P < 0.022$), and phosphate (0.020) were significant and selected as explanatory variables, and therefore used in variation partitioning. Similarly, for total beta-diversity (Sorenson): conductivity ($P < 0.002$), pH (0.010), depth ($P < 0.010$), nitrates ($P < 0.008$), flow velocity (P <

0.018), moss ($P < 0.018$), phosphate ($P < 0.018$), and dissolved oxygen ($P < 0.024$) were significant and selected as explanatory variables, and therefore used in variation partitioning. For turnover component of beta-diversity (Simpson): conductivity ($P < 0.002$), depth ($P < 0.004$), nitrates ($P < 0.002$), moss ($P < 0.022$), canopy cover ($P < 0.008$), and macrophytes ($P < 0.026$) were significant and selected as explanatory variables, and therefore used in variation partitioning. For Sorenson nestedness resultant as response: no environmental variable was selected by the model, and this implied that no variable was significantly related with nestedness-resultant community composition.

Variation partitioning revealed a relatively large pure fractions for environmental variable for Bray-Curtis, total, and turnover components as their pure fraction values were 14 %, 14 %, and 10 % respectively **(Figures 3, 4, and 5)**. However, small pure fractions were associated with geographical variables for Bray-Curtis, total, and turnover components with values of 3 %, 4 %, and 3 %, respectively. Similarly, the shared effects of environmental variables and geographical coordinates for Bray-Curtis, total, and turnover components were negligible as they all were associated with 0 % shared effects. Conversely, no variable was related with nestedness-related community composition.

The dbRDA plot based on Bray-Curtis as response revealed strong variation in species composition with flow, nitrates, conductivity, and moss, while the dbRDA plot based on Sorenson revealed that variation in species composition was mostly influenced by conductivity, flow velocity and northings (latitude) (**Figures 6 and 7).** The taxon accumulation curve revealed that there were some taxa that were mixing, probably because they were not sampled or considered **(Figure 8)**. This is evident in the nature of the curve which didn't reach any clear plateau.

Discussion

The macroinvertebrates encountered in these study streams are composed of the majority of taxa widely distributed elsewhere in Nigeria, (Emere and Nasiru, 2009; Odume *et al*. 2012; Akaahan 2014; Arimoro *et al.,* 2015; Arimoro and Keke, 2016; Keke *et al.,* 2017) and these taxa are also among the widely distributed species with particular important roles across the food web in the freshwater biotic communities. However, majority of the previous studies in this regard targeted only biota in single freshwater bodies. To the knowledge of the author, this is about the second study with direct focus on the multivariate analysis of ecological communities, besides the study of Tonkin *et al.,* (2016) that explored stream communities in the Niger Deltan area of Nigeria.

The analyses based on both abundance and presence-absence revealed that these study streams harbored varied macroinvertebrates communities. This variability in the composition of macroinvertebrates communities clearly support the idea that near-pristine/headwater streams are highly heterogeneous at multiple spatial scales (Heino *et al.,* 2013). This is also in support of the notion that environmental factors at different scales filter species from the regional pool to those that coexist at a locality (Heino *et al.,* 2013). Similarly, the species accumulation curve and decomposition of beta-diversity further supported this assertion. The beta diversity analysis showed that the total diversity was chiefly factored by the turnover component of beta-diversity, while the nestedness effect was almost negligible. This high degree of species turnover and variation in community composition were strongly associated with the environmental variables, even though the geographical coordinates had slight association explained. It is easier at this point to infer that species sorting was probably the most important factor that structured the macroinvertebrates community composition and diversity. Previous studies have associated small-bodied organisms, such as rotifers and cladocerans with high dispersal mechanisms over long distances, and hence negate the influence of spatial processes and mechanisms in their community assemblage (Padial *et al.,* 2014; Rocha *et al.,* 2017). These small-bodied organisms often occur in high population densities, such that they are less subject to local extinction events and allow for a very large production of propagules with high dispersal potentials (Fenchel and Finlay, 2004). These features associated with the small-bodied organisms may have contributed to the strong species sorting association.

Mykra *et al*. (2007), Bennett *et al*. (2010) and Heino (2011) had reported that geographical coordinates (as spatial factors and structures) and limited dispersal related mechanisms are always more important in large-scale studies (over 2000 km long geographical gradient). However, this study differed with this assertion in its entirety as the variation observed in study tended more to environmental variables than the geographical coordinates. However, the smaller kilometer gradient covered in this study in contrast to the over 2000 km long geographical gradient may have been responsible for the deviance in the above conjectures. Also, there was no observed account of variation influence from shared effect of environmental variables and geographical coordinates as the value of the shared effect equaled zero in all the multiple site dissimilarity matrix employed as responses, including Bray-curtis. It is, therefore, plausible to affirm that species sorting was solely responsible for structuring the patterns of macroinvertebrates community observed, and that many factors may have co-varied with the geographical coordinates of the streams that resulted in pure fraction effects accounted for by the geographical coorinates. This finding from this study is in support of the recent assertion by Rocha *et al.* (2017) that most of the variations observed in macrophyte-associated cladoceran communities were explained by the environmental variables alone. This study, as well as that of Rocha *et al.* (2017) disagrees with the report that metacommuities are driven by influences from both species sorting and spatial processes (Bennett *et al.,* 2010; Heino *et al.,* 2010).

Even though the findings from this study revealed that macroinvertebrate community structure and assemblages are driven essentially by environmental variables as expected, same study also revealed that there were a considerable amount of variation that the model could not explain. This considerable amount of unexplained variation is not unconnected from reasons that may include missing environmental metric and stochastic effects (Heino *et al.,* 2015b; Rocha, 2017). The reason for the considerably low amount of unexplained variation by our model is also not farfetched as this, or even unexplained values critically higher than this, are typical of studies that employed constrained ordination analysis when adjusted R^2 are considered (Peres-Neto *et al.,* 2006). Similarly, studies from Cottenie (2005), Nabout *et al.* (2009), Heino and Mykra (2008), Landeiro *et al.* (2012), Heino *et al* (2012), Souffreau *et al.* (2015), Heino *et al.* (2015b), and Rocha *et al.,* 2017 have found unexplained variation values that were of similar magnitude to that observed in this study, yet it never foreclosed or threatened the important aspects about community structure, beta diversity, and their drivers.

