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UNIVERSITE FELIX HOUPHOUËT-BOIGNY

Academic Year: 2022-2023 **Order Number :**

A Thesis Submitted for the award of the Degree of Doctor of Philosophy of the University Félix HOUPHOUËT-BOIGNY

Specialty: Climate Change and Biodiversity

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METACOMMUNITY STRUCTURE AND ASSEMBLAGE PROCESSES OF FISH, MACROINVERTEBRATE AND PHYTOPLANKTON IN THE LOWER NIGER RIVER BASIN, NIGERIA

Public Defense on 15th June, 2023

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Thèse présentée pour l'obtention du grade de Docteur de l'Université Félix HOUPHOUËT-BOIGNY

Spécialité: Changement Climatique et Biodiversité

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STRUCTURE DES MÉTACOMMUNAUTÉS ET PROCESSUS D'ASSEMBLAGE DES POISSONS, DES MACROINVERTÉBRÉS ET DU PHYTOPLANCTON DANS LE BASSIN INFÉRIEUR DU FLEUVE NIGER, AU NIGERIA

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DEDICATION

I dedicate this thesis to God the Father, God the Son and God the Holy Spirit for the grace and benevolence throughout my journey in this PhD studies.

ACKNOWLEDGEMENTS

First, I wish to acknowledge the West African Science Service Centre on Climate Change and Adapted Land Use (WASCAL), for the award of full PhD fellowship, financed by the German Federal Ministry for Education and Research (BMBF), in Climate Change and Biodiversity.

I would like to express my deepest gratitude to my supervisory team: Prof. AFFIAN Kouadio for encouragement, advice, and useful contributions to the success of this thesis. Thank you Prof for your commitments and sacrifices. To Prof. Omoigberale, O. Michael, I say a very big thank you for being ever ready for any kind of advice needed throughout this PhD journey. You were more like a father than an ordinary supervisor. Thank you once again. I also express my gratitude to Prof. Dr. Ralf B. Schäfer hosting me at the Institute for Environmental Sciences, University Koblenz-Landau, Germany, for a 5-month scientific visit during the period of this PhD program. Prof. your contributions towards the success of this is appreciated. The success story of this thesis will not be complete without mentioning PD. Dr Thomas MEHNER of the Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB) for his inputs and expertise, especially in the aspect of ecological statistics. I remain indebted to you Thomas.

I will also like to acknowledge the entire management and staff of WASCAL center in Abidjan, ably lead by Dr Kouassi Edouard and Dr Ngolo Kone for their leadership prowess in ensuring the smooth running of the Graduate Research Program in Climate change and Biodiversity.

To my colleagues and newfound families (Isaac, Alpha, Aly, Aboubacar, Jessica, Mariama, Zainabou, Rashida and Raila), I remain indebted to you people for the support, encouragement and cooperation throughout this PhD journey. I am glad our paths crossed.

To my parents who gave in all they have for me to have a firm foundation, I appreciate them. To my amiable wife (Chekwube) for sacrificing all to ensure that I am confortable, I deeply appreciate you. To my lovely children (Simdi, OG and Zitel), for holding forth in my absence, I say thank you. And to my adourable siblings (Chiedu and the wife - Blessing, Ikenna, Chidinma and Ekene), I say thank you for your prayers and supports.

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ABSTRACT

Understanding ecological processes that drive metacommunity dynamics is essential for elucidating the mechanisms of community assembly and for guiding biodiversity conservation. To this end, the relative influence of local environmental and spatial factors in structuring the community composition of fish, macroinvertebrate and phytoplankton at 15 sampling sites along the longitudinal gradient of the Lower Niger River Basin (LNRB) was investigated in dry and rainy seasons. In addition, the beta diversity and its components (species replacement and richness difference) of the species and their underlying drivers were examined. The result of Redundancy analysis indicated that the community compositions (fish, phytoplankton and macroinvertebrate) in the upper region were influenced by high nutrient concentrations, attributable to arable and nomadic farming within the region. In contrast, downstream sites were characterized by high concentrations of suspended solids indicative of flooding and mining effects. Fish and phytoplankton community compositions strongly differed between the upper and lower regions probably because of the presence of dams along the channel of the river that may have interrupted migration and dispersal. However, macroinvertebrate community composition was homogenized despite the presence of barrier (dam) in the river channel. Probable explanation to this observation may be the arial dispersal mode of most macroinvertebrate species that allow them to track suitable environment for their survival. Variation partitioning revealed higher contributions of spatial than environmental predictors on fish and phytoplankton community compositions (revealing the effect of dispersal limitations), but the total predicted variance was higher during dry season. Differences in flow dynamics between upper and lower regions as attributable to black and white floods in the LNRB modify the connectivity between sites. Dispersal among sites may be more limited downstream than in the upper region, particularly in dry season, certainly because damming in the upper region also interrupts the natural flood regime such that there are low water levels in the lower region, which spatially isolate fish and phytoplankton communities at certain sampling sites. Environmental predictors were the determinants of macroinvertebrate community composition reflecting the strength of species sorting in structuring macroinvertebrate community in the LNRB. This study revealed weak beta diversity for all the species studied indicating low species turnover. The replacement component contributed most to the overall beta diversity and its components for all the studied species in the LNRB, an indication of the importance of species sorting. Whereas, spatial predictors explained fish total beta diversity and its components, environmental filtering was the primary driver of macroinvertebrate and phytoplankton total beta diversity and its replacement component. However, their richness difference components were explained by spatial factors. The varying local contribution to biodiversity (LCBD) by different sites shows that some sites along the longitudinal gradient of the LNRB requires restoration measures (e.g. Awuru) while others require conservation actions (e.g Jebba). Overall, the results of this study indicated that damming induced changes in physiochemical variables (e.g. nutrients), accompanied by alterations in flow regime and longitudinal connectivity, increased replacement and loss of taxa. These changes have consequently led to alteration of species community dissimilarity and affected the relative effects of environmental and spatial factors on local community compositions, beta diversity and its components. These findings suggested that conservation of fish, phytoplankton and macroinvertebrate diversity in afro-tropical rivers requires maintenance of both habitat heterogeneity (spatial variation in habitat conditions) and connectivity at the scale of entire river basins.

Keywords: Community structure; Species sorting, Beta diversity, Spatial determinants, Lower Niger River Basin

RESUME

La compréhension des processus écologiques qui régissent la dynamique des métacommunautés est essentielle pour élucider les mécanismes d'assemblage des communautés et pour guider la conservation de la biodiversité. A cette fin, l'influence relative des facteurs environnementaux et spatiaux locaux dans la structuration de la composition des communautés de poissons, de macro-invertébrés et de phytoplancton dans 15 sites d'échantillonnage le long du gradient longitudinal du bassin inférieur du fleuve Niger (LNRB) a été étudiée en saisons sèche et pluvieuse. En outre, la diversité bêta et ses composantes (remplacement d'espèces et différence de richesse) des espèces et leurs moteurs sous-jacents ont été examinés. Les resultats ont indiqué que les compositions des communautés (poissons, phytoplancton et macroinvertébrés) dans la région supérieure étaient influencées par des concentrations élevées de nutriments, attribuables à l'agriculture arable et nomade dans la région. En revanche, les sites en aval étaient caractérisés par des concentrations élevées de solides en suspension, indiquant les effets des inondations et de l'exploitation minière. Les compositions des communautés de poissons et de phytoplanctons différaient fortement entre les régions supérieure et inférieure, probablement en raison de la présence de barrages le long du canal de la rivière qui ont pu interrompre la migration et la dispersion. Cependant, la composition des communautés de macroinvertébrés était homogène malgré la présence de barrage sur le fleuve. L'explication probable de cette observation peut être le mode de dispersion aérienne de la plupart des espèces de macroinvertébrés qui leur permet de rechercher un environnement approprié pour leur survie. Le partitionnement de la variation a révélé des contributions plus élevées des prédicteurs spatiaux que des prédicteurs environnementaux sur les compositions des communautés de poissons et de phytoplancton (révélant l'effet des limitations de dispersion), mais la variance totale prédite était plus élevée pendant la saison sèche. Les différences dans la dynamique des flux entre les régions supérieures et inférieures, attribuables aux crues noires et blanches dans la LNRB, modifient la connectivité entre les sites. La dispersion entre les sites peut être plus limitée en aval que dans la région supérieure, en particulier pendant la saison sèche, certainement parce que la construction de barrages dans la région supérieure interrompt également le régime naturel des crues, de sorte que les niveaux d'eau sont bas dans la région inférieure, ce qui isole spatialement les communautés de poissons et de phytoplancton dans certains sites d'échantillonnage. Les prédicteurs environnementaux étaient les déterminants de la composition de la communauté de macroinvertébrés, reflétant la force du tri des espèces qui instruit la communauté de macroinvertébrés dans la LNRB. Cette étude a révélé une faible diversité bêta pour toutes les espèces étudiées, indiquant un faible renouvellement des espèces. La composante de remplacement a contribué le plus à la diversité bêta globale et à ses composantes pour toutes les espèces étudiées dans la LNRB, ce qui indique l'importance du tri des espèces. Alors que les prédicteurs spatiaux expliquaient la diversité bêta totale des poissons et ses composantes, le filtrage environnemental était le principal moteur de la diversité bêta totale des macroinvertébrés et du phytoplancton et de sa composante de remplacement. Cependant, leurs composantes de différence de richesse ont été expliquées par des facteurs spatiaux. Les contributions variables de la LCBD par différents sites montrent que certains sites le long du gradient longitudinal de la LNRB nécessitent des mesures de restauration (par exemple Awuru) tandis que d'autres nécessitent des actions de conservation (par exemple Jebba). Dans l'ensemble, les résultats de cette étude indiquent que les changements induits par les barrages sur les variables physiochimiques (par exemple, les nutriments), accompagnés d'altérations du régime d'écoulement et de la connectivité longitudinale, ont augmenté le remplacement et la perte de taxons. Ces changements ont par conséquent conduit à une altération de la dissimilarité des communautés d'espèces et ont affecté les effets relatifs des facteurs environnementaux et spatiaux sur les compositions des communautés locales, la diversité bêta et ses composantes. Ces résultats suggèrent que la conservation de la diversité des poissons, du phytoplancton et des macroinvertébrés dans les rivières afro-tropicales nécessite le maintien à la fois de l'hétérogénéité de l'habitat (variation spatiale des conditions d'habitat) et de la connectivité à l'échelle de bassins fluviaux entiers.

Mots clés: Structure de la communauté; Tri des espèces, Diversité bêta, Déterminants spatiaux, bassin inférieur du fleuve Niger

CHAPTER ONE: GENERAL INTRODUCTION

1. Introduction

River ecosystem possess many unique physical properties that allow disproportionately high biodiversity to flourish in the relatively small area they occupy on the surface of the Earth (**Dudgeon *et al*., 2006; Tonkin *et al*., 2017**). These river ecosystems constitute dendritic habitats embedded within the terrestrial landscape, with water, solutes, and organisms moving predominantly downstream (**Allan, 2004; Allan and Castillo, 2007; Brown and Swan, 2010; Grönroos *et al*., 2013; Cañedo-Argüelles *et al*., 2015**). They are also one of the most heavily exploited natural resources for a wide range of ecosystem goods and services (**Maltby and Ormerod, 2011**). However, these ecosystems are largely impaired by human activities and are one of the most threatened ecosystems on Earth (**Dudgeon, 2019**). Climate and land-use changes are major threats to river ecosystems because they alter flow and sediment regimes, temperature, habitat, and water quality (**Allan *et al*., 1997; Meyer *et al*., 1999; Lefcheck *et al*., 2015**). These alterations cascade into the distribution of species and arrangement of communities across the landscape (**Oliver and Morecroft, 2014; Mouton *et al*., 2020**). However, how community assembly is affected by spatial factors has been a major challenge for community ecology (**Datry *et al*., 2016a; Chase *et al*., 2020; Liu *et al*., 2021**). Yet, the metacommunity concept is a useful framework to examine spatial patterns in biodiversity (**Tonkin *et al*., 2016; He *et al*., 2020**).

Metacommunity theory has emerged as a framework to investigate the spatial distribution of species and dynamics of spatially structured ecosystems (**Leibold *et al*., 2004; Massol *et al*., 2011; Guichard, 2017**). Species sorting, acting at the local scale and dispersal acting at the regional scale are the main processes structuring metacommunities (**Lindström and Langenheder, 2012**). Species sorting includes both environmental filtering (selection of well-adapted species) and species interactions (i.e., competition, grazing, or predation) (**Chase and Leibold, 2003; Leibold *et al*., 2004; Soininen, 2014; Heino *et al*., 2014; Jamoneau *et al*., 2017**). Dispersal, defined as the movement of individuals between local communities scattered in a landscape, is a pivotal regional process allowing species to reach their preferred habitats, including mass effects and dispersal limitations (**Leibold *et al*., 2004; Brown and Swan, 2010; Heino and Tolonen, 2017; Jamoneau *et al*., 2017**). Generally, the respective roles in each process are explored through the distance decay of community dissimilarity along environmental or spatial distances (**Nekola and White, 1999; Soininen *et al*., 2007; Nekola and McGill, 2014; Heino and Tolonen, 2017**); here, environmental distance reflects the species sorting progress, and spatial distance (i.e., distance between sites) is the distance between pairwise combinations of sites and reflects dispersal progress (**Cañedo-Argüelles *et al*., 2015; Datry *et al*., 2016a**).

In river ecosystems, species sorting (**Leibold *et al*., 2004**) has long been assumed as the main process explaining metacommunity patterns and dynamics (**Cottenie, 2005; Heino *et al*., 2015b; Soininen, 2016**). However, growing evidence suggests that in river systems experiencing substantial levels of environmental harshness, such as drying rivers (**Cid *et al*., 2020; Gauthier *et al*., 2020**), braided rivers (**Vorste *et al*., 2015**), or high-elevation streams (**Datry *et al*., 2016b**), the role of dispersal can become dominant over species sorting. Accordingly, the relative importance of species sorting and dispersal in shaping communities could vary with the levels of anthropogenic impacts, although this aspect has not been explored. Nevertheless, identifying which processes underlie metacommunity patterns is a major avenue to improve the management of river ecosystems, from the accuracy of biomonitoring methods (**Heino, 2013; Cid *et al*., 2020**) to the efficiency of restoration efforts (**Swan and Brown, 2017; Cid *et al*., 2021**).

Furthermore, given the dynamical nature of most ecosystems, especially in tropical river systems (**Datry *et al*., 2016a**), ecological studies have frequently emphasized that mechanisms governing community assembly varied among seasons. **Fernandes *et al*. (2013)** reported that seasonality is a crucial driver of environmental heterogeneity and connectivity among habitats. For instance, increased water level and flow velocity during the rainy season increases connectivity between habitats with the consequence that aquatic organisms may expand their ranges into adjacent sites (**Sarremejane *et al*., 2017**). In this regard, the contribution of spatial predictors to community composition would be expected to decrease during rainy seasons due to sufficient dispersal under high hydraulic connectivity (**Cottenie *et al*., 2003**).

Parallel to the development of metacommunity theory, beta diversity has become a foundational concept to shed light on assembly processes governing distributional patterns in the different realms of life (**Chase and Myers, 2011; Legendre, 2014**). Beta diversity refers to variation in community composition across space and time (**Anderson *et al*., 2011**) and can be examined for different facets of biodiversity, such as taxonomic, functional, or phylogenetic beta diversity (**Villéger *et al*., 2013; Li *et al*., 2020**). Beta diversity also provides a direct link between local alpha and regional gamma diversity (**Anderson *et al*., 2011; Mori *et al*., 2018**). **Baselga (2010)** suggested that beta diversity can be partitioned into turnover and nestedness components, the former refers to beta diversity resulting from species replacement, whereas the latter is attributed to species gain or loss (**Baselga, 2010; Baselga and Orme, 2012**). However, **Podani and Schmera (2011)** proposed beta diversity can be decomposed into replacement and richness difference fractions (**Podani and Schmera, 2011; Carvalho *et al*., 2013; Podani and Schmera, 2016**). Differences in richness may be due to species thinning causing nestedness or to other ecological processes (e.g. physical barriers) (**Legendre, 2014**). These two frameworks represent alternative approaches with different conceptual and mathematical backgrounds (**Legendre, 2014**). Spatial turnover can reflect species sorting by environmental filtering or dispersal processes, whereas nestedness can reflect colonization and extinction patterns (**Si *et al*., 2016; Soininen *et al*., 2018; Fontana *et al*., 2020**). The two components are complementary and together contribute to beta diversity (**Gianuca *et al*., 2017; Hill *et al*., 2017; Li *et al*., 2020a**), and these complementary components can facilitate the perception of more complex ecological patterns in space and time (**Lansac-Tôha *et al*., 2019**). Therefore, understanding the drivers of the aquatic biodiversity and consequent variation in community composition of aquatic species especially in the afro-tropical freshwater river system where such information is scanty, will guide practical regional conservation strategies and management decisions (**Gothe *et al*., 2017**). For instance, higher turnover would require the conservation of multiple sites at the landscape scale. In contrast, higher nestedness would suggest that conserving species-rich sites might be enough for regional biodiversity conservation (**Baselga, 2010; Gianuca *et al*., 2017; Hill *et al*., 2017**).