Bini *et al*. (2014) and Heino *et al.* (2015b) posited that beta diversity is expected to increase with increasing spatial extent for the following four reasons. First, larger areas encompass higher environmental heterogeneity than small areas. Therefore, an increase in environmental heterogeneity is hypothesized to be positively related to the strength of species sorting processes, although evidence for such a relationship is scant (Landeiro *et* *al*., 2012; Gr€onroos *et al*., 2013). Second, the effect of dispersal limitation, promoting differences in species composition among sites, is expected to increase with spatial extent (Cottenie, 2005; Heino, 2011). Third, a positive relationship between beta diversity and spatial extent may arise from sampling different regional species pools (Heino *et al*., 2015a). Fourth, the relationship between beta diversity and spatial extent is also expected due to a negative relationship between pairwise similarity in assemblage composition and geographic distance (i.e., the distance decay of similarity; Nekola and White, 1999). Following these reasons, it is not strange that our finding is opposite to this, since there were no large variation in spatial extent among the metacommunities we studied, since the underlying factors for such reasons were birthed on very large spatial extent among metacommunites.

The findings from this research have demonstrated that species sorting is very important in structuring ecological community, while the effect of spatial factors and mechanisms like the geographical coordinates of latitude and longitude are largely ineffective in metacommunity assemblages. Nonetheless, the spatial factors (e.g longitude and latitude) may assume significance in structuring variations, but such variations are negligible and could be attributed to co-variance with other unexplained factors. However, even as environmental variables were largely important in structuring macroinvertebrates communities, they is also a very high fraction of variation that cannot be explained.

References

Akaahan, T. J. A. (2014). Studies on Benthic fauna as bioindicators of pollution in river Benue at Makurdi, Benue State, Nigeria. *Int Res J Environ Sci*, 3(7), 33 – 38.

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D. & Freestone, A. L. (2011). Navigating the multiple meanings of b diversity: a roadmap for the practicing ecologist. *Ecology Letters*, 14, 19–28.

APHA (1995) Standard methods for the examination of water and wastewater. American Public Health Association, Washington, DC

Arimoro, F. O. & Keke, N. U. (2016). The intensity of human-induced impacts on the distribution and diversity of macroinvertebrates and water quality of Gbako River, North Central, Nigeria. *Energy, Ecology, and Environment (Springer)*. DOI 10.1007/s40974-016-0025-8

Arimoro, F. O., & James, H. M. (2008). *Preliminary pictorial guide to the macroinvertebrates of Delta State Rivers, Southern Nigeria.* Grahamstown: Albany Museum.

Arimoro, F. O., Obi-Iyeke, G. E., Obukeni, P. J. O. (2012). Spatiotemporal variation of macroinvertebrates in relation to canopy cover and other environmental factors in Eriora River, Niger Delta, Nigeria. *Environmental Monitoring Assessment,* 184, 6449–6461. doi:10.1007/s10661-011-2432-9

Arimoro, F. O., Odume, N. O., Uhunoma, S. I. & Edegbene, A. O. (2015). Anthropogenic impact on water chemistry and benthic macroinvertebrate associated changes in a southern Nigeria stream. *Environmental Monitoring Assessment,* 187, 1–14.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19, 134 – 143.

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, 21, 1223–1232.

Baselga, A., Orme, C. D. L., Villeger, S., De Bortoli, J. & Leprieur, F. (2017). Betapart: partitioning beta diversity into turnover and nestedness components. R package version 1.4. Available at: http://CRAN.R-project.org/package=betapart.

Bennett, J. R., Cumming, B. F., Ginn, B. K. & Smol, J. P. (2010) Broad-scale environmental response and niche conservatism in lacustrine diatom communities. *Global Ecology and Biogeography*, 19, 724–732.

Bini, L. M., Diniz-Filho, J. A. F. & Hawkins, B. A. (2004). Macroecological explanations for differences in species richness gradients: a canonical analysis of South American birds. *Journal of Biogeography*, 31, 1819–1827.

Blanchet, F. G., Legendre, P. & Borcard, D. (2008b) Forward selection of explanatory variables. *Ecology*, 89, 2623–2632.

Borcard, D., Legendre, P. & Drapeau P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, 73, 1045–1055.

Brown, B. L. & Swan, C. M. (2010). Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology*, 79: 571–580.

Clarke, A., Mac Nally, R., Bond, N. & Lake, P. S. (2008). Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology*, 53:1707–1721.

Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters*, 8, 1175 – 1182.

Datry T., Pella H., Leigh C., Bonada N. & Hugueny B. (2016a) A landscape approach to advance intermittent river ecology. *Freshwater Biology*, 61, 1200–1213.

Day, J. A., Harrison, A. D., & De Moor, I. J. (2002). *Guides to the freshwater invertebrates of Southern Africa*, vol. 9, DipteraTT 201/02 Pretoria: Water Research Commission.

De Moor, I. J., Day, J. A. & De Moor, F. C. (2003). *Guides to the freshwater invertebrates of Southern Africa*, vol. 7. Insecta I (Ephemeroptera, Odonata and Plecoptera) TT. Pretoria: Water Research Commission.

Donohue, I., Donohue, L.A., Ni Ainin, B., and Irvine, K. (2009). Assessment of eutrophication pressure on lakes using littoral invertebrates. *Hydrobiologia*, **633**(1): 105–122. doi:10.1007/s10750-009-9868-8.

Emere, M. C. & Nasiru, C. E. (2009). Macroinvertebrates as indicators of the water quality of an urbanized stream, Kaduna Nigeria. *Natural Science*, 7(1), 1–7.

Fenchel, T. O. M. & Finlay, B. J. (2004) The ubiquity of small species: patterns of local and global diversity. *BioScience*, 54, 777–784.

Field, R., Hawkins, B. A., Cornell, H. V., Currie, D. J., Diniz-Filho, J. A. F., Gue´Gan, J. F., Kaufman, D. M. Kerr, J. T., Mittelbach, G. G., Oberdorff, T. O'brien, E. M. & Turner, J. R. G. (2009). Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, 36: 132–147.

Fritz, K. M., Glime, J. M., Hribljan, J., Greenwood, J. L. (2009). Can bryophytes be used to characterize hydrologic permanence in forested headwater streams? *Ecological Indicators* 9, 681–692.

Gr€onroos, M., J., Heino, T., Siqueira, V. L., Landeiro, J., Kotanen, J & Bini, L. M. (2013). Metacommunity structuring in stream networks: roles of dispersal mode, distance type and regional environmental context. *Ecology and Evolution,* 3, 4473–4487.

Grenouillet, G., Brosse, S., Tudeque, L., Lek, S., Baraille´, Loot, G. (2008). Concordance among stream assemblages and spatial autocorrelation along a fragmented gradient. *Diversity and Distributions* 14, 592–603.

Griffith, M. B., Hill, B. H., Herlihy, A. T., Kaufmann, P. R. (2002). Multivariate analysis of periphyton assemblages in relation to environmental gradients in Colorado Rocky Mountain streams. *Journal of Phycology* 38, 83–95.