Locally, aquatic communities (fish, plankton, macroinvertebrate) are modified by resource availability and physico-chemical characteristics (e.g., temperature, flow velocity, pH, dissolved oxygen etc.) of their habitat (**Shukla and Bhat, 2018**). The community structure of aquatic organisms at the macro-habitat scale is mostly influenced by geographical and land-use patterns (Sarkar and Bain, 2007). Studies on the relative importance of local environmental drivers and spatial determinants in structuring the community composition of riverine organisms are gaining traction in different regions of the world, especially in the temperate (e.g. **Gothe *et al*., 2017; Cilleros *et al*., 2017**) and subtropical river ecosystems (**Shukla and Bhat, 2017; Lopez-Delgado *et al*., 2020; Mondal and Bhat, 2022**). However, there is still a major knowledge gap for afro-tropical river ecosystems. Most research on community composition in afro-tropical freshwater ecosystems focused on measuring the impact of anthropogenic perturbations on fish assemblages (e.g. **Odo *et al*., 2009; Oguntade *et al*., 2014; Abiodun and John, 2017, Agbugui *et al*., 2019**). Information on the spatial predictors of community composition and the influence of season on spatial processes in afro-tropical river ecosystems are scanty (**Isabwe *et al*., 2018**). Although research findings from temperate river systems or other tropical regions could certainly help inform conservation action in the afro-tropical river ecosystems, **Fugere *et al*. (2018)** suggested that location/region-based knowledge is very important given the unique structure and functions of afro-tropical river ecosystem in terms of its geological history, flow regime and geomorphology.

Niger River basin, one of the most important rivers in West Africa (**Babatolu, 1998**) was used as a case study, with particular focus on the Lower Niger River Basin (LNRB) in Nigeria. The riparian, rural populations within the catchment of the river benefit from its important fish resources. Its floodplains and tributaries are used for agricultural and pasture purposes (**Ogilvie *et al*., 2010**). The river is reported to be under heavy degradation due to mutually reinforcing unsustainable socioeconomic development, unregulated/unplanned urbanization and agricultural land-use **(Ezeonyejiaku *et al*., 2017**). Recently, the fish diversity of the river and its tributaries have been reported to be declining due to a combination of over-exploitation and anthropogenic activities (**Agbugui *et al*., 2019**).

The river experiences two unique ("black and white flood") types of annual flooding (Adeniji and Mbagwu, 1998) that structure its hydrology and make the Niger River different from most other afro-tropical rivers. The "black flood" originates from the headwaters of the Niger River and its peak discharge usually coincides with the peak of dry season (**Balogun and Ibeun, 1995**), thus, increasing the water velocity and level of the upper region during this period. This is contrary to the expectations that the water velocity of most tropical rivers should be low during the dry season owing to reduced rainfall events and evaporation (**Sagua and Fregene, 1979**). The "white flood" that originates from local runoffs around the catchments of the upper region of the LNRB, occurs from August to November (rainy season). In addition, there are two hydroelectric dams located in the upper region of the river that have transformed these regions from lotic to lentic ecosystems with its characteristic features of increased water depth and width, and reduced flow velocity (**Henderson, 1973**). This transformation is expected to cause a change in the community composition of species contrary to what is expected in natural upper reaches of a tropical river ecosystem (**Oberdorff *et al*., 1993**). Therefore, understanding how aquatic communities in these systems are structured spatially and temporally and the processes driving this diversity is imperative (**Carol *et al*., 2006**) to identify sites with high conservation values or sites in the need of restoration (**Legendre and De Cáceres, 2013**).

1.2 Aim and objectives of the study

1.2.1 Aim

The aim of this study is to provide information on the ecological mechanisms structuring the local community composition and beta diversity of fish, macroinvertebrates and phytoplankton along the longitudinal gradient of the Lower Niger River Basin, Nigeria.

1.2.2 Hypotheses

1. It is expected that the presence of dams along the main channel of the river would induce community composition to differ between the upper and lower regions because they interrupt the migration and dispersal of organisms (**Araujo *et al*., 2009**).

2. Given the flow dynamics within the LNRB as a result of "black and white floods", hydraulic connectivity between sites should be high in both dry and wet seasons, such that spatial factors would affect community composition only marginally.

3. Within region or sub-basin, given that sites are more interconnected, it is expected that high dispersal rates should give rise to a strong mass effect that tends to reduce beta diversity. As a result, species turnover should be relatively low, with spatial differences in species richness likely to reflect a nested pattern. Conversely, between regions, given that, environmental heterogeneity is high and dispersal rate should be low because of distance between regions and probably because of the dam in the river channel, it is expected that species track suitable environmental conditions, hence, beta diversity should be high as a result of species replacement owing to species sorting.

1.2.3 Research questions

1. What is the relative importance of local environmental conditions and spatial processes in structuring the community composition of fish, macroinvertebrates and phytoplankton in an afro-tropical river system?

2. Does the community structure of different trophic levels vary seasonally and spatially within the study basin?

3. Which mechanism is the determinant of the dissimilarities in the local community composition (species turnover) of the different trophic levels?

1.3.4 Objectives of the study

1. Understand the relative importance of spatial and local environmental factors in structuring the community composition of fish, macroinvertebrates and phytoplankton.

2. Explore the spatio-temporal distribution pattern of the community composition of the different trophic levels.

3. Assess the prevailing pattern explaining species turnover among the different trophic levels studied.

CHAPTER TWO: LITERATURE REVIEW

2. Concept of community ecology

Community ecology as a discipline is concerned with explaining the patterns of distribution, abundance and interaction of species (**Leibold *et al*., 2004**). Such patterns occur at different spatial scales and can vary with the scale of observation, suggesting that different principles might apply at different scales (**Maurer, 1999; Chase and Leibold, 2002**). Within local communities, populations are assumed to interact directly by affecting each other's birth and mortality rates, as modelled by population dynamic models such as the classic Lotka-Volterra equations and their extensions (**Pimm and Lawton, 1978; McCann *et al*., 1998**). It has been recognized, however, that other ecological processes involving species interactions occur at other scales (**Holt, 1993; Maurer, 1999; Hubbell, 2001**). For example, species interactions can occur in a network of local communities where they affect colonization probabilities and extinction patterns at a larger scale than those typically addressed by population dynamic equations (**Holt, 1997; Mouquet and Loreau, 2003**). The interactions and demography of local communities could also be influenced by other kinds of spatial dynamics, such as the flow of individuals that create mass effects (**Shmida and Wilson, 1985**) and source–sink dynamics (**Holt 1985; Pulliam, 1988**). These dynamics involve interactions among local communities at larger scales referred to as metacommunities.

Metacommunity is defined as a set of local communities that are linked by dispersal of multiple potentially interacting species (**Gilpin and Hanski, 1991; Wilson, 1992**). Metacommunity theory describes processes that occur at the metacommunity scale and suggests novel ways of thinking about species interactions. Currently, the concept of the metacommunity is mostly theoretical and has received relatively little empirical attention. It is easy to define local communities wherein species interact by affecting each other's demographic rates and a metacommunity as a set of local communities that exchange colonists of multiple species (**Wilson, 1992**). This definition posits that there are at least two discrete levels of community integration. At the local level, a lot of literature on species interactions, including conventional Lotka-Volterra models as well as their elaborations account for nonlinear interactions and trophic structure (**Holt and Polis, 1997**), as well as food web interactions of the kind that may be seen in more speciose local communities (**McCann *et al*., 1998; Holt, 2002; Bolker *et al*., 2003**). At the regional level, dispersal among local communities occurs and can occur with variable rates. When dispersal rates are low, the primary effects will involve colonization events that can regulate the assembly history of local communities (**Chase, 2003; Steiner and Leibold, 2004**). Effect of high dispersal rates and the roles of mass effects (**Shmida and Wilson, 1985**) and rescue effects (**Brown and Kodric-Brown, 1977**) have also been investigated. These mass and rescue effects modify both species abundance (e.g. source– sink dynamics; **Pulliam, 1988**) and species interactions (**Holt, 1985; Danielson, 1991**), and consequently both could affect community structure and dynamics (**Holt *et al*., 2003**). For species that are capable of driving another species locally extinct (e.g. natural enemies or superior competitors) metapopulation theory suggests that there are both lower and upper bounds on interpatch dispersal rates at which regional persistence of both species is possible (**Amarasekare and Nisbet, 2001; Mouquet and Loreau, 2002, 2003**).

2.1. Primers of metacommunity ecology's basic processes

In a metacommunity, four core processes determine the occurrence and abundance of species across the landscape: (1) environmental filtering of species according to local abiotic conditions, (2) biotic interactions resulting from competition and trophic interactions, (3) dispersal among habitat patches, and (4) ecological drift resulting from demographic stochasticity (**Vellend, 2017**). Critically, these basic processes occur in an explicit spatio-temporal context and across scales (**Leibold and Chase, 2017**). Within local habitat patches, population size and local species coexistence are determined by abiotic conditions, biotic interactions, and demographic stochasticity. Under unfavorable local conditions, species have negative growth rates and are eventually filtered out, unless dispersal from the regional species pool (i.e., immigration) compensates for this negative growth. At the regional scale, environmental heterogeneity among habitat patches provides additional niche space for species, and dispersal across the landscape allows species to persist under suitable environmental conditions. Hence, regional environmental heterogeneity, biotic interactions in local patches, and dispersal interact to influence regional species coexistence. Abiotic and biotic processes are often considered under the umbrella of "niche selection" (**Vellend, 2017**) as an analogy with selection in population genetics, but often, for clarity, abiotic and biotic processes are separated, as both generate different kinds of dynamics relevant to conservation biology.

2.1.1. Environmental filtering

A species' niche is defined by the set of environmental conditions under which species have intrinsic positive growth rate (**Chase and Leibold, 2003; Holt, 2009**). Niche differentiation among species leads to deterministic fitness differences that influence the likelihood of local coexistence and the geographical distribution of species across spatial scales. This is supported by theoretical formulations of local species coexistence when there are trade-offs in resource utilization and response (**Tilman, 1982; Chesson, 2000; Chase and Leibold, 2003**) and by empirical evidence of species distributions (**Peterson *et al*., 2011**), species richness (**Stein *et al*., 2014**) and community compositional variation along environmental gradients (**Cottenie, 2005; Soininen, 2014**).

While environmental filtering typically assumed a primary process limiting species distribution, it is clear that a number of other processes, including biotic interactions, dispersal limitation, and ecological drift act in conjunction with, and sometimes in opposition to, environmental filtering (**Leibold *et al*., 2004**). Furthermore, it is important to recognize that the relative importance of environmental filtering depends on the spatial (and temporal) scale in which observations are made. At small scales, and where environmental heterogeneity is minimal, the signal of ecological drift will be stronger than when scales are larger and/or heterogeneity is higher (**Chase, 2014; Viana and Chase, 2019**).

2.1.2. Biotic interactions

Individuals of the same or different species interact with each other, typically in a density-dependent way, affecting the relative abundance and composition of species among local communities (**Chase *et al*., 2020**). Competitive interactions have been central in community ecology since its inception (**Lotka, 1922**) and are the key element in species coexistence theory (**Chesson, 2000**). Similar principles for coexistence typically form the basis for the majority of metacommunity theories where competitive interactions interplay with spatial processes, including dispersal, and with scale (**Leibold *et al*., 2004**). Despite a focus on competitive interactions, recent efforts have extended the metacommunity perspective to incorporate trophic interactions (**Toju *et al*., 2017; Guzman *et al*., 2018**). Thus, the abiotic environment does not only determine habitat suitability, but also by the presence and abundance of interacting species (**Gravel *et al*., 2011**).

2.1.3. Dispersal

Dispersal connects habitat patches to each other and to the regional species pool. Differences in dispersal rates depend on both landscape connectivity and movement ability of organisms, and underlie a wide range of possible metacommunity dynamics (**Mouquet and Loreau, 2003; Leibold and Chase, 2017**). When dispersal is limited, environmental tracking can be disrupted, demographic stochasticity can increase local population extinction, and species occupancy and diversity can be lower. On the other hand, high rates of dispersal can override environmental filtering by allowing species to occupy habitat patches where their intrinsic growth rate would be otherwise negative (i.e., mass effects) (**Ng *et al.*, 2009**). Especially in highly heterogeneous landscapes, mass effects can generate source-sink dynamics with spillover of individuals from high- to low-quality habitat patches; where diversity is maintained by transient dynamics (sinks). This can drive more locally adapted species toward rarity or extinction. In addition, within a conservation context, dispersal itself often allows species to persist within a metacommunity. For example, many rare species are specialists within habitats that emerge following disturbances (**Pavlovic, 1994; Warren and Büttner, 2008**) and are able to persist in a spatial context by dispersing more rapidly to these habitats, or by tolerating disturbances better than competitors that must reinvade.

2.1.4. Ecological drift

In any given local population, each of the demographic parameters of interest (birth, death, immigration, and emigration rates) are realized with some degree of stochasticity (i.e., pulled from a distribution), which in turn influences metacommunity assembly processes (**Shoemaker *et al.*, 2019**). Small populations are relatively more susceptible to stochasticity, which can ultimately lead to higher chances of local extirpation and altered patterns of species interactions, occupancy, and coexistence (**Hubbell, 2005; Orrock and Fletcher, 2005**). The effect of demographic stochasticity can also be higher in more isolated communities, where regional dispersal is less likely to rescue populations from local extinction. Environmental stochasticity can also impose abundance fluctuations, but via deterministic environmental filtering. Although both types of stochasticity affect metacommunity functioning, their effects can be substantially different (**Shoemaker *et al.*, 2019**).

2.2. Anthropogenic drivers altering metacommunity processes

The main global anthropogenic drivers of biodiversity change, and thus the main conservation challenges for the 21st century, include land-use change and water management (including habitat loss and fragmentation), climate change, biological invasions, pollution, and overexploitation (**Butchart *et al*., 2010; IPBES, 2019**). For example, changing climate and physico-chemical properties directly influence environmental filtering; changing regional biotas and biological invasions alter biotic interactions; and changing landscapes affect dispersal among habitat patches. Furthermore, demographic stochasticity and ecological drift can amplify the effects of other drivers by altering local extinction probabilities of small populations affected by a given anthropogenic pressure. Although there is still a long way to go to fully understand the effects of disturbance on metacommunity functioning and in turn on biodiversity, some general mechanisms for each of the main global change drivers are discussed in this thesis.

2.2.1. Land-use change and water management

Global land use change such as conversion of forests into agricultural fields and pastures is a major driver of biodiversity change in both terrestrial and aquatic systems (**Sala *et al*., 2000; Foley *et al*., 2005; Millennium Ecosystem Assessment, 2005**). Although often overlooked in conservation planning and land management schemes, aquatic ecosystems are especially affected by forest conversion because they receive terrestrial inputs such as sediment, nutrients, and contaminants via runoff in their watershed (**Dudgeon *et al*., 2006; Abell *et al*., 2007; Strayer and Dudgeon, 2010**). Common effects of agricultural land use on streams and rivers include sedimentation and siltation linked to catchment erosion, increased nutrient and pollutant concentrations associated with fertilizer and pesticide runoff, and decreased habitat quality for stream organisms due to such factors as elevated water temperature and lower dissolved oxygen (DO) concentration (**Allan, 2004**). Because of these influences on aquatic habitat integrity and water quality, land use change is consistently listed as one of the most important threats both to the biodiversity of rivers and to the important ecosystem services that they provide (**Sala *et al*., 2000; Dudgeon *et al*., 2006; Dugan *et al*., 2010; Vörösmarty *et al*., 2010; Collen *et al*., 2014**).

Many studies from both temperate and tropical regions have demonstrated that declines in water quality associated with land use often lower aquatic species richness and/or other indicators of alpha diversity (**Allan 2004; Ramirez *et al*., 2008**). Land use changes may also influence beta diversity (i.e., variation in assemblage composition across the landscape; **Whittaker, 1960, 1972**), a component of biodiversity that has received comparatively less attention until recently despite its obvious relevance for conservation planning (**Ferrier, 2002; McKnight *et al*., 2007; Anderson *et al*., 2011**). Effects of forest conversion on aquatic beta diversity are much harder to predict, both because empirical studies are few and because competing theories suggest opposite responses. On one hand, cultural eutrophication (i.e., a rise in nutrient concentration and primary productivity associated with agricultural land use in a watershed) may increase beta diversity by strengthening stochastic processes during community assembly (**Chase and Leibold, 2002; Chase, 2010; Bini *et al*., 2014**). Indeed, if a larger proportion of the regional species pool can persist in more productive than less productive environments, stochasticity in colonization history can lead to "multiple stable equilibria" of community structure, thereby increasing beta diversity (**Chase, 2010**). On the other hand, deforestation also causes habitat degradation that negatively affects many pollution-intolerant taxa; this should allow a smaller, not larger, fraction of the regional species pool to maintain viable populations at deforested sites, thus lowering beta diversity. Moreover, some abiotic effects of forest conversion on rivers such as silt deposition on the riverbed and loss of woody debris could reduce habitat heterogeneity among rivers, leading to biotic homogenization and lower beta diversity (e.g., **Passy and Blanchet, 2007; Donohue *et al*., 2009**). Finally, deforestation could influence the dispersal of aquatic taxa with terrestrial, aerial life stages (e.g., **aquatic insects; Petersen *et al*., 2004; Smith *et al*., 2009**), which would also affect stream beta diversity (**Matthiessen and Hillebrand, 2006; Heino *et al*., 2015a**). Of course, multiple mechanisms could be simultaneously at play, such that their combined effects remain unknown. Indeed, the few recent studies that have examined effects of land use on stream beta diversity have reached contradictory conclusions (**Heino *et al*., 2009; Gutiérrez-Cánovas *et al*., 2013; Bini *et al*., 2014; Johnson and Angeler, 2014; Larsen and Ormerod, 2014; Hawkins *et al*., 2015**).

2.2.2. Climate change

Climate change directly affects metacommunities as an environmental filter, but also indirectly via complex community assembly processes and interactions (**Chase *et al*., 2020**). Species are extirpated from habitat patches and regions by climatic filtering if they are not able to adapt or disperse to regions with suitable climatic conditions (**Nogués-Bravo *et al*., 2018**). Changing regions experience both emigration and immigration of individuals, which leads to compositional change and the emergence of novel biotic interactions. For example, a field experiment showed that novel competitors arriving from lower altitudes strongly reduced the performance of plants that failed to disperse upward to colder climates (in contrast to transplanted plants that could track environmental change) (**Alexander *et al*., 2015**). Another indirect biotic effect of climate change is the phenological mismatch between consumers and associated trophic resources (**Renner and Zohner, 2018**), which may also affect dispersal if the synchronization between dispersal vectors and propagule production is affected (**Rafferty *et al*., 2015**).

In freshwater ecosystem, anthropogenic climate change represents a profound and insidious threat to freshwater biodiversity. Impacts will arise from rising temperatures, but changes in flow and inundation patterns due to shifts in rainfall, medium-term effects such as glacial melt, and an increased frequency of extreme events (**Milly *et al*., 2008**) will be relatively important in fresh waters because life cycles are often closely linked to hydrology. The 'fingerprint' of global climate change is already clear (**Scheffers *et al*., 2016**): 23 out of 31 measured freshwater ecological processes show evidence of being altered. If water bodies become too warm for riverine species, and they cannot adapt, dispersal to cooler habitat (at higher altitudes, or further north) will be necessary, subject to limitations imposed by topography, habitat availability upstream, the presence of dams, and so on. Compensatory movements will be especially difficult for isolated lacustrine species that cannot disperse overland or through river networks. The extent of displacement needed to adjust to the upper range of warming predicted for the next century appears insurmountable for most freshwater animals (**Bickford *et al*., 2010**).

2.2.3. Biological invasions

Invasive species directly impact biotic interactions in the metacommunity. Nonnative species compete with native species for resources, potentially reducing their performance and causing regional extinctions, as observed in both plants (**Rafferty *et al*., 2015**) and animals (**Harris and Macdonald, 2007**). Likewise, invasive species can establish novel trophic interactions, such as predation (**Doherty *et al*., 2016**) and disease (**Vilcinskas, 2015**). Examples of invasion-driven extinctions are particularly prominent on islands, where species are often evolutionarily naive to these sorts of interactions (**Sax and Gaines, 2008**). In addition, invasive species can be physical ecosystem engineers, having profound effects on habitats that create environmental filtering for native species (**Sousa *et al*., 2009**). In aquatic ecosystem, the impacts of alien invasive species depend on the identity of the invader and characteristics of the receiving community (**Strayer,**

2010). Example, carnivores are especially problematic if native prey lack appropriate anti-predator adaptations. Competition for food or space may occur, especially if invaders make habitat conditions less suitable for native species. Alien species can introduce diseases to recipient communities or may themselves be pathogens. Hybridization poses a threat if there is a close evolutionary relationship between alien and native species.

2.2.4. Pollution

Pollution causes habitat alteration and degradation, working directly as a strong abiotic filter through effects on fitness via changes in growth, health, and behavior (**Winner and Atkinson, 1986; Saaristo *et al.*, 2018**). It also affects habitat connectivity and suitability by increasing matrix hostility (**Willson and Hopkins, 2013**) and reducing services, such as pollination (e.g., lethal toxicity due to pesticides) (**Brittain and Potts, 2011**). Pollution, especially via pesticides, can also interact with spatial processes within metacommunities to repeatedly and cumulatively influence impact, recovery, and regeneration processes (**Trekels *et al.*, 2011**). Furthermore, pollution occurs in a host of forms, reflecting its multiple origins, with consequences that can be ubiquitous (the syndrome of eutrophication) and as in the case of the 'cocktail' of contaminants and pollutants affecting an individual site unique to a particular location. The non-chemical alteration of water body falls into this category, such as warming (thermal pollution) caused by cooling-water discharge from power stations. Pollution can arise from 'end-of-the-pipe' point sources. For instance, discharge from a factory, a mining operation, or more diffuse run-off from agricultural land, and may be organic or inorganic compounds, or a mixture thereof, consisting of livestock waste and sewage (including pharmaceuticals), factory discharges, landfill seepage, oily run-offs from roads and impermeable surfaces, agrochemicals (fertilizers or pesticides), macro- and microplastics, and so on (**Lebreton *et al.*, 2017; Burns *et al.*, 2018**). The effects of pollutants can be direct or indirect, lethal or sub-lethal, and their interactions may cause unexpected consequences. Pollution burdens can be expected to increase in the near future as a result of increasing wastewater discharge due to urbanization and intensification of livestock farming (**Wen *et al.*, 2017**).

2.3. Status of the fish biodiversity of the Niger River

The fish communities of the Niger River belong to the Nilo-Sudanian Province. The Upper Niger and Central Delta harbor about 130 to 140 species (**Daget, 1954; Lévêque *et al.*, 1990**), which belong to 62 genera and 26 families. In the middle Niger, 98 species belonging to 22 families, have been recorded (**Daget, 1962; Bacalbasa-Dobrovici, 1971; Coenen, 1986**). Among these species, 83 are regularly fished while 15 are of a very small size and/or are very rare. In the lower Niger, 160 species have been recorded in Lake Kainji (**Balon and Coche, 1974; Ita, 1978, 1993**), with 9 fish families of economic importance. On the Benue River (one of the largest tributary of the LNRB), 113 species were collected in the Mayo-kebbi (**Blache *et al*., 1964**) versus 128 in the Benue River (**Stauch, 1966**). **Welman (1948)** identified 181 species of fish from the major river systems of Nigeria and Lake Chad including some estuarine and marine species which frequent the rivers. **Banks *et al.* (1965)** identified and described about 139 species of fish along the upper Niger within the then proposed Kainji Reservoir Basin. **Reed *et al.* (1967)** also identified and described about 160 fish species within the then northern region of Nigeria. Since then, numerous studies both in Kainji and other man-made and natural lakes in Nigeria have led to the description of new species and identification of species described earlier by scientists associated with the Kainji Lake Research Project and the National Institute for Freshwater Fisheries Research. The checklist produced in **White (1965)** covers the upper Niger within the then proposed Kainji Lake Basin and lists about 145 species. Species in the Anambra, Kaduna and Sokoto/Rima, which are major tributaries of the Niger, are low in diversity as would with 23, 28 and 22 species respectively. Compared with the major investigations of **Reed *et al.* (1967)** and **White (1965)** which were funded internationally, the duration and extent of investigations by national institutions are usually limited by inadequate funding. The same constraints also limited the investigations into the Cross River, and rivers Ogun and Oshun with 39, 23 and 23 species respectively. In most cases, the identification of species was limited to genus. Until recently, the fauna of the Niger Delta was largely ignored, due to the inaccessibility of the riverine and swampy areas. The Delta has a lower diversity of freshwater fish than recorded in equivalent biotopes in West Africa. By 2002, there were 311 freshwater fish species recorded from the rivers and lakes of Nigeria (**Ita, 1993).**

All these species have adapted the seasonal and inter-annual variations of the hydrological cycle of the river both in freshwater and brackish water ecosystems involving a succession of favorable and unfavorable environments and the appearance and disappearance of natural habitats (**Odo *et al*., 2009**). Feeding, growth and mortality are closely linked to the seasons. For instance, spawning of most of the species takes place at the beginning of floods (**Benech and Dansoko, 1994**), growth is restricted to rising and high waters, while mortality rates are higher during the declining water level and dry season. Fish breeding and feeding migrations are dependent on water discharges (**Eyo and Mgbenka, 1992**). In response to the variations in the hydrological cycle, fish community composition and abundance can change greatly from one season or one year to another.

Over the past decade a fluctuation and decline has been recorded in LNRB by researchers indicating the total loss or decline of some fish species. (**Solomon *et al*., 2012; Agbugui *et al*., 2019**). This decline is a gradual indication that species are becoming threatened, endangered and the possibility of extinction. The world's population is geometrically increasing, while food production both from agriculture and livestock only multiples arithmetically. This constant demand for food and aquaculture produce especially freshwater fish is overstretching the catch efforts, survival, and management regims of fishes. Other factors that possibly affect this consumer satisfaction include overfishing, habitat loss and degradation, pollution and global warming. **Stiassny (1998)** estimated that about 300 species will become extinct in the next 20 - 30 years (i.e. by 2028). This means that if care and management is not appropriately deployed, this sector will depreciate and not contribute adequately to curbing hunger and meeting the need of mankind. The River Niger is one of the Rivers in Nigeria that has experienced fluctuation in fish fauna. So far, there is the inadequacy of data, institutional policies and inadequate conservation methods to alleviate the problem of threatened fish fauna. Furthermore, there is the absence of observed fishing laws and penalties to assist in the drive for fish conservation.

2.4. Ecological concepts underpinning the distribution and abundance of aquatic biodiversity

2.4.1. River continuum concept

The development of the river continuum concept (RCC) (**Vannote *et al*., 1980**) was an important step in river ecology, as it was the first attempt to describe both the structural and functional characteristics of stream communities along the entire length of a river. The concept was developed specifically in reference to naturally undisturbed river ecosystems in North America. The RCC argues that the biotic stream community adapts its structural and functional characteristics to the abiotic environment, which presents a continuous gradient from headwaters to river mouth. This is expressed by the distribution of organic matter and macroinvertebrate functional feeding groups. In general, rivers can be divided into three parts based on stream size: headwaters (stream orders

1 – 3), medium-sized streams (orders 4 – 6) and large rivers (order greater than 6). The headwaters of rivers are strongly influenced by riparian vegetation. Primary production is low because of shading, and the vegetation contributes large amounts of allochthonous detritus. Thus, the ratio of gross primary productivity to respiration of the aquatic community is small (P/R< 1). The size of particulate organic matter is rather large, consisting mainly of dead leaves and woody debris (coarse particulate organic matter (CPOM) <1 mm). The influence of the riparian zone diminishes moving downstream; both the importance of terrestrial organic input and the degree of shading decreases, whereas primary production and transport of organic matter from upstream increases. This is reflected by an increase in the P/R ratio (from P/R<1 to P/R>1). The size of organic matter decreases to fine particulate organic matter (FPOM, 50 – 1 mm) and ultrafine particulate organic matter (UPOM, 0.5 – 50 mm). Large rivers receive organic matter, mainly from upstream, which has already been processed to a small size. Primary production is often limited by depth and turbidity. Therefore, the P/R ratio decreases again (P/R<1).

Changes in the size of organic matter along the length of the river are reflected in the distribution of functional feeding groups of invertebrates. In the headwaters, shredders are codominant with collectors. Shredders process CPOM, such as leaf litter and the associated biomass. Collectors obtain their food by filtering it out of the water or gathering from the sediment FPOM and UPOM, which has been processed from CPOM by shredders. Collectors and grazers (or scrapers), which shear attached algae from surfaces, dominate the middle part of the river. In the lower reaches, the invertebrate assemblage consists mainly of collectors.

Since its development, the applicability of the RCC has been tested on various river systems. Several field observations agreed with the RCC (**Cushing *et al*., 1983; Minshall *et al*., 1983; Naiman, 1983; Conners and Naiman, 1984**). In the cases where the concept did not comply with field observations, this could be explained by the dominant role of tributaries, climate, geology, local conditions, water quality or human disturbance (**Winterbourn *et al*., 1981; Minshall *et al*., 1983; 1985; Bruns *et al*., 1984; Conners and Naiman, 1984; Cummins *et al*., 1984, 1995; Magdych, 1984; Sedell and Frogatt, 1984**). **Minshall *et al*. (1985)** stress the intention of the RCC as a standard for natural, unperturbed lotic systems, in which general conditions and relationships can be identified and used to study and compare existing streams. It provides a framework for understanding the ecology of streams and rivers and is not intended as a description of the biological components of all rivers individually.

2.4.2. Resource spiraling concept

The resource spiraling concept extends on the RCC by elaborating the processing of organic matter along the length of the river. The downstream flow of rivers adds a spatial dimension to resource cycles in stream ecosystems through downstream displacement of material. This results in partially open cycles or 'spiraling' (**Wallace *et al.*, 1977; Newbold *et al.*, 1981, Newbold *et al.*, 1982a, b; Elwood *et al.*, 1983; Newbold, 1992**). Spiraling can be measured with the unit 'spiraling length' (S), defined as the average distance along which the river flows during one cycle of a nutrient element, such as carbon. The shorter the spiraling length, the more efficiently the nutrient is utilized, i.e. the more times a nutrient is recycled within a given reach of stream (**Newbold *et al.*, 1981; 1982a**). Spiraling is a function of both downstream transport rate and retention processes (**Minshall *et al.*, 1983**). A high transport rate, determined largely by water flow, will increase the spiraling length, whereas retention mechanisms, such as physical storage (e.g. wood debris, boulders, macrophyte beds, sedimentation) and biological uptake and storage will decrease the spiraling length. This biological retention is the recycling of nutrients in the ecosystem, which is largely controlled by environmental conditions, such as oxygen, temperature, nutrient availability and the structure and species composition of the food web (**Minshall *et al.*, 1983**).

In general, the spiraling length increases with stream size. Forested headwaters tend to conserve or store resources, because of their high biological activity and high retention of organic matter through debris dams (**Lorenz *et al.*, 1997**). In downstream parts of rivers, flow velocities increase and organic carbon is processed into successively smaller (and more transportable) particle sizes (**Newbold *et al.*, 1982a; Johnson *et al.*, 1995**). In side channels and floodplains, the spiraling length may decrease, because of a high retention, both physically (e.g. sedimentation, woody debris, riparian vegetation) and biologically (e.g. high productivity) (**Pinay *et al.*, 1990**).

2.5.3. Serial discontinuity concept

Another concept associated with the RCC is the serial discontinuity concept (**Ward and Stanford, 1983**). This addresses the effects of dams on rivers. Dams disrupt the continuum and cause upstream–downstream shifts in abiotic and biotic parameters and processes. The effect is related to the position of the dam along the continuum. TheWa serial discontinuum concept defines two parameters that may be used to evaluate the relative effect of a dam on the riverine ecosystem structure and function (**Ward and Stanford, 1983**). First, the discontinuity distance, which is the distance over which the expected value of a physical or biological variable is shifted in downstream or upstream direction as a consequence of the discontinuity introduced by the dam. Secondly, the intensity, which is the absolute change in the variable as a consequence of regulation (i.e., the difference between the unregulated versus the regulated response at the same point along the longitudinal profile).

In general, dams increase the homogeneity of a variable between two discontinuities (**Ward and Stanford, 1995**). In the lentic water from a reservoir, temperature is more uniformly distributed than in flowing water. The transport of large organic matter particles, such as CPOM, will be blocked, whereas smaller particles (FPOM) can pass the dam more easily. Furthermore, dams reduce the ecological connectivity between the main-stream and the riparian zone. In the first place, the blocking of CPOM originating from the riparian vegetation decouples the linkage between allochthonous inputs upstream and processing of organic matter downstream. In the second place, dam building is frequently associated with river regulation, which isolates river channels from their floodplain and riparian forest. Tests of the serial discontinuity concept in regulated rivers showed discontinuities in abiotic (temperature) (**Stanford *et al*., 1988**) and biotic variables (**Hauer and Stanford, 1982; Stanford *et al*., 1988, Araujo *et al*., 2009**).

2.4.4. Flood pulse concept

The RCC predicts a diminishing influence of the riparian zone from headwaters to the downstream river. This, however, holds only for large rivers, that are confined to the riverbed. Large floodplain rivers are significantly influenced by regular floods of the main stream into the bordering floodplains. The flood pulse concept (FPC) (**Junk *et al*., 1989**) describes the effects of floods on both the river channel and its floodplain in an unmodified, large river–floodplain system.

Floodplains tend to establish their own nutrient cycles since organisms and environmental conditions differ considerably from the main channel. Nutrients originate mainly from river water. Release and storage of nutrients in the floodplain depend on the flood cycle, vegetation cover and, in temperate regions, the growth cycle of the vegetation. During floods, a layer of sediment, composed of nutrients and particulate organic and inorganic matter, is deposited on the floodplain. The quality of the sediment determines the fertility of the floodplain. The carbon exchange between floodplain and main channel will depend on three factors: the presence of retention mechanisms keeping carbon in the floodplain and reducing leakage to the river channel (e.g. sedimentation, uptake by organisms, and retention by macrophytes and terrestrial vegetation); the duration and flushing rate of the flood; and the growth cycle of floodplain vegetation in temperate regions. **Pinay *et al*. (1990)** report that annual direct litter inputs to large rivers range between 10 and 40 g/m2 of water surface.