Heino J. (2011) A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology*, 56, 1703–1722.

Heino J., Bini, L. M., Karjalainen, S. M., Mykr€a, H., Soininen, J., Vieira & L. C. G. (2010). Geographical patterns of micro-organismal community structure: are diatoms ubiquitously distributed across boreal streams? *Oikos*, 119, 129–137.

Heino, J & Mykr€a, H. (2008). Control of stream insect assemblages: roles of spatial configuration and local environmental variables. *Ecological Entomology*, 33, 614 – 622.

Heino, J. & Alahuhta, J. (2015) Elements of regional beetle faunas: faunal variation and compositional breakpoints along climate, land cover and geographical gradients. *Journal of Animal Ecology*, 84, 427–441.

Heino, J. (2011). A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology,* 56, 1703–1722.

Heino, J., & Mykra, H. (2008). Control of stream insect assemblages: roles of spatial configuration and local environmental variables. *Ecological Entomology*, 33, 614–622.

Heino, J., Gro, M., Nroos, M., Soininen, J., Virtanen, R. & Muotka, T. (2012). Context dependency and metacommunity structuring in boreal headwater streams. *Oikos*, 121, 537–544.

Heino, J., Gronroos, M., Ilmonen, J., Karhu, T., Niva, M. & Paasivirta, L. (2013). Environmental heterogeineity and β diversity of stream macroinvertebrate communities at intermediate spatial scales. *Freshwater Science,* 32(1), 412-154.

Heino, J., Melo, A. S. & Bini, L. M. (2015). Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. *Freshwater Biology*, 60, 223 – 235.

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S. & Bini, L. M. (2015a). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology*, 21, 45-56.

Heino, J., Melo, A., Bini, L., Altermatt, F., Al-Shami, S., Angeler, D., Bonada, N., Brand, C. Callisto, M., Cottenie, K. Dangles, O., Dudgeon, D., Encalada, A., G€othe. E., Gr€onroos, M., Hamada, N., Jacobsen, Landeiro, V., Ligeiro, R., Martins, R., Miserendino, M., Rawi, C., Rodrigues, M., Roque, F., Sandin, L., Schmera, D., Sgarbi, F., Simaika. J., Siqueira, T., Thompson, R., Townsend, C. (2015b). A comparative analysis reveals weak relationships between ecological factors and beta diversity of stream insect metacommunities at two spatial levels. *Ecology and Evolution*, 1-7.

Heino, J., Muotka, T., Mykra¨, H., Paavola, R., Ha¨ma¨ la¨inen, H., Koskenniemi, E. (2003a). Defining macroinvertebrate community types of headwater streams: implications for bioassessment and conservation. *Ecological Applications,* 13, 842–852.

Heino, J., Parviainen, J., Paavola, R., Jehle, M., Louhi, P. & Muotka, T. (2005) Characterizing macroinvertebrate assemblage structure in relation to stream size and tributary position. *Hydrobiologia*, 539, 121–130.

Heino, J., Soininen, J. (2005). Assembly rules and community models for unicellular organisms: patterns in diatoms of boreal streams. *Freshwater Biology*, 50, 567–577.

Jeffries, M., & Mills, D. (1990). *Freshwater ecology principles and applications*. London: Belhaven Press.

Johnson, R. K., and Hering, D. 2009. Response of taxonomic groups in streams to gradients in resource and habitat characteristics. *J. Appl. Ecol.* **46**(1): 175–186. doi:10.1111/j.1365-2664.2008.01583.x.

Keke, U. N.,Arimoro, F. O., Auta, Y. I. & Ayanwale, A. V. (2017). Temporal and Spatial variability in Macroinvertebrate community structure in relation to environmental variables in Gbako River, Niger State, Nigeria. *Tropical Ecology*, 58(2), 229–240

Kennard M.J., Pusey B.J., Olden J.D., Mackay S.J., Stein J.L. & Marsh N. (2010) Classification of natural flow regimes in Australia to support environmental flow management. *Freshwater Biology*, 55, 171–193.

Koleff, P., Gaston, K. J. & Lennon, J. J. (2003). Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, 72:367–382.

Koperski, P. (2010*a*). Diversity of macrobenthos in lowland streams: ecological determinants and taxonomic specificity. *Journal of Limnology,* **69**: 1–14. doi:10.3274/JL10-69-1-08.

Koperski, P. (2011). Diversity of freshwater macrobenthos and its use in biological assessment: a critical review of current applications. *Environmental Revision,* **19**, 16–31.

Landeiro, V. L., Bini, L. M., Melo, A. S. Pes, A. M. O. & Magnusson, W. E. (2012). The roles of dispersal limitation and environmental conditions in controlling caddisfly (Trichoptera) assemblages. *Freshwater Biology*, 57, 1554–1564.

Legendre P. (2014) Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography, 23, 1324–1334.

Legendre, P. & Legendre, L. (2012). *Numerical Ecology*, 3rd edn. Elsevier: Amsterdam.

Legendre, P., Borcard, D. & Peres-Neto, P. R. (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, 75, 435 – 450.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M. & Hoopes, M. F. (2014). The metacommunity concept: a framework for multi-scale community ecology. *Ecological Lett,* 7, 601-613.

Magurran, A. E. (2004). *Measuring Biological Diversity*. Oxford: Blackwell Publishing.

Merritt, R. W., & Cummins, K. W. (1996). *An introduction to the aquatic insects of North America* (3rded.). IOWA, Dubuque: Kendall-Hunt.

Moore, A. A. & Palmer, M. A. (2005). Invertebrate biodiversity in agricultural and urban headwater streams: implication for conservation and management. *Ecological Appl*ication, **15**(4): 1169–1177.doi:10.1890/04-1484.

Mykra, H., Aroviita, J., Hama¨ la¨inen, H., Kotanen, J., Vuori, K.-M., Muotka, T. (2008). Assessing stream condition using macroinvertebrates and macrophytes: concordance of community responses to human impact. *Fundamental and Applied Limnology*, 172, 191–203.

Mykra, H., Heino, J. & Muotka, T. (2007) Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Global Ecology and Biogeography*, 16, 149–159.

Nabout, J. C., Siqueira, T., Bini L. M. & Nogueira, I .D. S. (2009). No evidence for environmental and spatial processes in structuring phytoplankton communities. *Acta Oecologica*, 35, 720–726.