With regard to biological productivity, a high P/R ratio is predicted for a large river–floodplain system, because of a high production in the floodplain and low import of organic matter from upstream. The flood-pulse affects the primary production and respiration in the floodplain by determining the occurrence, life cycle and abundance of organisms. Furthermore, the change between the terrestrial and aquatic phase accelerates the decomposition of organic material.

River–floodplain systems show a high diversity of habitats. Sediments, deposited in the floodplain, form bars, levees, swales, ox-bows, backwaters and side channels. Differences in the duration of flooding, soil structure and vegetation result in many different small-scale habitats and physicochemical conditions of oxygen, temperature and dissolved and suspended matter. These habitats can be unstable because of changing water-levels, sediment deposition and erosion. **Amoros *et al*. (1987)** and **Bravard *et al*. (1986)** have carried out extensive studies on the geomorphological processes underlying the habitat diversity in floodplains on the Rhone system. As a consequence of the large variation in habitats, species diversity in river–floodplain systems is high. The flood-pulse is expected to limit sedentary terrestrial and aquatic species, because of the physical stress of the flood, but will favor mobile organisms, such as fish and non-aquatic birds, which are able to avoid this stress.

CHAPTER THREE: MATERIALS AND METHODS

3. Study area

The lower Niger River Basin (LNRB) is located between latitude 7° N and 12° N and longitudes 3° and 9° E (Figure 1). The river has its source in the Fouta Djallon Mountains in the south of Guinea at an altitude of about 800 m (**Oguntunde *et al*., 2014**) and flows for a total length of about 4,100 km, through Mali, Niger and about 1,200 km through Nigeria (**Iloeje, 1976**), before reaching the Atlantic Ocean. The LNRB occupies about 562,372 km^2 (44%) of the total basin of Niger River and constitutes about 66.74 million (62%) of human population within the basin (UNPD, 2006). The growth rate of the population occupying the basin is estimated at 3.2% (**Bana and Conde, 2008; Guengant, 2009**). Population density in the basin is four to five times greater than the national average, given that people concentrate along River as they depend on the river's resources for their livelihood (**UNPD, 2006**). A massive rural exodus, as well as a century-old migration from the inland to coastal areas (**Ogilvie, 2010**) exacerbate urbanization within the river basin. The basin experiences two major seasons: the rainy season (which varies in amount of rainfall from 100 mm in the north to 1300 mm in the south) commences in the month of April, attaining its peak around September and ends in October (**Oguntunde *et al*., 2014**). The dry season lasts between the months of November and March (**Otache *et al*., 2016**). The main channel of the river crisscrossed three different agro-climatic zones: Guinea savanna (the largest zone within the basin) in the northern part of Nigeria where arable crop and nomadic system of farming is dominant, the rainforest zone mainly dominated by unplanned/unregulated urban settlement and farming, and the mangrove/delta region where oil exploration is taking place, before emptying into the Atlantic. Two consecutive dams, Kainji and Jebba, constructed for hydropower generation, transformed the river in the headwater site into Lakes Kainji and Jebba, respectively.

LNRB experiences two distinct floods annually. The first is the "Black flood" which occurs in dry season (December to March), originates from the high rainfall area at the headwaters and travels for a period of six months before reaching Kainji Lake section of the LNRB. On its way to the LNRB, the water drains the swamp of Timbuktu (in Mali) where it loses 65% of its water to evaporation and infiltration (**NEDECO and Balfour, 1961**). Having deposited its silt in these swampy areas, the water becomes relatively clean and appears black from distance, hence, the name "black flood". The black flood arrives at Kainji Lake in December and lasts until March at Jebba Lake after attaining a peak discharge rate of 2000 cubic meters per second in February

(**Balogun and Ibeun, 1995**). The flood recedes to 200 and 400 cubic meters per second in May and August respectively, when the "White flood" takes over (**Adeniji and Mbagwu, 1998**). This "White flood" originates from local runoffs around the catchments of Kainji Lakes (upper reach of the LNRB). It occurs from August to November (mid to late rainy season). The flood carries a lot of silt and mud giving it the milky look from which it gets its name. It reaches its peak at about end of September and it is much higher than that of the "black flood". Its peak discharge is about 4,000 cubic meters per second and levels down to 1,500 cubic meters per second in November before "black flood" takes over again (**Adeniji and Mbagwu, 1998**). The annual flow of the LNRB may reach about 80 000 million m^3 in a year of high flow, of which 47 000 million is obtained from the "white flood" and the balance, 33 000 million, in the "black flood". However, "black flood" is relatively constant from year to year while the "white flood" may be reduced by as much as one third in dry years (**Imevbore, 1970**). The river basin is currently undergoing rapid urbanization leading to fast population growth, accompanied by fast economic development. Urbanization has led to large-scale deforestation, additional demand for water for agricultural and municipal use, siltation and increase in relative amount of drainage basin area, which is made impervious (**Babatolu and Akinnubi, 2014**).

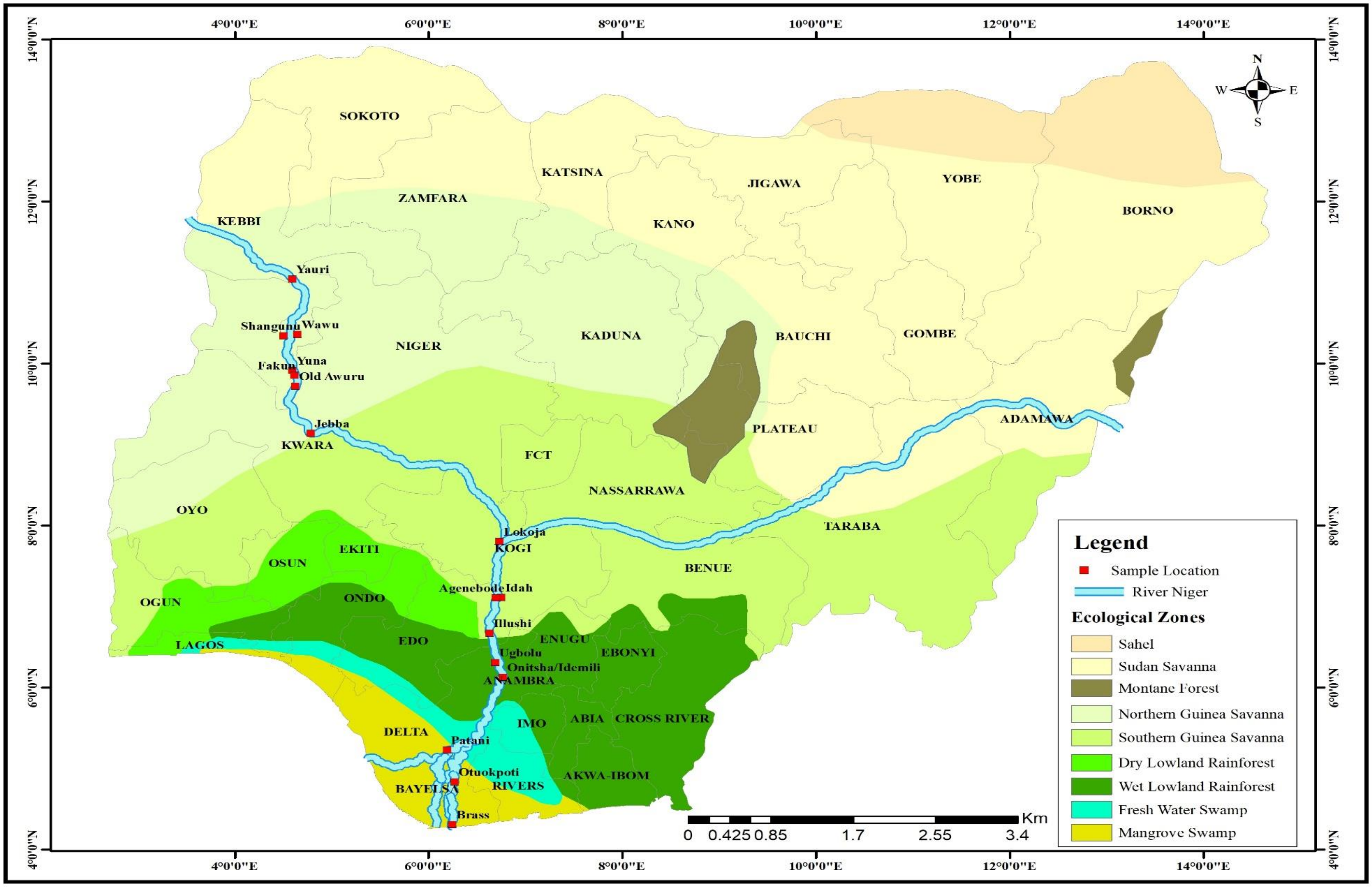

***Figure 1*:** Map of the study area showing the sampling sites and the different ecological zones along the longitudinal gradient of the river

3.2. Sampling sites

This study was conducted at fifteen (15) sampling sites along the longitudinal gradient of the LNRB (Figure 1). The river was divided into upper and lower region. The upper region is made up of seven (7) sites. The sites include: Yauri, Wawu, Shagunu, Yuna, Fakun, Awuru and Jebba. These sites are located in the section of the river that is within the Guinea savanna in the northern part of Nigeria where arable crop and nomadic system of farming is dominant. This region is also characterized by the presence of Kainji and Jebba hydroelectric dams. The lower region is made up of the sites that are below the dams (eigth sites). The sites are namely: Lokoja, Idah, Agenebode, Ilushi, Ugbolu, Onitsha, Patani and Ogbia. This region lies within the rainforest and mangrove zone of the southern Nigeria where unplanned urbanization, farming activities and oil exploration is taking place. Sampling occurred over one year, and seasonally in the dry (January to March 2021) and rainy (July to August 2021) seasons. Dry and rainy seasons represent the major seasonal changes in Nigeria. Samples were collected twice (once within the dry and rainy seasons respectively). The sampling sites were selected based on sites already established by previous researchers along the longitudinal gradient of the river. This was done based on reconnaissance survey of the study area.

3.3. Sample collection and analysis

3.3.1. Water sampling and physico-chemical measurements

Surface water samples were collected in 250 ml polyethylene bottles from three different points at each site during each field campaign for physico-chemical analyses. Water quality parameters such water temperature (°C), dissolved oxygen (mg/l), conductivity (µS/cm) and pH were measured *in situ* with a multi-parameter water quality-monitoring instrument (YSI, model 85, Cole-Parmer, USA). Biological oxygen demand (BOD_5) (mg/l), total dissolved solids (mg/l), total suspended solids (mg/l), turbidity (NTU), chloride (mg/l), acidity (mg/l), total hardness (mg/l), alkalinity (mg/l), sulphate (mg/l), phosphate (mg/l), nitrate (mg/l) and nitrite (mg/l) were measured following **APHA (2005).**

3.3.2. Fish sample collection and identification

Fish sampling protocols were as recommended by **Odo *et al.* (2009)**. We engaged the services of three artisanal fishermen per site who used gill nets (mesh size = 75 mm, width = 50 m, height =

2 m) and cast nets (mesh size = 50 mm, length = 3.5 m, circumference = 15 m). Four Malian traps (100 mm mesh size) and five hook and line systems (hook size 13) were also used to achieve a good representation of all species. Three gill nets were deployed between 4:00 am and 4:30 am, and the catches recovered between 10:00 am and 10:30 am (fishing duration of approximately six hours). Cast net fishing (15 throws) was conducted for three hours (7 am to 10 am) covering about 300 m stretch in each sampling sites. To ensure equal fishing efforts in all sampling sites, we used the same set of fishing gears and spent equal amount of time in all the stations. The catches were transported to the laboratory in an icebox. At the laboratory, the fish were identified to species level using fish identification keys by **Olaosebikan and Raji (1998)**. For each sampling site, the total counts of specimens per species were recorded and used for further analysis.

3.3.3. Phytoplankton sample collection and identification

Phytoplankton samples were collected by passing one hundred (100 L) liters of surface water through phytoplankton net made of bolting silk no. 25 in the early hours of the day between (7 am to 9 am) as recommended by **Jesna *et al*. (2021)**. The filtered plankton samples were preserved in 4% formalin (v/v) in an airtight bottle and transported to the laboratory for identification and enumeration. At the laboratory, the phytoplankton were identified with an inverted microscope of Olympus CKX41 model (x 400 magnification) using standard protocols (**Needham and Needham, 1962; APHA, 1992; Tsarenko, 2011; Komarek *et al*., 2014; Guiry and Guiry, 2020**). The identified phytoplankton were then enumerated with a Sedgwick-Rafter Counting Cell (**Saxena, 1987**). The phytoplankton cell density was calculated in accordance with **Welch (1948)** and expressed as cells/liter of the water body as follows:

$$N = (A \times 100)\ C/L$$

Where N is the number of phytoplankton per liter of water; C is the volume of original concentrate in milliliter; A is the average numbers of phytoplankton in all counts in the counting cells and L is the volume of water filtered through the plankton net.

3.3.4. Macroinvertebrates sample collection and identification

Littoral macroinvertebrates were sampled using a kick net (dimension 300 x 300 mm frame and 1000 µm mesh) according to the South African Scoring System (SASS) 5 protocol (**Dickens and Graham, 2002**). SASS 5 protocol requires the collection of macroinvertebrates from three distinct biotopes: stones (in-current and out-of-current) for 3 min, sediments (gravel, sand, and mud) for 1 min, and 2 m and 1m^2 of marginal and aquatic vegetation, respectively. At each sampling event, samples were collected within the sites but not necessarily the same spot was sampled repeatedly. After each collection, samples were preserved in 4% formalin (v/v) in an airtight-labelled 500 ml polyethylene sample bottles and transported to the laboratory for sorting and identification.

In the laboratory, all macroinvertebrate specimens for each site and season were sorted and identified to the lowest possible level (generally to genus or species) under a dissecting microscope using available keys (**Day and de Moor, 2002; de Moor *et al*., 2003**).

3.3.5. Disturbance score

We used a score-based disturbance index as described by **Shukla and Baht (2018)**, with modifications to quantify anthropogenic perturbation of each of the sampling sites within the river basin. The features were categorized to include proximity to human settlement, activities along river bank, agriculture/farming, sand mining, proximity to forested area, distance from dams, river modification (in the form of dams, channel obstructions etc.) and waste disposal. Stations were scored 3 (highest) for a feature/activity if it was observed on site, 2 if it was upstream to the site and 1 if it was observed downstream. Activity that was absent was scored 0. Features and activities with most likely negative impacts on river ecology were assigned positive values while activities with likely positive impacts were assigned negative values (e.g., whereas - 3 was assigned to forest on site, +3 was assigned to agriculture/farming on site). We estimated the disturbance index for each site by summing the scores obtained on each site. Sites with high scores indicate strong negative impacts (Table I).

Table I: Disturbance scoring method. Sites were ranked by presence of activity recorded during sampling periods

Activities	Disturbance score		
	-3 or 3	-2 or 2	-1 or 1
Proximity to human settlement (meter)	<100	<500	<1000
Activities along stream bank[a]	<3	<6	>6
Agriculture/farming (distance from stream bank to farm in meters)	<100	100–500	>500 or absent
Sand extraction/mining	On site	Upstream	Downstream
Distance from forested area (meter)	>500	100–500	<100
Effect of dams (distance from dams in meters)	<500	<1000	>1000
Stream modification[b]	3	>1	0
Waste dump	On site	Upstream	Downstream

Activities recorded at site were given a score of 3 or – 3, upstream of site as 2 or – 2, downstream as 1 or – 1 and absence of any activity as 0. Positive values are assigned to activities with negative impacts on the river ecosystem.

[a] Fishing, cremation/religious activities, cattle, bathing/washing clothes, road/bridge construction, boating, Market

[b] River diversion, modification of river bank, unregulated pumping of stream water

Source: Shukla and Baht (2018)

3.4. Data analyses

The spatial and temporal differences in the community structure between the upper and lower regions and between seasons (dry and rainy) were tested using a non-parametric permutation-based one-way analysis of similarity (ANOSIM; **Clarke, 1993**). ANOSIM is similar to univariate analysis of variance (ANOVA), as it tests for significant differences among groups. However, unlike ANOVA, ANOSIM is performed on a similarity matrix rather than the raw data; significance is based on comparisons of this matrix to random permutations of the matrix (**Clarke and Warwick, 1994**), with the degree of dissimilarity associated with each factor being measured by an *R* statistic (comparable to the *F* statistic of ANOVA).

Next, Nonmetric multidimensional scaling (NMDS) was used to identify groupings of observations. A similarity breakdown procedure (SIMPER) was further used to identify the species that contributed most to any among-group dissimilarity and to quantify and rank species that on average contribute strongly to community structuring (**Clarke, 1993**). The procedure also allowed the quantification of the average contribution of each species to the overall measure of dissimilarity between regions within season and between seasons within region. In order to accomplish these ends, the procedure uses the standard deviation of the site by distance matrix, attributed to a species, for all species pairs and compares that with the average contribution of a species to the dissimilarity.