Odume, O. N., Muller, W. J., Arimoro, F. O. & Palmer, C. G. (2012). The impact of water quality deterioration on macroinvertebrate communities in Swartkops River, South Africa: a multimetric approach. *African Journal of Aquatic Sciences*, 37(2), 191–200.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R. O'Hara, R. B. Simpson, L. G., Solymos, P., Henry, M., Stevens, H. Szoecs, E. & Wagner, H. (2017). *Vegan: Community Ecology Package. R package version 2.4-3*. Available at: http:// CRAN.R-project.org/package=vegan.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R. & O'Hara, R. B. (2013). *vegan: Community Ecology Package.* R package version 2.0-10. Available at: http:// CRAN.R-project.org/package=vegan.

Olden J. D. & Poff, N. L. (2003) Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Research and Applications*, 19, 101–121.

Paavola, R., Muotka, T., Virtanen, R., Heino, J. & Kreivi, P. (2003). Are biological classifications of headwater streams concordant across multiple taxonomic groups? *Freshwater Biology*, 48, 1912–1923.

Padial, A. A., Ceschin, F., Declerck, S.A.J., De Meester L., Bonecker C.C., Lansac-T^oha F.A. et al. (2014) Dispersal ability determines the role of environmental, spatial and temporal drivers of metacommunity structure. *PLoS ONE*, 9, 11-22.

Peres-Neto, P. R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, 87, 2614–2625.

Petchey, O.L., Downing, A.L., Mittelbach, G.G., Persson, L., Steiner, C.F., Warren, P.H., and Woodward, G. (2004). Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos*, **104**(3): 467–478. doi:10.1111/j.0030-1299.2004. 13257.x.

Petrin, A., Laudon, H., and Malmqvist, B. (2007). Does freshwater macroinvertebrate diversity along a pH-gradient reflect adaptation to low pH? Freshw. Biol. **52**(11): 2172–2183. doi:10.1111/j.1365-2427.2007.01845.x.

R Core Team. (2017). *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna*. Available at: http://www.R-project.org/.

Rocha, M., Heino, J., Machado-Velho, L., Lansac-Toha, F. & Lansac-Toha, F. A. (2017). Fine spatial grain, large spatial extent and biogeography of macrophyte-associated cladoceran communities across Neotropical floodplains. *Freshwater Biology,* 62, 559-569.

Rolls, R. J., Heino, J.& Chessman, B. C. (2016). Unravelling the joint effects of flow regime, climatic variability and dispersal mode on beta diversity of riverine communities. *Freshwater Biology,* 61, 1350–1364.

Sandin, L. (2003). Benthic macroinvertebrates in Swedish streams: community structure, taxon richness, and environmental relations. *Ecography,* **26**(3): 269–282. doi:10.1034/j.1600-0587. 2003.03380.x.

Sandin, L. & Johnson, R. K. (2004). Local, landscape and regional factors structuring benthic macroinvertebrate communities in Swedish streams. *Landscape Ecology*, 19, 501–511.

Soininen, J., Macdonald, R. & Hillebrand, H. (2007). The distance decay of similarity in ecological communities. *Ecography*, 30:3–12.

Souffreau, C., Van der Gucht, K., Van-Gremberghe, I., Kosten, S., Lacerot, G., Lob~ao, L. M. (2015). Environmental rather than spatial factors structure bacterioplankton communities in shallow lakes along a > 6000 km latitudinal gradient in South America. *Environmental Microbiology*, 17, 2336–2351.

Tixier, G., and Guerold, F. (2005). Plecoptera response to acidification in several headwater streams in the Vosges Mountains (northeastern France). *Biodiversity Conservation,* **14**(6): 1525–1539. doi:10.1007/s10531-004-9790-3.

Tonkin, J. D., Arimoro, F. O. & Haase, P. (2016). Exploring stream communities in a tropical biodiversity hotspot: biodiversity, regional occupancy, niche characteristics, and environmental correlates. *Biodiversity and Conservation,* 25, 975-993.

Tuomisto, H. (2010). A diversity of beta diversity: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, 22:2–22.

Velle L.G., Nilsen L.S., Norderhaug A. & Vandvik V. (2014) Does prescribed burning result in biotic homogenization of coastal heathlands? Global Change Biology, 20, 1429 – 1440.

Voelz, N. J. & McArthur, J. V. (2000). An exploration of factors influencing lotic insect species richness. *Biodiversity Conservation*, **9**(11): 1543–1570. doi:10.1023/A:1008984802844.

Ward, J. V. (1992). *Aquatic insects ecology*. NewYork: John Wiley and Sons Inc.

Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, **21**(2/3): 213–251. doi:10.2307/1218190.

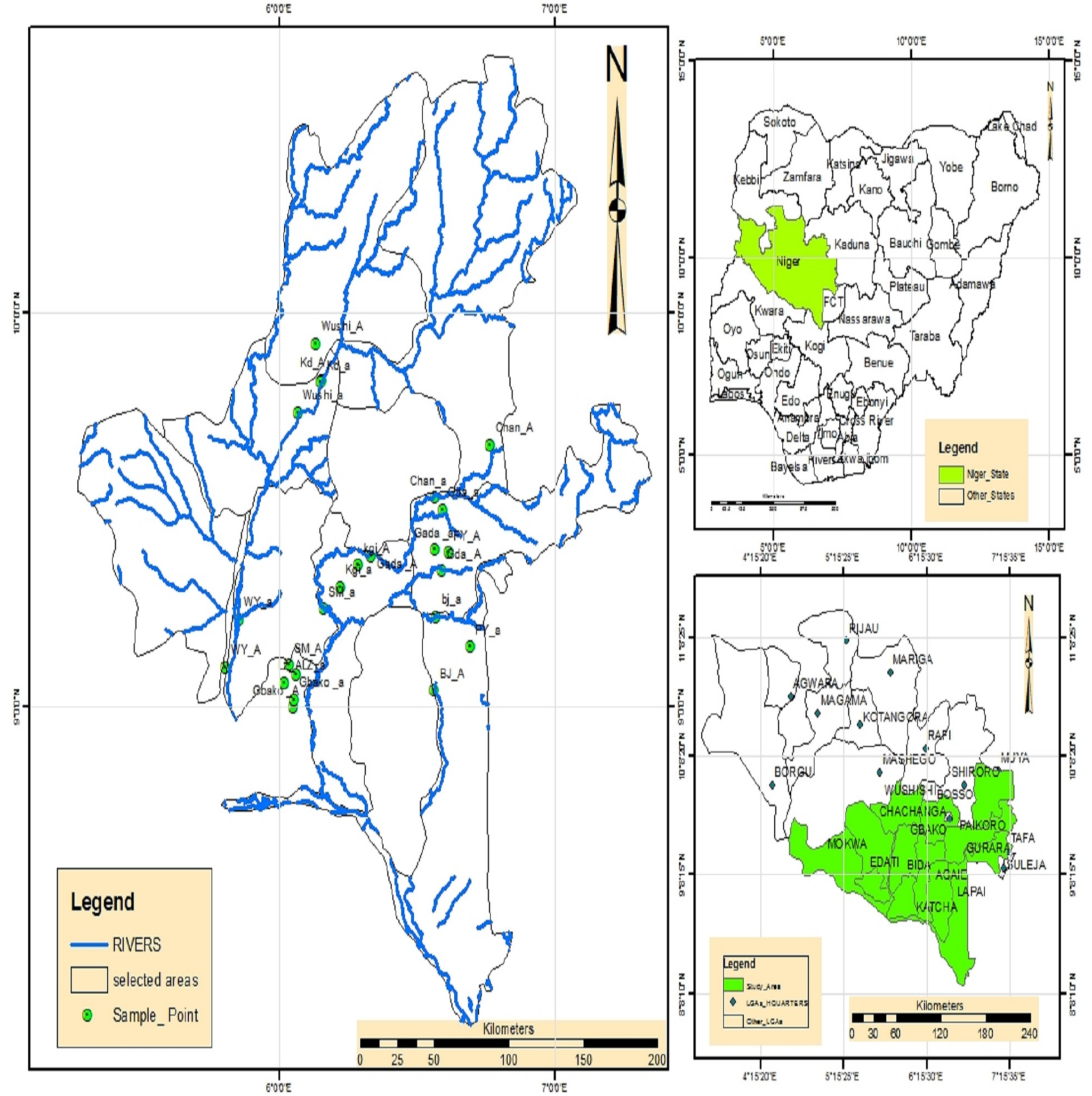

Figure 1. Map of the study area showing sampled locations

Source: Geography department, Federal University of Technology, Minna.

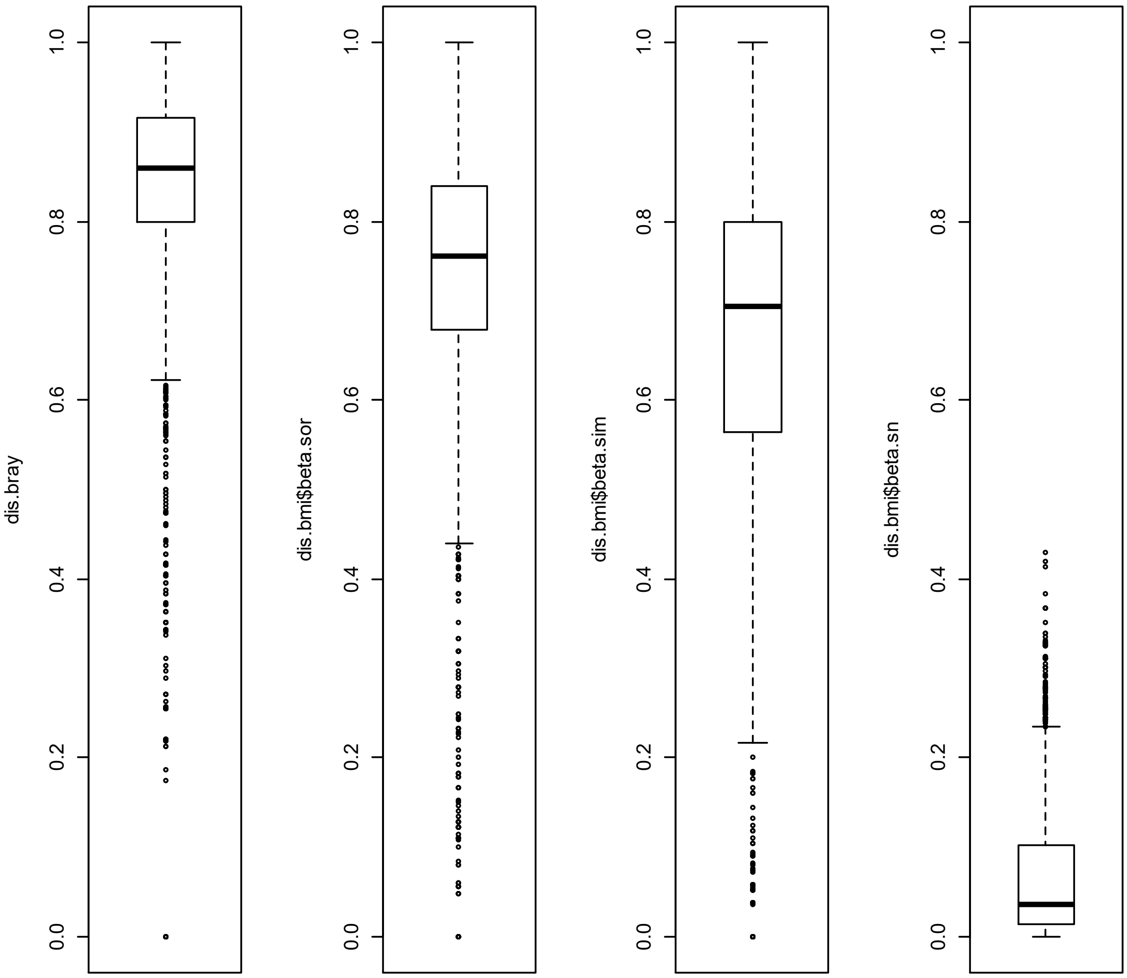

Figure 2: Boxplots of variation in between-site pairwise dissimilarity matrices for presence-absence based on the total beta diversity (beta.sorensen), turnover (beta.simpson) and nestedness-resultant (beta.nestedness) for the reference sites