To assess the relative importance of environmental and spatial factors structuring the species composition in the LNRB, Redundancy Analysis (RDA), partial Redundancy Analysis (pRDA) and variation partitioning analysis were used. The response variables consisted of species count data. The species count data were Hellinger transformed prior to RDA (**Legendre and Gallagher, 2001**). Two sets of predictor variables were used in the RDA. The first set of variables consisted of environmental data (water quality variables). These environmental variables were log transformed to approximate normal distributions. The second set of predictor variables consisted of spatial data (matrix of spatial distances between sampling sites along the longitudinal length of the LNRB obtained from a map of the studied river using QGIS version 3.2.6) generated through principal coordinate analysis of neighbor matrices (PCNM). The PCNM proposed by **Bocard and Legendre (2002)** were used to model spatial variation. Generation of spatial variables was done using the *pcnm* function from the vegan package (**Oksanen *et al*., 2018**) in R package (version 4.2.1).

3.4.1. Model selection

To reduce the number of environmental variables used in the final RDA model, the approach suggested by **Zuur *et al*. (2010)** was followed. First a full model of RDA using *rda* function in vegan package (Oksanen *et al*., 2018), was performed with all the predictor variables. After this, variance inflation factors (VIFs) were calculated for each explanatory variable of the model. Then, the variable with the highest VIF from the model were removed and the RDA repeated with the remaining variables. The procedure was sequentially repeated until all the VIFs of the variables were below a predetermined threshold value of VIF<5, to minimize the effect of multicollinearity among the environmental variables. After removing the environmental variables with multicollinearity, next was a stepwise (backward) variable selection applying the Akaike Information Criterion (AIC) using *ordistep* in vegan package (**Oksanen *et al*., 2018**) for the remaining variables. The variables selected by the AIC were then used as the explanatory variables in the final RDA as response variables. In the backward selection procedure, the selected variables had to be significant at alpha ≤ 0.05, and the *adjusted* R^2 of the final model had to be lower than the *adjusted* R^2 of the global model. The VIF procedure, however, was not feasible for the selection of spatial variables given that these variables are by default uncorrelated with each other. Therefore, in order to reduce the number of spatial variables in the final RDA models, an RDA was performed with the full set of spatial variables. Afterwards, a backward AIC variable selection for the model was ran. The spatial variables chosen based on the AIC were used in the final RDA model. The retained environmental and spatial variables from the RDA model were then used for variation partitioning and pRDA analysis, in which the unique fraction of total variation in species abundance explained by each set of explanatory variables and the significance of the fractions explained were estimated, respectively. All the analyses were performed separately for the dry and rainy seasons.

3.4.2. Variation partitioning by partial redundancy analysis (pRDA)

To determine the fractions of the variance in species abundance that could be explained by local environmental factors, E, and spatial factors, S, variance partitioning using partial redundancy analysis (pRDA) was performed (**Peres-Neto *et al*., 2006**). Redundancy analysis shows associations between species count and a set of explanatory variables (E or S). The pRDA is an extension of RDA, which allows testing for effects of one set of explanatory variables, at the same time partialling out effects of a second set of explanatory variables. The total variation in species count was divided into the fraction of variation in species abundance that can be explained by the spatial factor independently of any environmental factors (S|E), the fraction of variation of species abundance that can be explained by the environmental factors independently of any spatial factor (E|S), the spatial structure in species abundance shared by the environmental data (E ∩ S) and unexplained variation [1 – (E + S)]. According to **Clappe *et al*. (2018)**, this method is routinely used in ecology to assess the importance of environmental and spatial variables on meta-communities. The pure environmental variation without a spatial component represents the strength of species sorting, while the pure spatial variation without an environmental component is interpreted as the effect of dispersal limitation. Significance of the partitions was tested by an ANOVA-like permutation for the pRDA with 999 permutation and alpha = 0.05. *Adjusted* R^2 values was used to estimate the percentage of variation explained since this is the only unbiased measure (**Peres-Neto *et al*., 2006**). The pRDA and variation partitioning analyses were performed with functions *rda* and *varpar*t in R package (version 4.2.1) vegan, respectively (**Oksanen *et al*., 2018**).

3.4.3. Beta diversity decomposition

Data analyses were conducted at the entire basin and reach levels (upper and lower region). At the basin level, the overall data set from the entire basin (15 sites) were included and at the reach level, data from the sites within each given reaches (upper and lower region) along the longitudinal gradient of the river were used. At each reach, the sum of the total of species collected from the sites within the reach formed the regional species pool for that reach. This approach was used to test whether beta diversity patterns differ depending on position along the longitudinal gradient of the river.

Site-by-species matrices with species count data and Jaccard dissimilarity coefficients were used to assess beta diversity. Firstly, the species count data were Hellinger-transformed to minimize differences because of the high abundance of some species. The beta diversity was then partitioned using the Podani family decompositions into components of species richness difference and species replacement as described by **Legendre (2014)**, using the function *beta.div.comp* from the library adespatial (**Dray *et al*., 2017**) in R (Version 4.1.2). Once beta diversity and its components (richness difference and replacement) were estimated, the next step was to identify if these values differ as function of the position along the longitudinal gradient of the river. Permutational analysis of multivariate dispersion "PERMDISP" (**Anderson *et al*., 2006**), an analysis that tests if beta diversity and its components (response variables) differ between upper and lower reaches (factors) was used. To test for significant pairwise differences between the river regions, ANOVA was used. Both PERMDISP and ANOVA tests were performed using the *betadisper* function from the vegan package (**Oksanen *et al*., 2018**) in R.

3.4.4. Local contributions to beta diversity (LCBD)

To measure the contribution of each site to beta diversity, LCBD index was calculated as an estimate of the compositional uniqueness of local assemblages relative to the basin-wide metacommunity. LCBD indices were calculated for the beta diversity and its components (richness difference and replacement) using the function *LCBD-comp* from the adespatial package in R. Large LCBD values indicate sites that may have high conservation status for their particular species combinations or sites with a very low number of species that may be candidates for ecological restoration (**Legendre and De Cáceres, 2013**). Spearman correlation test were performed using *cor.test* function to identify if LCBD values were related to local richness and abundance.

3.4.5. Explaining variation in beta diversity and its components

To test if variation in community dissimilarity matrices (beta diversity, species richness difference, species replacement) were related to environmental and/or spatial factors along the longitudinal gradient of the river, distance-based redundancy analysis (db-RDA) method (**Legendre and Anderson, 1999**) was used. Because db-RDA works well when the dissimilarity matrix is Euclidean, Podani's family decomposition method was used. **Legendre (2014)** reported that matrices generated by Podoni's family are Euclidean and can be fully represented in the Euclidean space without transformation. db-RDA was calculated using the function dbRDA. This function produces an F-test of significance for the response data matrix (beta diversity and its components) and a set of explanatory variables (environmental and spatial).

To select environmental and spatial variables that were significantly related to beta diversity and its components, a stepwise (backward) selection procedure was performed using each of the dissimilarity matrices as response data (one by one) and the environmental and spatial variables (separated) as explanatory data as described by **Legendre (2014)**. Prior to performing the db-RDA and stepwise procedure, environmental variables were Hellinger transformed because they were measured using different units. Variables expressed as proportions were transformed to the arcsine of their square root. The remaining variables (response variables) were log-transformed, with the exception of ordinal and categorical data, for which no transformation was performed. The function *forward.sel* from the adespatial package in R was used with 999 permutations and significance at alpha = 0.05 for the explanatory variables.

3.4.6. Variation partitioning

Variance partitioning procedure was used to determine the relative influence of environmental and spatial variables on each of the dissimilarity matrices (**Peres-Neto *et al*., 2006**). Because dissimilarity matrices are being used as response data, db-RDA was used to partition the variation into the pure components of environment, space, and their shared contribution to the explanation of beta diversity and its components. To test the significance of each testable component, an ANOVA-like permutation test for the db-RDA was performed with 999 permutations and alpha = 0.05. These analyses were carried out using the functions *varpart* and *anova* from the vegan package in R.

CHAPTER FOUR: RESULTS AND DISCUSSION

4. Results

4.1. Fish community structure

In total, 3807 fishes representing 42 species belonging to 17 families and 10 orders were collected in the Lower Niger River Basin (Appendix 1). A total of 40 and 34 species were recorded in the dry and rainy seasons, respectively. While 34 fish species were recorded in both the dry and rainy seasons, 41 species were obtained in the lower region of the river basin. In the upper region, during the dry season (Appendix 2), the family Clariidae (32.78 %) recorded the highest abundance while *Oreochromis niloticus* (20.17%) was the most abundance species. The family Polypteridae with abundance of 0.11 % and the species *Polypterus senegalus* (0.11 %) were the least abundant family and species, respectively. In the rainy season, the family Synodontidae (17.45 %) were the most abundant while *Synodontis membranaceus* was recorded as the most abundance species with a total of 88 (13.13 %) individuals. *Heterobranchus bidorsalis* and *Brycinus macrolepidotus* with 0.14 % percentage abundance each were recorded as the least abundance species at the upper region during the rainy season. Polypteridae was the least abundance family with percentage abundance of 0.29 % (Appendix 3). Families Osteoglosidae, Channidae and Tetraodontidae were observed to be absent at the upper region during the dry season but were present at the rainy season. In the same vein, the families Protoptridae, Gymarchidae and Malapteruridae which were found to be absent in the rainy season at the upper region, are present during the dry season.

At the lower region of the river, during the dry season, the family Bagridae with percentage abundance of 16.54 % was the most abundant family while Malapteruridae (0.18 %) was the least abundant family. *Citharinus citharius* (10.6%) and *Labeo senegalensis* (0.12%) were the most and least abundant species, respectively (Appendix 4). During the rainy season, Synodontidae (25.8%) and *Synodontis schall* (17.97%) were the most family and species, respectively. The least abundant and the most abundant family and species are Malapteruridae (0.46%) and *Synodontis couteti* (0.31%) (Apendix 5).

Generally, Shagunu (upper region) and Onitsha (lower region) sites had the highest richness with 29 species each while Awuru (upper region) recorded the lowest richness with nine species. Whereas families Alestidae (6), Mormyridae (6), Bagridae (5) and Synodontidae (5) had the highest number of species, Tetraodontidae, Channidae, Polypteridae, Protopteridae, Centropomidae and Gymnarchidae occurred rarely with only one species each. Fish species such as *Mormyrus rume*, *Oreochromis niloticus*, *Chrysichthys nigrodigitatus*, *Citharinus citharus*, *Labeo coubie* and *Lates niloticus* occurred in most of the sampled stations. Some species were recorded in only one or two stations. For example, *Protopterus annectens* (Wawu site), *Tetraodon lineatus* (Onitsha and Ogbia sites) and *Parailla pellucida* (Ilushi site). The occurrence of *Heterotis niloticus* (Osteoglosidae), *Sarotherodon galilaeus* (Cichlidae), *Tetraodon lineatus* (Tetraodontidae), and some species of Synodontidae (*Synodontis occelifer*, *S. couteti* and *S. eupterus*) were restricted to the lower region of the basin. Omnivorous fish species were distributed in almost all the sites within the upper and lower region of the basin. The upper region recorded few species of herbivores. However, many species of omnivores were recorded in transition sites (Jebba, Lokoja and Idah) from upper to lower region.

ANOSIM showed that fish community structure differed significantly at both basin and reach scales in the rainy and dry seasons (Table II), indicating the influence of season and space on the community structure of the river basin. During the rainy season, we recorded absent of catches from Wawu and Awuru stations in the upper reaches of the basin. The result of the non-metric multidimensional scaling (NMDS) analysis showed some levels of distinctness in the community structure of the upper and lower reaches. However, the community structuring had a considerable level of overlap seasonally at both upper and lower basin (Figure 2).

SIMPER analysis revealed that at basin level, *Synodontis schall*, *Bagrus bayad*, *Synodontis membranaceus* and *Oreochromis niloticus* contributed 6.2%, 4.6%, 4.5 and 4.2% respectively, to the dissimilarity between upper and lower reaches during the rainy season, while *Oreochromis niloticus* (4.1 %), *Sarotherodon galilaeus* (3.7) and *Labeo coubie* (3.1%) contributed the most in dry season. At reach scale, whereas, *Oreochromis niloticus* (7.8%), *Sarotherodon galilaeus* (4.9%), *Citharinus citharus* (4.9%) contributed the most to the community dissimilarity at the upper reaches in both rainy and dry season, *Synodontis schall* (3.6 %), *Labeo cubie* (3.4%) and *Synodontis membranaeceus* (3.0%) were identified as the species with the greatest contribution at the lower reach of the river.

4.1.1. Phytoplankton and macroinvertebrates community structure

A total of 49 species of phytoplankton with 148,520 individuals belonging to 4 families (Baccillanophyceae, Chlorophyceae, Cyanophyceae and Pyrrophyceae) were recorded from the LNRB. At the upper region, during the dry season, Cyanophyceae was the most abundant family with percentage abundance value of 46.12 %, while Pyrrophyceae (0.95 %) was recorded as the least abundant family. At species level, *Athrospira* sp. (24.64 %) recorded the highest abundance, while *Ophiocytium parculum* (0.25 %) was the least abundant species (Appendix 7). In the rainy season, at the upper region, Chlorophyceae (43.33 %) was recorded as the most abundant family, while Pyrrophyceae (1.73 %) was the least abundant family. *Athrospira* sp. with percentage abundance of 19.33 % was the most abundant species while *Ceratulinia pelagica* (0.05 %) was the least abundant species (Appendix 8). At the lower region, the family Chlorophyceae (dry season – 55.69%, rainy season – 53.64%) and the species *Chlorella* sp. (dry season – 16.96%, rainy season – 19.24%) were the most abundant during the dry and rainy seasons. Pyrrophyceae was recorded as the least abundant family in both seasons at the lower region (Appendix 9 and 10). *Pinnularia gibba* (0.22%) and *Selenastrium* sp. (0.22%) were the least abundant species during the dry season, while *Ophiocytium parculum* and *Pinnularia gibba* with 0.1 % abundance were recorded as the least abundance species during the rainy season. Considering the entire basin, Chlorophyceae is the most abundant group with 19 species comprising 74,660 (50.27%) individuals, Pyrrophyceae represented by 3 species (1930 individuals) with 1.30% abundance was the least abundance group. Cyanophyceae represents 30.36% abundance with 10 species comprising of 45,100 individuals. Baccillariophyceae represented by 17 species (26,830 individuals) consisted of 18.06%. Some species from the family Baccillariophyceae (e.g. *Achnanthes clevei*, *Asteronella* sp., *Cymbella similis*, *Cylindrotheca closterium*, *Leptocylindricus* sp.) and Chlorophyceae (e.g. *Zygnema* sp., *Microspora* sp., *Actinastrum gracilum* and *Cerastrias staurastria*) were restricted to the lower region while *Microcytis* sp. (Cyanophyceae), *Melosira granulata* (Baccillariophyceae), *Fragillana* sp. (Baccillariophyceae), *Tetrospora* sp. (Chlorophyceae), *Pediastrium* sp. (Chlorophyceae) and *Homidium* sp. (Chlorophyceae) were commonly distributed in the entire river basin. However, *Pediastrium* sp. (Chlorophyceae) and *Homidium* sp. (Chlorophyceae) were absent at Patani and Ogbia stations (both in lower region) (Appendix 11). The community structure differed significantly at basin scales in both rainy and dry seasons (Table II), indicating the influence of season and space on the community structure of the river basin. At the reach scale, community structure within upper reaches and lower reaches in both dry and rainy season respectively, did not vary significantly ($p>0.05$). However, the community composition between upper and lower reaches in both dry and rainy seasons were significantly different ($p<0.05$).

Non-metric multidimensional scaling (NMDS) analysis showed that the phytoplankton community structure of the upper and lower reaches were distinct. However, the community structuring had a considerable level of overlap seasonal wise at both upper and lower basin (Figure 3). SIMPER analysis revealed that *Athrospira and Chlorella* contributed about 4% each to the phytoplankton community dissimilarity during the rainy and dry season at the basin level. At reach scale, whereas, *Athrospira* (4.7%), *Chlorella* (4.3%) and *Spirogyra* (3.2%), contributed the most to the community dissimilarity between upper and lower reaches in dry season, *Chlorella* (5.3 %), *Athrospira* (4.8%) and *Tetraspora* (3.4%) were identified as the species with the greatest contribution to the community dissimilarity between upper and lower reaches in the rainy season. When the community compositions between lower reaches in dry and rainy season respectively, were compared, *Chlorella* with 3.1 % was found to have the largest contribution to the community dissimilarities.

Across the 15 sampling sites, a total of 2457 macroinvertebrates were identified, belonging to 40 taxa. Overall, 40 taxa, belonged to 9 orders and 27 families. Abundances ranged from 21 to 156 individuals per taxa, and taxonomic richness ranged from 1 to 5 taxa. The most abundant taxa were *Chironomus sp*. (Diptera; relative abundance = 6.36%), *Afroaetis sp* (Ephemeroptera; relative abundance = 4.76%) and *Amphiops sp.* (Coleoptera; relative abundance = 3.26%) (Appendix 12). Moreover, macroinvertebrates community composition showed no significant ($p>0.05$) difference at both basin and reach scale, indicating that season and space have little or no effect on the macroinvertebrates community structure at the LNRB. NMDS analysis revealed that the macroinvertebrates community structure were overlapping in both seasons and reaches (Fig. 4).

SIMPER analysis for macroinvertebrates community structure in this study was not reported as the species contributed less than 1%.

Table II: R-statistic values and their significance levels for pair-wise comparisons of fish, phytoplankton and macroinvertebrate community structure between reaches for each season using ANOSIM in the LNRB

Species	Reaches	R-stat	P-value
Fish	Dry vs rainy	0.12	0.02*
	Upper vs. Lower (dry)	0.33	<0.001
	Upper vs. Lower (rainy)	0.22	0.03*
	Upper dry vs Upper rainy	0.33	0.01*
	Lower dry vs Lower rainy	0.21	0.03*
	Upper vs. Lower (combined)	0.23	0.01*
Phytoplankton	Dry vs rainy	0.46	<0.00**
	Upper vs. Lower (dry)	0.51	<0.00**
	Upper vs. Lower (rainy)	0.36	<0.00**
	Upper dry vs Upper rainy	-0.06	0.75
	Lower dry vs Lower rainy	-0.09	0.92
	Upper vs. Lower (combined)	0.55	<0.00**
Macroinvertebrate	Dry vs rainy	0.02	0.22
	Upper vs. Lower (dry)	-0.05	0.65
	Upper vs. Lower (rainy)	-0.02	0.52
	Upper dry vs Upper rainy	-0.14	0.97
	Lower dry vs Lower rainy	-0.10	0.89
	Upper vs. Lower (combined)	-0.04	0.60

*** P<0.05; ** P<0.01**

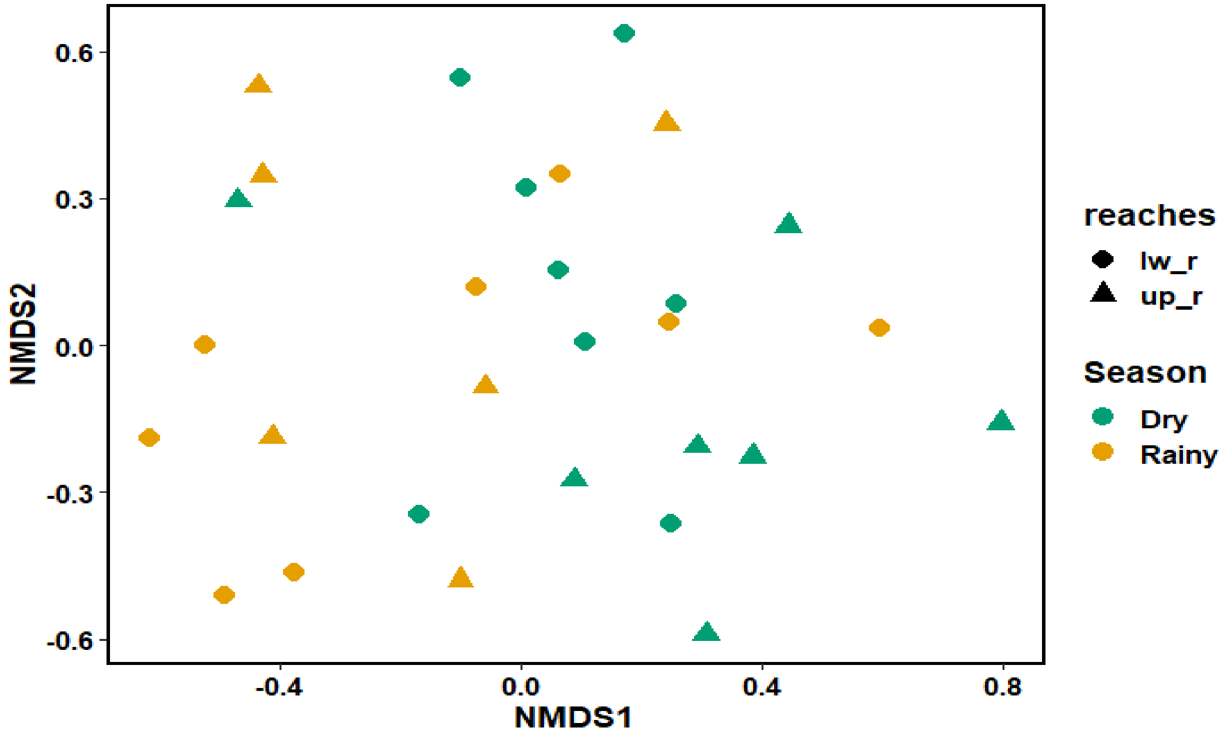

Figure 2: Non-metric multi-dimensional scaling (NMDS) by reaches and seasons for the fish community structure of the Lower Niger River Basin. lw_r = lower region, up_r = upper region.

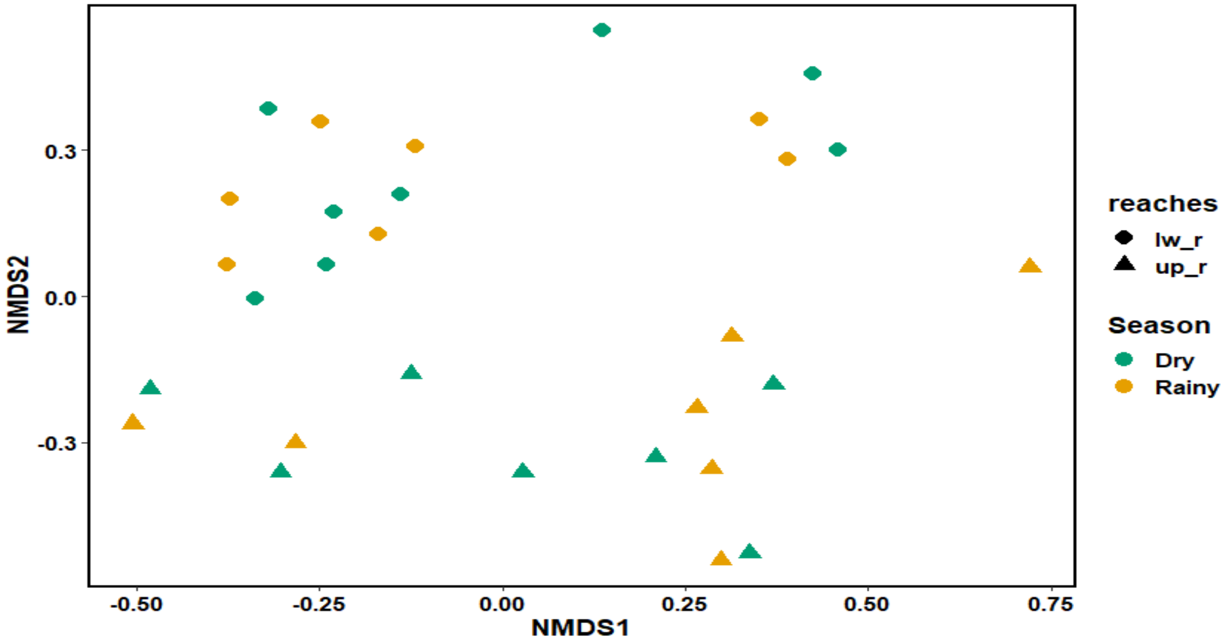

Figure 3: Non-metric multi-dimensional scaling (NMDS) by reaches and seasons for the phytoplankton community structure of the Lower Niger River Basin. lw_r = lower region, up_r = upper region

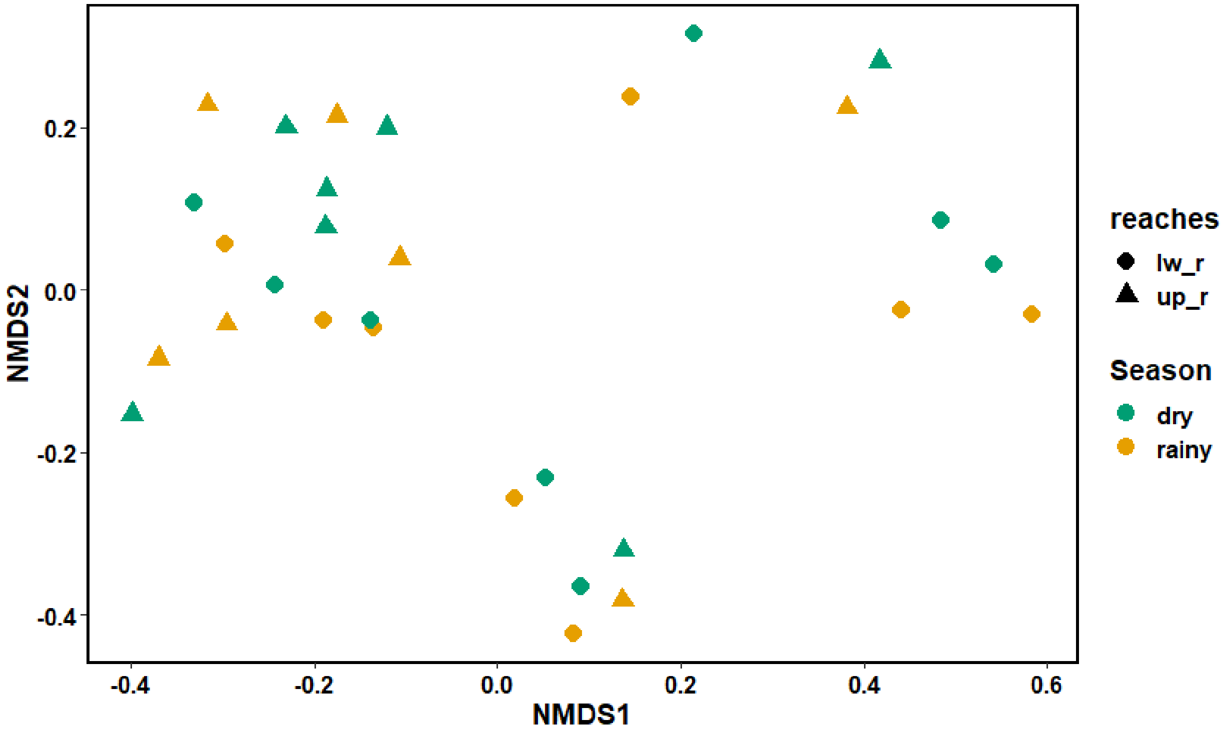

Figure 4: Non-metric multi-dimensional scaling (NMDS) by reaches and seasons for the macroinvertebrate community structure of the Lower Niger River Basin. lw_r = lower region, up_r = upper region

4.1.2. Environmental and spatial determinants of the community composition of fish, macroinvertebrates and phytoplankton in the LNRB, Nigeria

Stepwise model selection using permutation tests of RDA for environmental and spatial variables with fish count selected DO, phosphate, TDS, TSS, nitrite and water width (environmental variables), and PCNM6, PCNM4, PCNM1 and PCNM3 (spatial variables) as the most important variables influencing fish community composition during the dry season (Table III). In the rainy season, phosphate, nitrite and disturbance index (environmental variables), and PCNM2, PCNM5, PCNM1, PCNM4 and PCNM6 (spatial variables) were selected (Table III). While phosphate, disturbance index and TSS (environmental variables), and PCNM1 (spatial variables) were selected as the most important variables influencing phytoplankton community composition during the dry season, TDS, phosphate, river width, TSS and disturbance index (environmental variables); PCNM4, PCNM1, PCNM3, PCNM2, PCNM6 and PCNM5 (spatial variables) were selected in the rainy season (Table IV). For macroinvertebrates, disturbance index, nitrite and river width (environmental variables), PCNM7, PCNM4, PCNM1 and PCNM2 (spatial variables) were the most important variables influencing the community composition in the dry season, while, nitrate, phosphate and river width (environmental variables); PCNM8, PCNM7 and PCNM1 (spatial variables) were selected in the rainy season (Table IV). The RDA model of the fish, phytoplankton and macroinvertebrates with environmental and spatial variables after stepwise model selection in the dry and rainy seasons were all significant ($p < 0.05$) according to the permutation tests (999 random permutations) except for TDS and nitrate for phytoplankton and macroinvertebrate respectively in rainy season (Tables III and IV). The final models in the dry season ($R^2 = 0.69$; $Adj.R^2 = 0.25$; $p < 0.001$ for fish; $R^2 = 0.64$; $Adj.R^2 = 0.28$; p-value < 0.001 for phytoplankton; $R^2 = 0.48$; $Adj.R^2 = 0.28$; p-value < 0.001 for macroinvertebrates) and rainy season ($R^2 = 0.86$; $Adj.R^2 = 0.37$; $p < 0.001$ for fish; $R^2 = 0.57$; $Adj.R^2 = 0.24$; $p < 0.001$ for phytoplankton; $R^2 = 0.90$; $Adj.R^2 = 0.55$; $p < 0.001$ for macroinvertebrate) were all significant.

Table III: Summary statistics of the stepwise model selection in RDA, showing significant environmental and spatial variables correlated with fish species composition in the LNRB during the dry and rainy season. The variables are presented in the order they were selected

Environmental variables	AIC	F-stat	P-value	Spatial variables	AIC	F-stat	P-value
Dry season							
River width (m)	52.41	1.41	0.06	**PCNM6**	52.71	1.50	0.04
DO (mg/l)	52.66	1.48	0.05	**PCNM4**	53.01	1.59	0.02
Phosphate (mg/l)	52.60	1.46	0.04	**PCNM1**	53.40	1.71	0.01
TSS (mg/l)	53.69	1.08	<0.01	**PCNM2**	53.39	1.70	0.01
TDS (mg/l)	53.65	1.79	<0.01	**PCNM3**	55.05	2.26	<0.01
Nitrite (mg/l)	54.29	2.00	<0.01				
Rainy season							
Nitrite (mg/l)	54.88	1.45	0.08	**PCNM2**	55.26	1.64	0.04
Disturbance index	55.18	1.60	0.04	**PCNM5**	55.27	1.65	0.02
Phosphate (mg/l)	55.36	1.69	0.02	**PCNM1**	55.56	1.79	0.01
				PCNM4	55.79	1.91	<0.01
				PCNM6	56.39	2.24	<0.01

DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; AIC = Akaike Informatin Criterion

Table IV: Summary statistics of the stepwise selection procedure, showing significant environmental and spatial variables correlated with phytoplankton and macroinvertebrate species composition in dry and rainy season. The variables are presented in the order they were selected

Species	Environmental variables	F-stat	P-value	Spatial variable	F-stat	P-value
Phytoplankton	**Dry season**					
	Phosphate (mg/l)	1.36	0.12	PCNM1	2.80	<0.01
	Disturbance index	1.75	0.03			
	TSS (mg/l)	2.44	<0.01			
	Rainy season					
	TDS (mg/l)	1.61	0.08	PCNM4	1.58	0.09
	Wt_width (m)	1.65	0.08	PCNM1	1.91	0.04
	Phosphate (mg/l)	1.89	0.05	PCNM3	2.11	0.02
	Disturbance index	2.05	0.02	PCNM2	1.99	0.02
	TSS (mg/l)	2.03	0.02	PCNM6	2.10	0.01
				PCNM5	2.46	0.01
Macroinvertebrate	**Dry season**					
	Disturbance index	1.75	0.06	PCNM7	1.82	0.05
	Nitrite (mg/l)	2.65	0.01	PCNM4	2.12	0.03
	Wt_width (m)	2.50	<0.01	PCNM1	2.13	0.02
				PCNM2	2.62	<0.001
	Rainy season					
	Nitrate (mg/l)	1.20	0.02	PCNM8	1.57	0.07
	Phosphate (mg/l)	2.44	<0.01	PCNM7	2.00	0.01
	Wt_width (m)	2.67	<0.01	PCNM1	2.21	0.01

TSS = total suspended solid; TDS = total dissolved solid; Wt_water = river width

4.1.3. Environmental versus spatial predictors that explained the variation in the community composition of fish, phytoplankton and macroinvertebrate between upper versus lower region of the LNRB

The RDA plots (Fig. 5 and 6) showed the distribution pattern of the fish species in relation to the environmental and spatial variables within the river basin. For both seasons, fish community composition substantially differed between the upper and lower regions, reflected by the arrangement of sampling sites along RDA axis 1. It was observed that species such as *Brycinus macrolepidotus, Malapterurus electricus, Heterobranchus bidorsalis, Synodontis schall, S. eupterus, S. couteti* and *S. occelifer* were distributed within the lower region and were positively associated with TSS, TDS, PCNM1, PCNM4 and PCNM6. Species such as *Lates niloticus, Schilbe mystus, Brycinus nurse, Auchenoglanis occidentalis* and *Sarotherodon galilaeus* were mainly found within the upper region, and they were positively associated with DO, phosphate, nitrite, river width, PCNM2 and PCNM3. During the rainy season, the community composition in the lower region was positively associated with spatial variables, while the upper region had positive association with nitrite and phosphate (Figures 5 and 6). Species such as *Hemichromis fasciatus, Petrocephalus bane, Schilbe mystus, Auchenoglanis occidentalis* and *Sarotherodon galilaeus* are widely distributed within the upper region while species from the Synodontidae family (*Synodontis schall, S. eupterus, S. couteti* and *S. occelifer*), *Brycinus macrolepidotus* and *Malapterurus electricus* are widely distributed in the lower region.