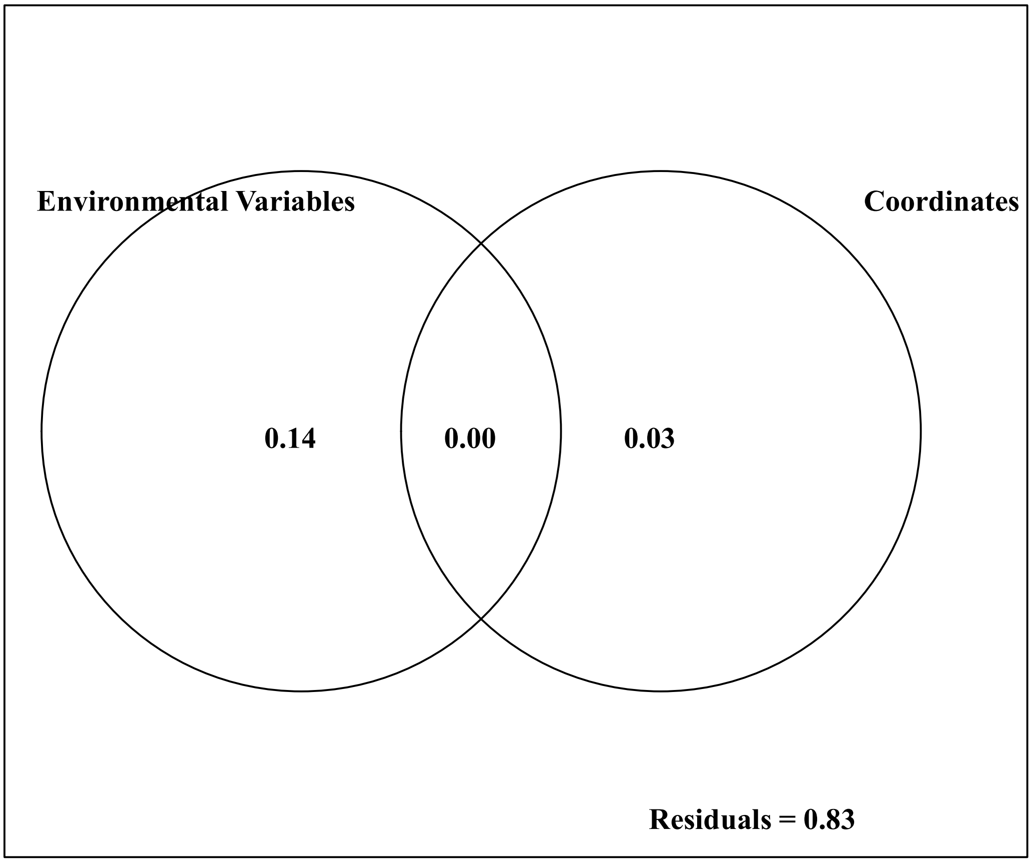

Figure 3: Plots of variation partitioning results based on Bray-Curtis dissimilarities for the reference sites. Shown are adjusted R^2 values

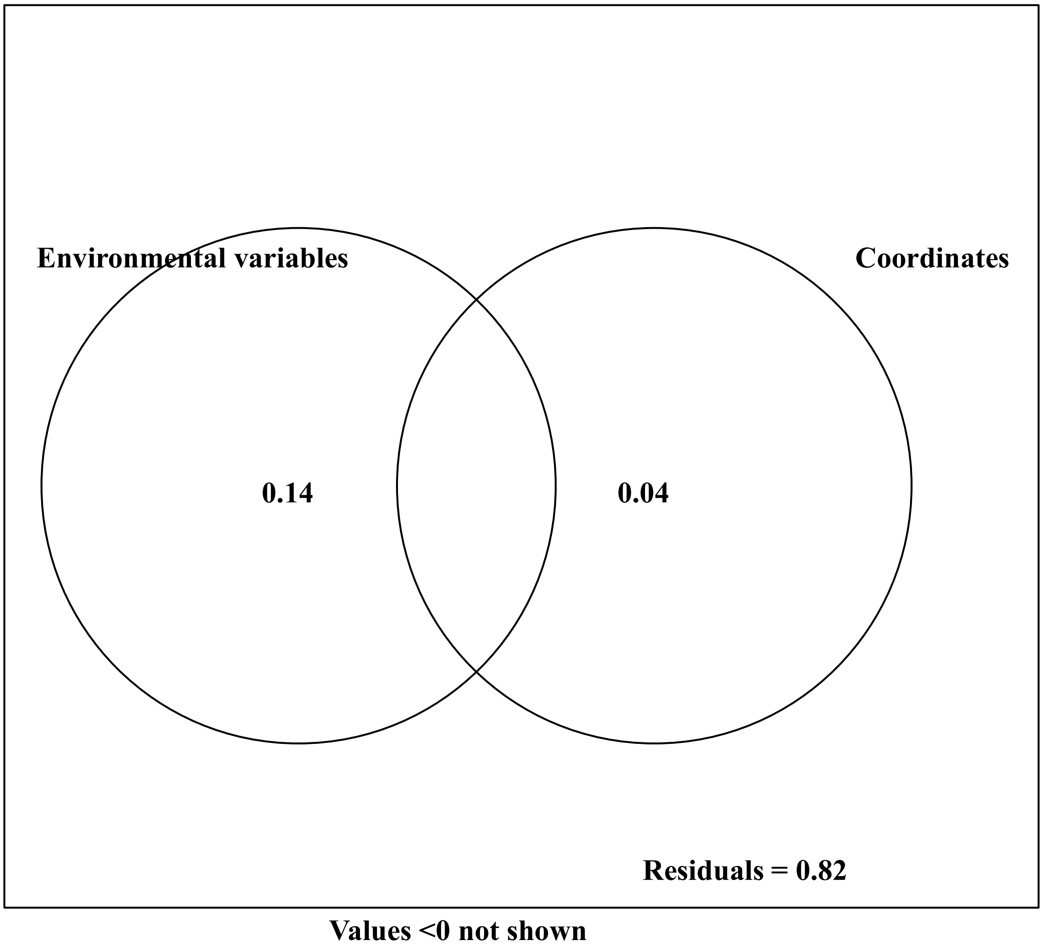

Figure 4: Plots of variation partitioning results based on total (Sorenson) dissimilarities for the reference sites. Shown are adjusted R^2 values