For phytoplankton community composition, the result suggests that during the dry season, phytoplankton composition within the upper region were positively associated with phosphate (nutrient), while, disturbance index (anthropogenic activities), TSS and PCNM1 are positively related with community composition of the lower region. Taxa such as *Athrospira*, *Hormidium*, *Chlorella*, *Melosira*, *Fragillana* and *Microcytis* were mainly distributed within the upper basin while *Asteronella*, *Zygnema*, *Cerastrias*, *Hematococcus*, *Quadrigula, Anabeana*, *Cylindrotheca*, *Cymbella,* and *Nitzchia* were largely found within the lower region of the basin (Fig. 7). During the rainy season, the community composition in the upper reaches (*Pediastrum*, *Amphidinium*, *Hormidium*, *Tetraspora*, *Selenastrium*, *Athrospira* and *Volvox*) were positively associated with phosphate (environmental variables), PCNM5 and PCNM6. *Surirella*, *Zygnema*, *Merismopedia*, *Aphanocapsa*, *Durvilla*, *Actinastrum*, *Meuniera*, *Pleurosigma*, and *Merismopedia* are distributed in the lower region and they are positively associated with disturbance index, TDS, river width, PCNM1, PCNM2, PCNM3 and PCNM4 (Fig. 8).

In the dry season, nitrite, river width and PCNM7 influenced macroinvertebrates community composition in the upper region of the basin, while, Disturbance index, PCNM1 and PCNM4 are positively related to the community composition of the lower region. Nutrients (phosphate and nitrate) showed positive association with the macroinvertebrate community composition in the upper region during the rainy season, river width, PCNM7 and PCNM1 are positively associated with the community composition of the lower region. In dry season, distribution of taxa such as *Orthetrum, Hyphydrus, Pseudocloeon, Orectogyrus, Tanypus, Chironomid* and *Cleon* are explained by river width, nitrite, PCNM7 and PCNM2 while *Afroaetis, Melanoides, Alladomyia, Simulium, Calapteryx, Tricorythus, Zyxoma* and *Enattagma* are positively associated with PCNM1 and PCNM4 (Fig 9). Disturbance index explains the distribution of *Naboandelus*, *Amphiops*, *Apassus* and *Caenis* in the river basin. In the rainy season, whereas, PCNM1 explained the distribution of *Afroaetis, Melanoides, Simulium, Calapteryx* and *Leptocerina*, nitrate, phosphate, river width, PCNM8 and PCNM7 have a positive association with *Pseudocloeon, Orthetrum, Cybister, Bugillisia, Thraulus, Orectogyrus, Atherix, Thalassius* and *Macrocoris* (Fig. 10).

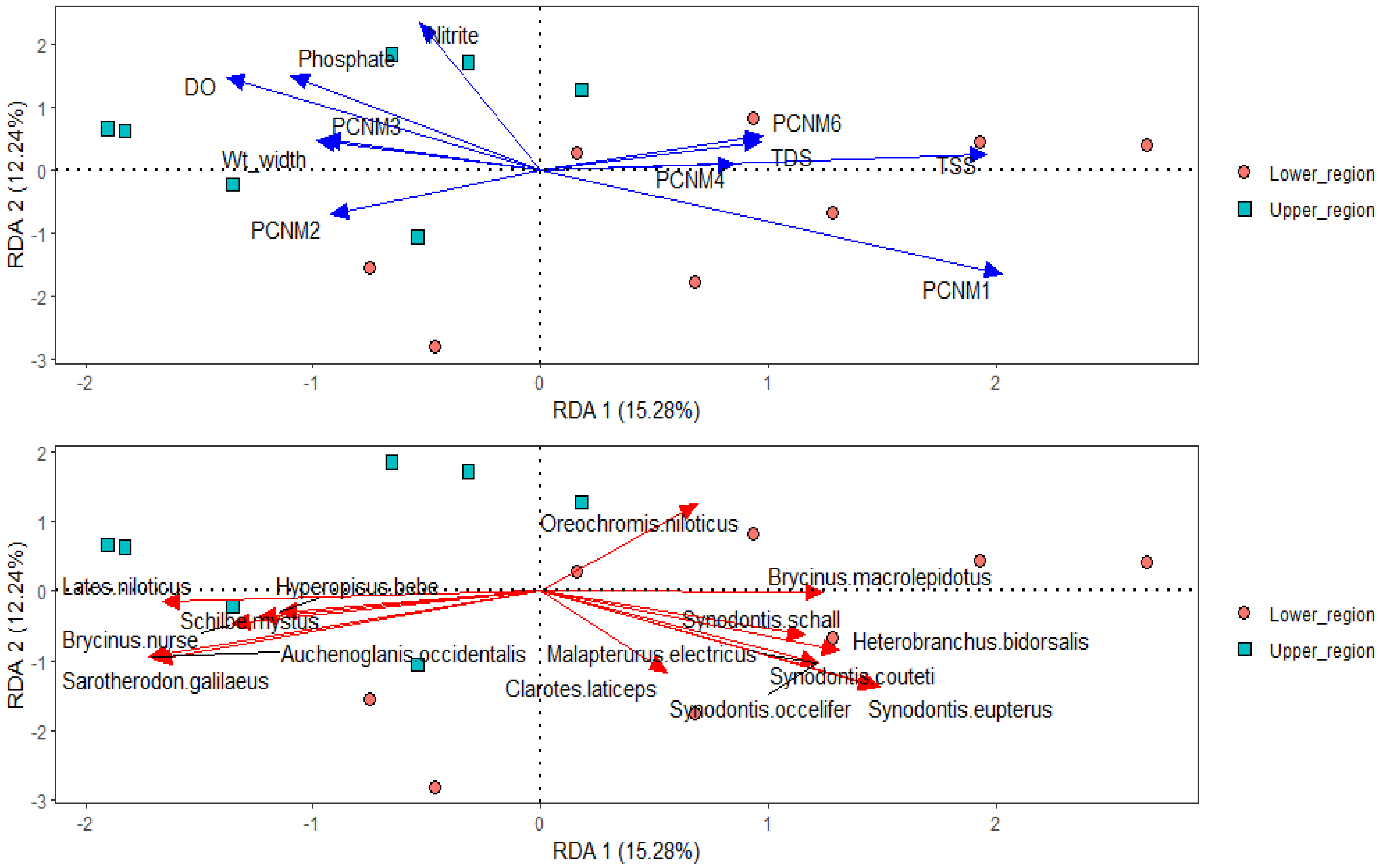

Figure 5: Redundancy analyses of fish community composition in relation to environmental and spatial factors during the dry season in the LNRB. The displayed species in the RDA plot were selected based on the value of their loadings in axes 1 and 2. Species with loading value of 0.35 and above were selected irrespective of sign (negative or positive)

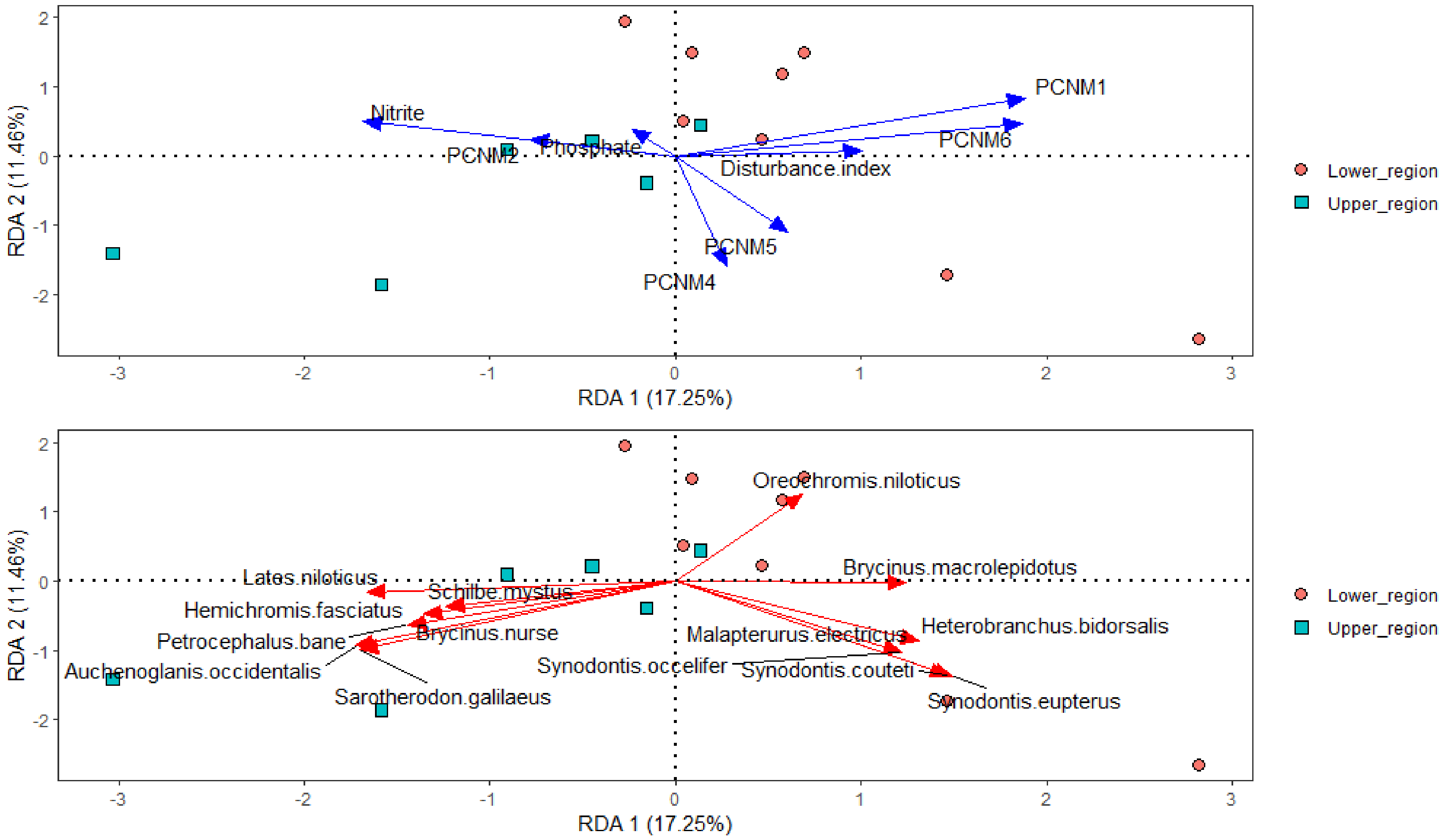

Figure 6: Redundancy analyses of fish community composition in relation to environmental and spatial factors during the rainy season in the LNRB. The displayed species in the RDA plot were selected based on the value of their loadings in axes 1 and 2. Species with loading values of 0.35 and above were selected irrespective of sign (negative or positive)

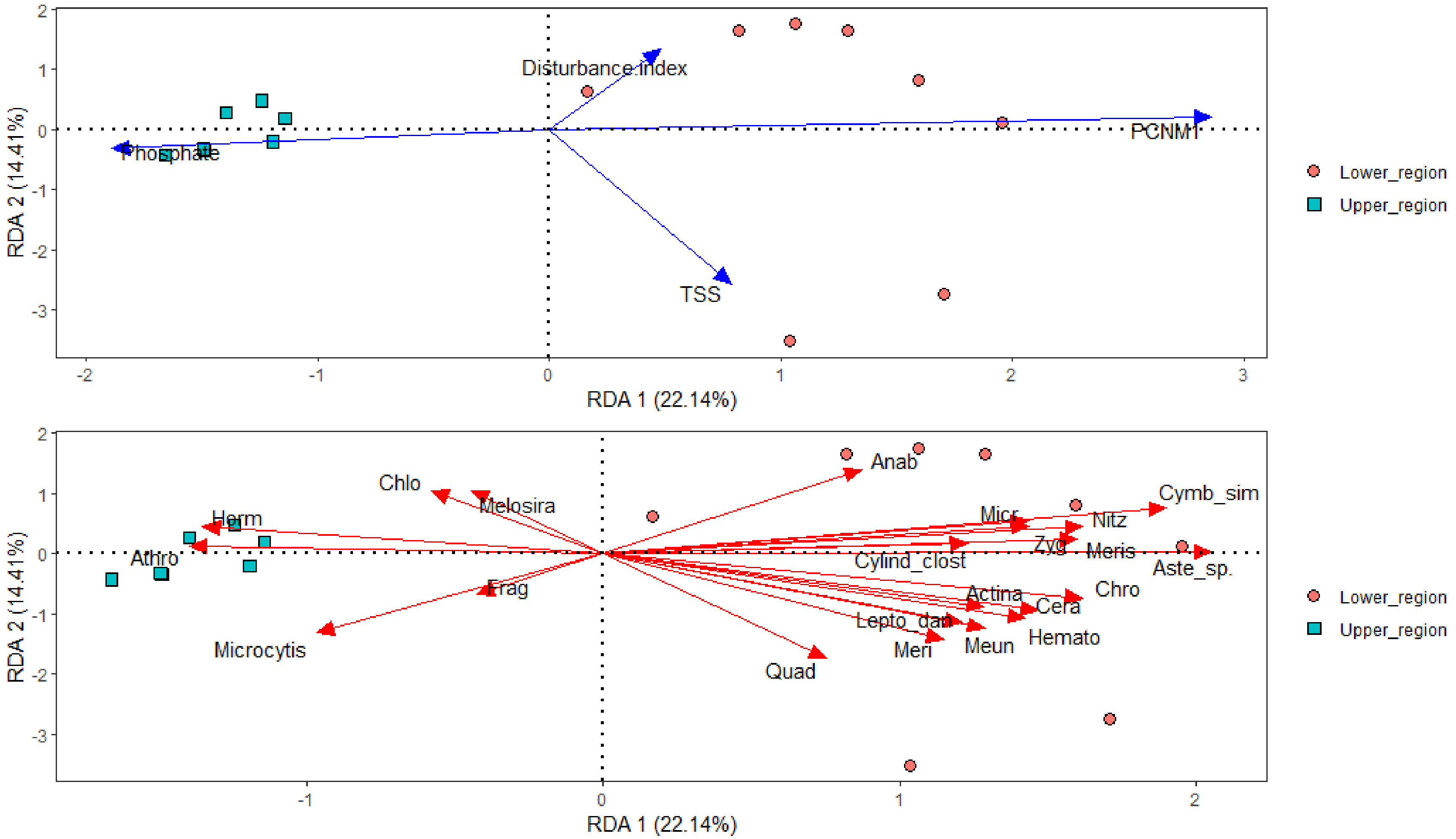

Figure 7: Redundancy analyses of phytoplankton assemblages in relation to environmental and spatial factors during dry season in the LNRB. The displayed species in the RDA plot were selected based on the value of their loadings in axes 1 and 2. Species with loading values of 0.35 and above were selected irrespective of sign (negative or positive)