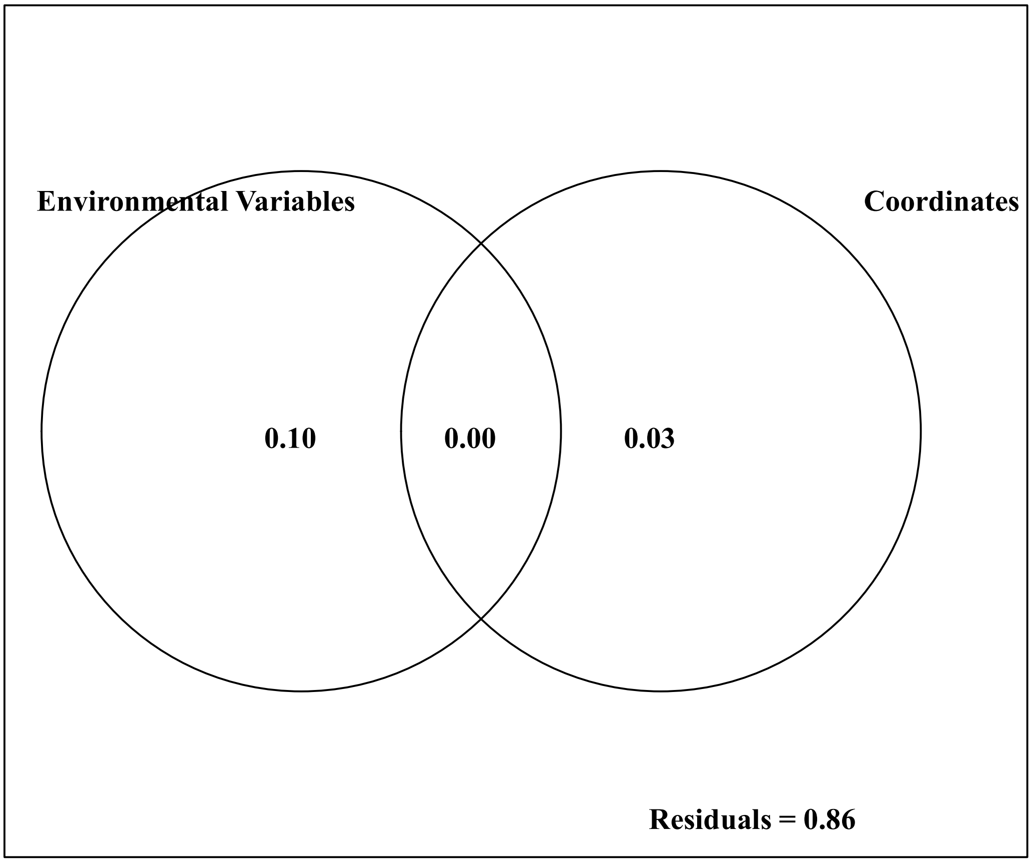

Figure 5: Plots of variation partitioning results based on turnover (Simpson) dissimilarities for the reference sites. Shown are adjusted R^2 values

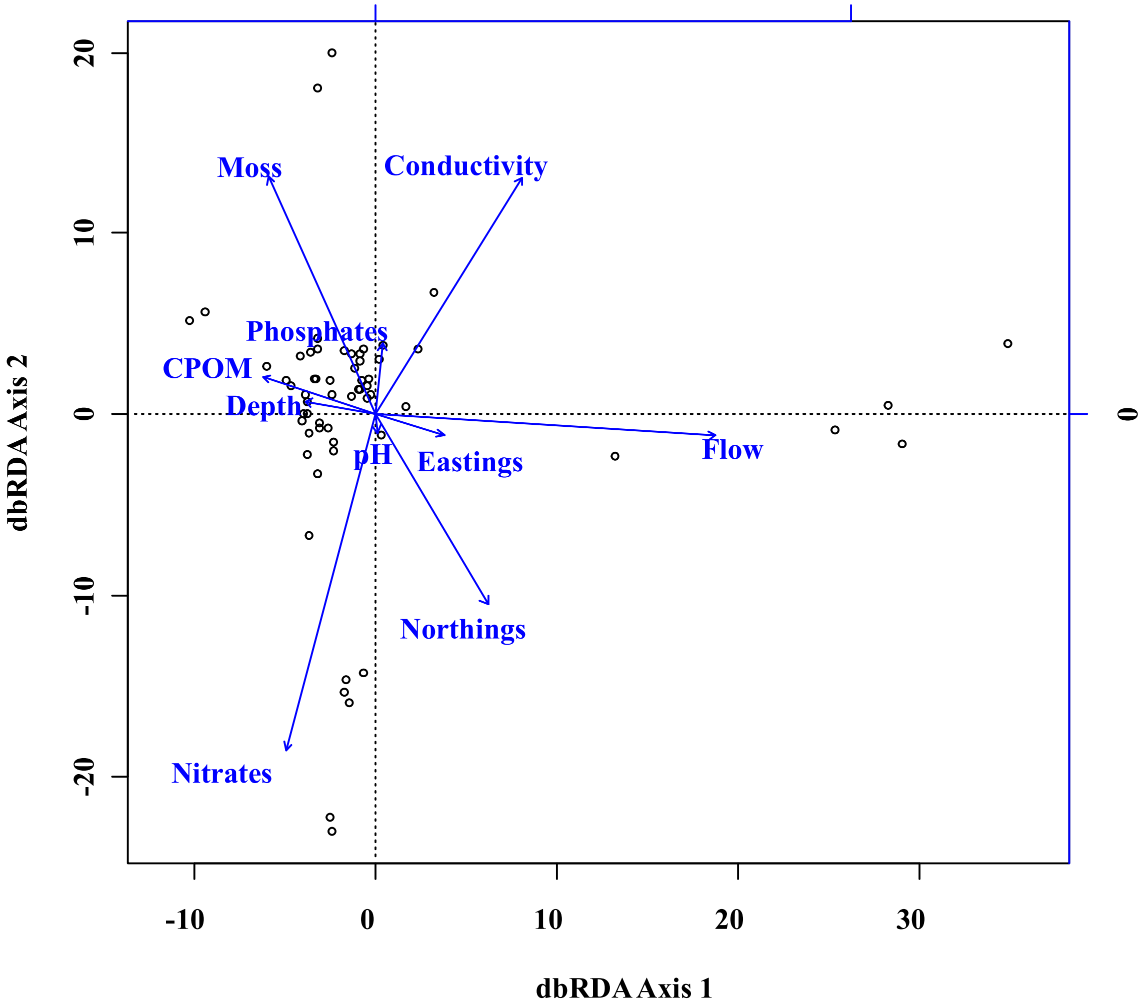

Figure 6: Distance-based Redundancy Analysis (dbRDA) ordination plots of macroinvertebrate using Bray–Curtis dissimilarity (abundance data). Open circle show site scores.

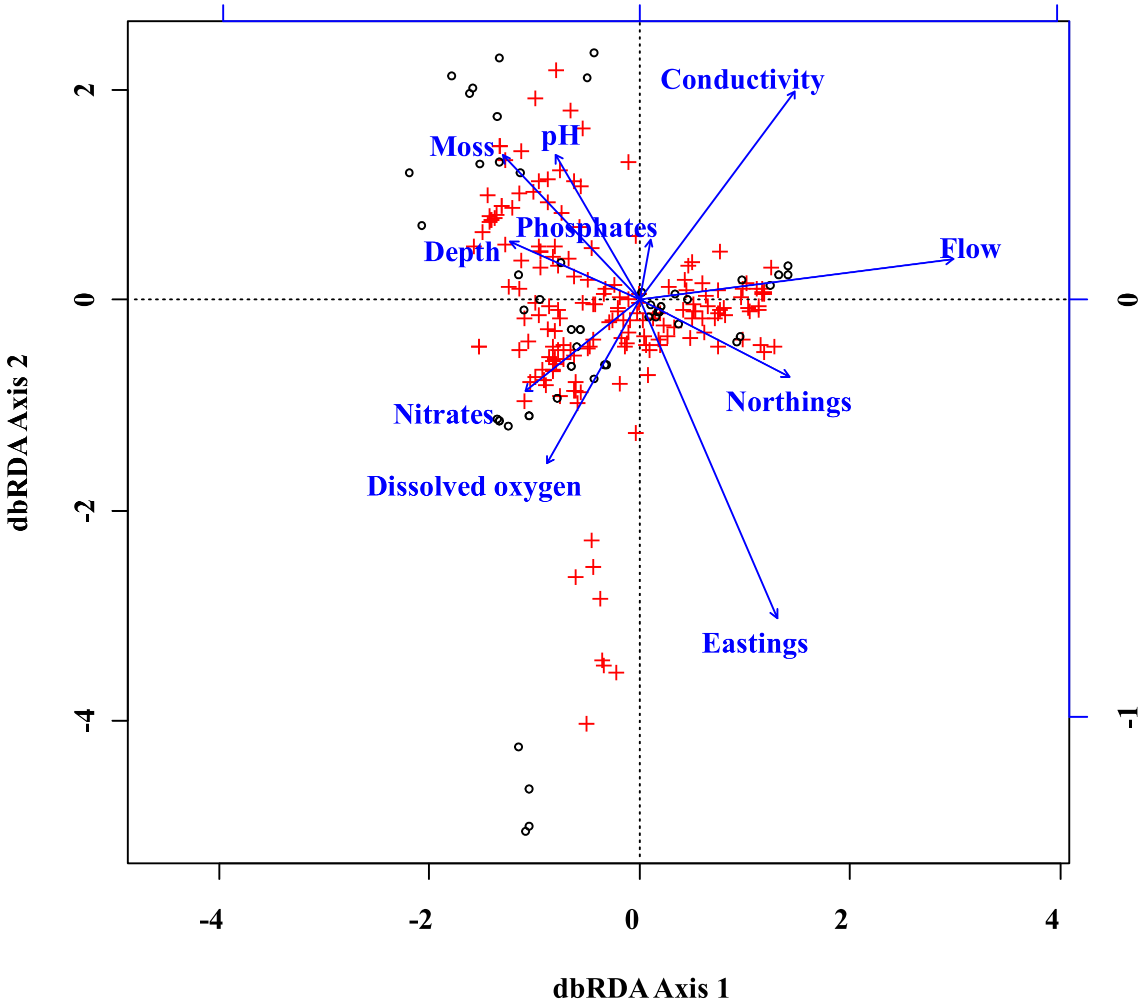

Figure 7: Distance-based Redundancy Analysis (dbRDA) ordination plots of macroinvertebrate using Sørensen dissimilarity (presence/absence data).

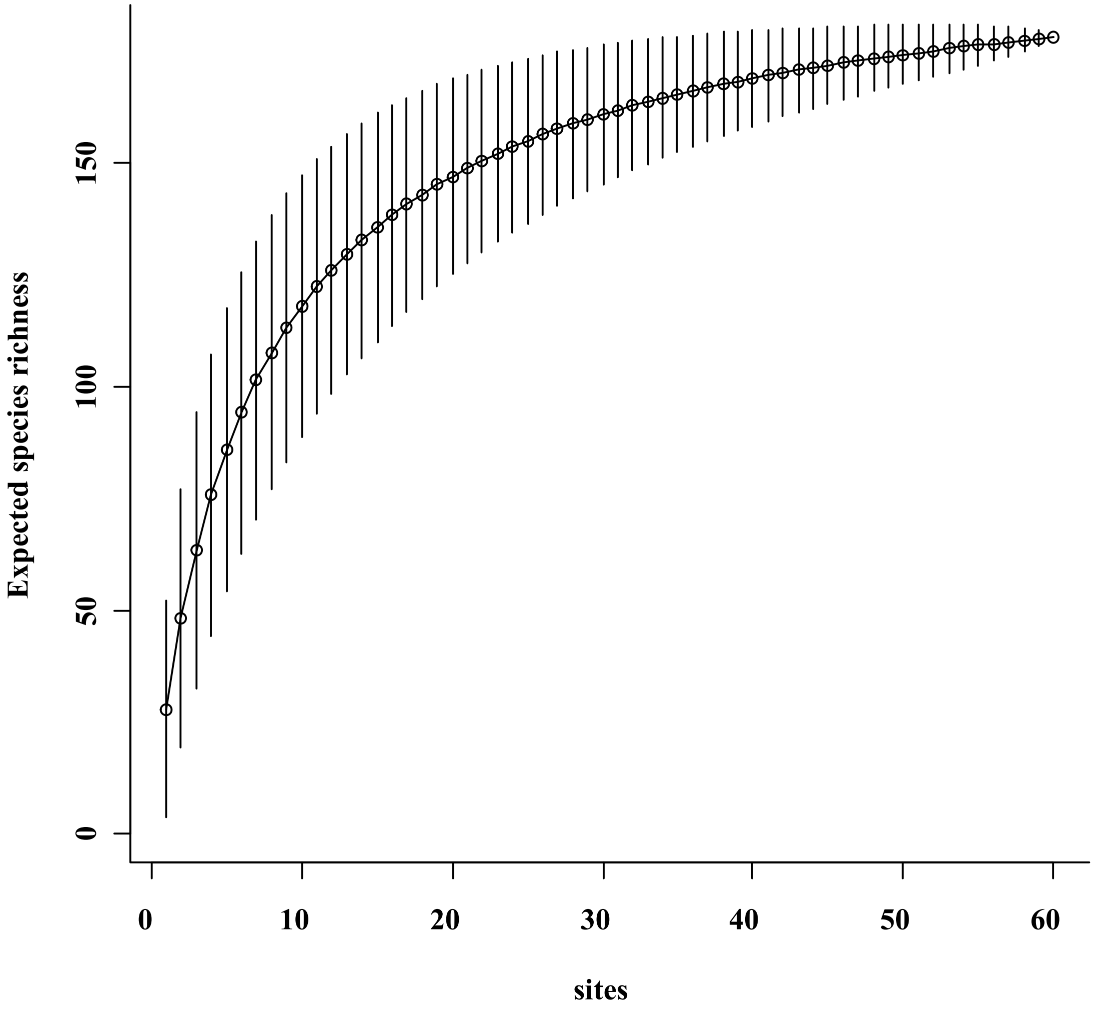

Figure 8: Taxon accumulation curve for macroinvertebrates of the reference sites