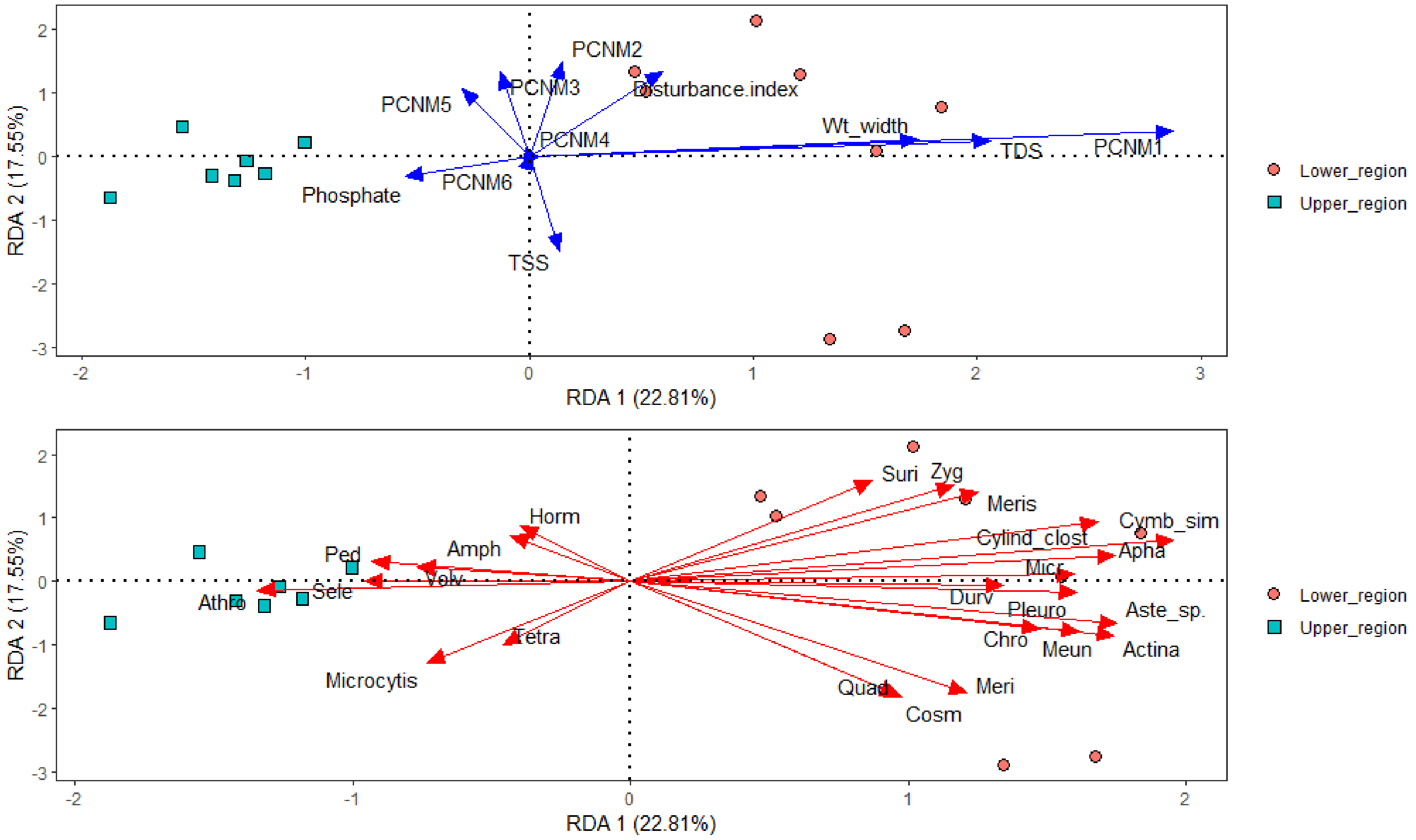

Figure 8: Redundancy analyses of phytoplankton assemblages in relation to environmental and spatial factors during rainy season in the LNRB. The displayed species in the RDA plot were selected based on the value of their loadings in axes 1 and 2. Species with loading values of 0.35 and above were selected irrespective of sign (negative or positive)

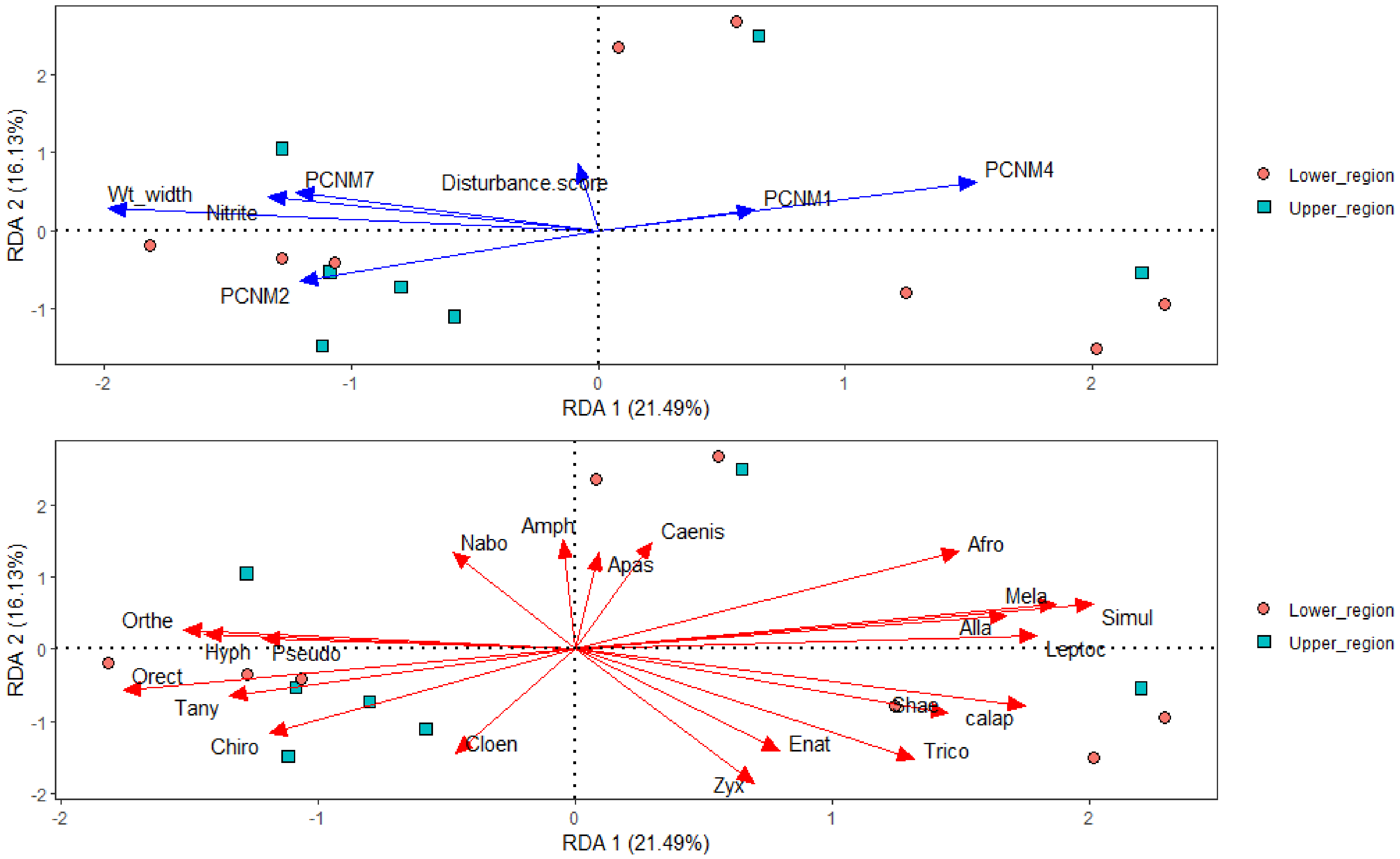

Figure 9: Redundancy analyses of macroinvertebrate community in relation to environmental and spatial factors during dry season in the LNRB. The displayed species in the RDA plot were selected based on the value of their loadings in axes 1 and 2. Species with loading values of 0.35 and above were selected irrespective of sign (negative or positive)

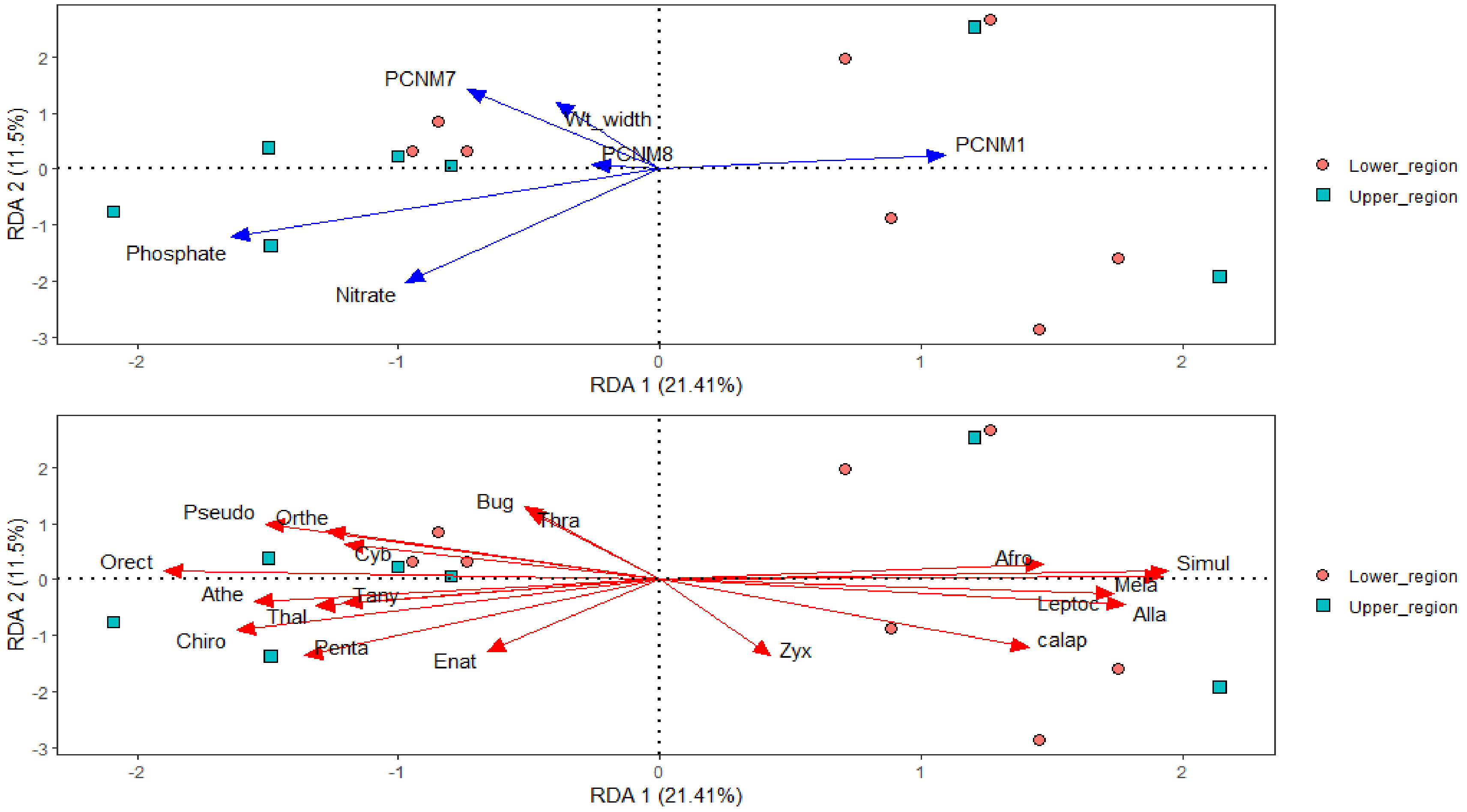

Figure 10: Redundancy analyses of macroinvertebrate community in relation to environmental and spatial factors during rainy season in the LNRB. The displayed species in the RDA plot were selected based on the value of their loadings in axes 1 and 2. Species with loading values of 0.35 and above were selected irrespective of sign (negative or positive)

4.1.4. Relative contribution of environmental versus spatial predictors to the explained variation in community composition of fish, phytoplankton and macroinvertebrate in dry and rainy season in the LNRB

Variation partitioning analysis showed that during the dry season, the fractions of variation in the community structure of fish that were explained by environmental factors independent of spatial factor (E|S) and spatial factors independent of environmental factor (S|E) were 28% and 32%, respectively (Fig. 11). While the spatial structure in species composition shared by the environmental and spatial factors (E ꓵ S) was -20%, unexplained variation [1 – (E + S)] in the structuring of fish community was 60%. During the rainy season, E|S was 6%, while 10% was recorded as S|E (Fig. 12). The proportion of unexplained variation in the community structure was 86% and -2% was the value for the overlap between environmental and spatial factors.

During the dry season, 17% and 18% were the relative contributions of environmental (E|S) and spatial (S|E) predictors respectively to the explained variation in the phytoplankton community structure in the LNRB. Whereas the overlap between environmental and spatial predictors (E ꓵ S) to the explained variation in the community composition is – 1%, unexplained variation [1 – (E + S)] in the structuring of phytoplankton community is 66% (Fig. 13). In the rainy season, the percentage of variation explained by environmental factor independent of spatial factor (E|S) is 27%, while 34% is recorded as the percentage of variation explained by spatial factor independent of environmental factor (S|E). The proportion of unexplained variation in the phytoplankton community structure is 43% and -35% was the value for the overlap between environmental and spatial factor (Fig. 14).

For the macroinvertebrates community composition in the dry season (Fig. 15), environmental factor (E|S) explained 25% of the variation while 19% is the percentage of variation in the community structure that were explained by spatial factor (S|E) independent of environmental factor. Whereas the percentage of the explained variation in species composition shared by the environmental and spatial factors (E ꓵ S) is -12%, unexplained variation [1 – (E + S)] in the structuring of the community is 69%. During the rainy season (Fig. 16), 24% is the percentage of variation explained by environmental factor independent of spatial factor (E|S), while spatial factor (S|E) explained 16% of the variation independent of environmental factor. The proportion of unexplained variation in the community structure is 74% and 15% is the percentage of the shared explained variation by environmental and spatial factor (E ∩ S).

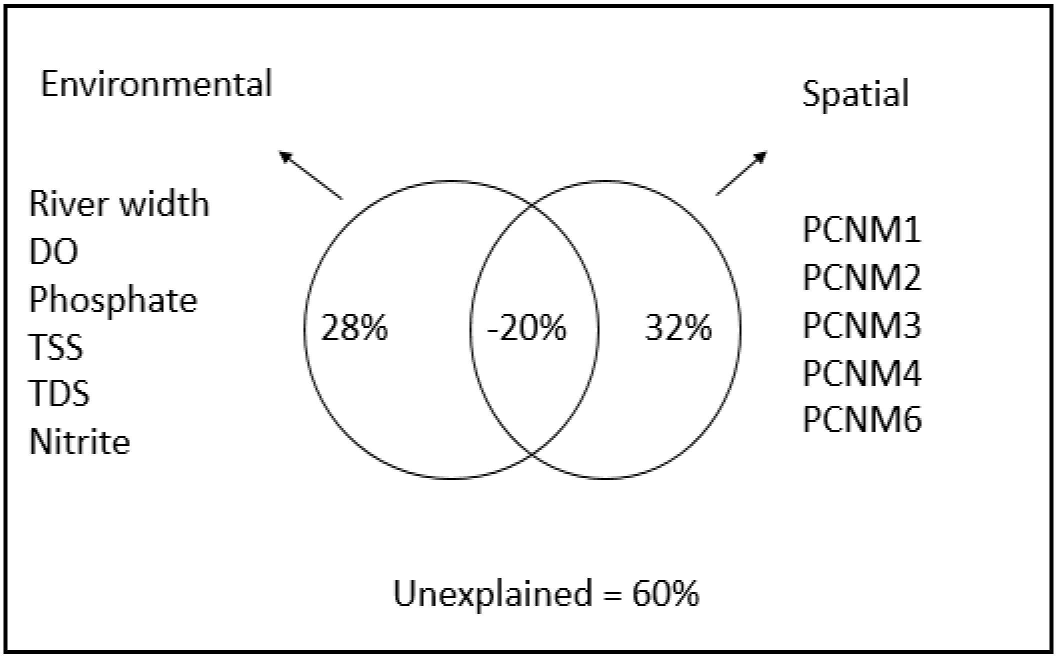

Figure 11: Venn diagram showing the result of variance partitioning analyses of predictors of fish community composition in the LNRB during the dry season**.** DO = Dissolved oxygen, TSS = Total suspended solids, TDS = Total dissolved solids

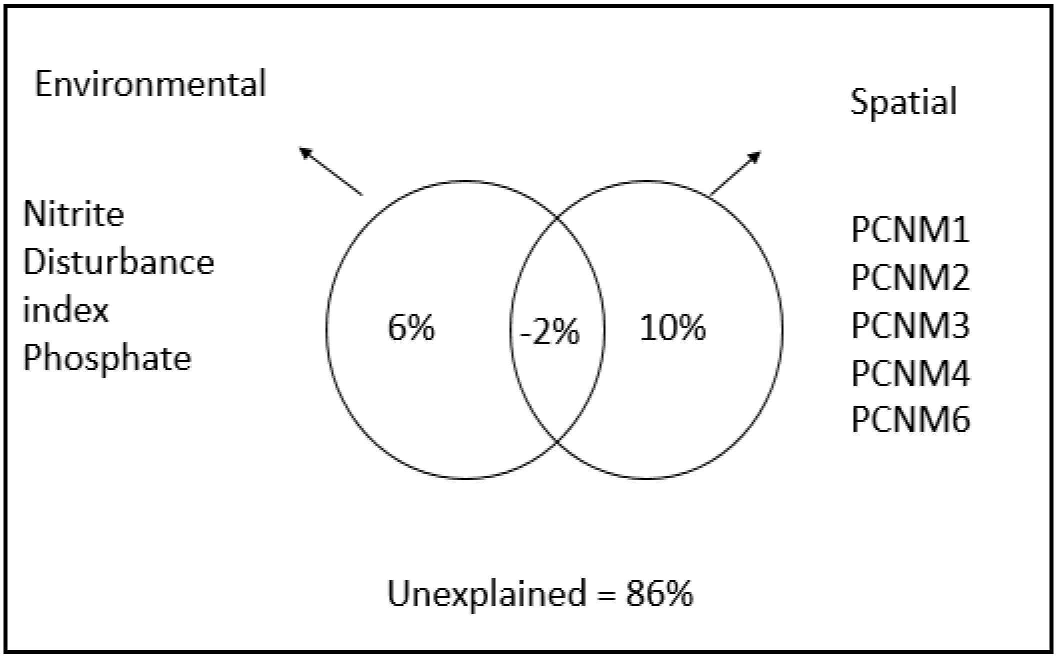

Figure 12: Venn diagram showing the results of variance partitioning analyses of predictors of fish community composition in the LNRB during the rainy season

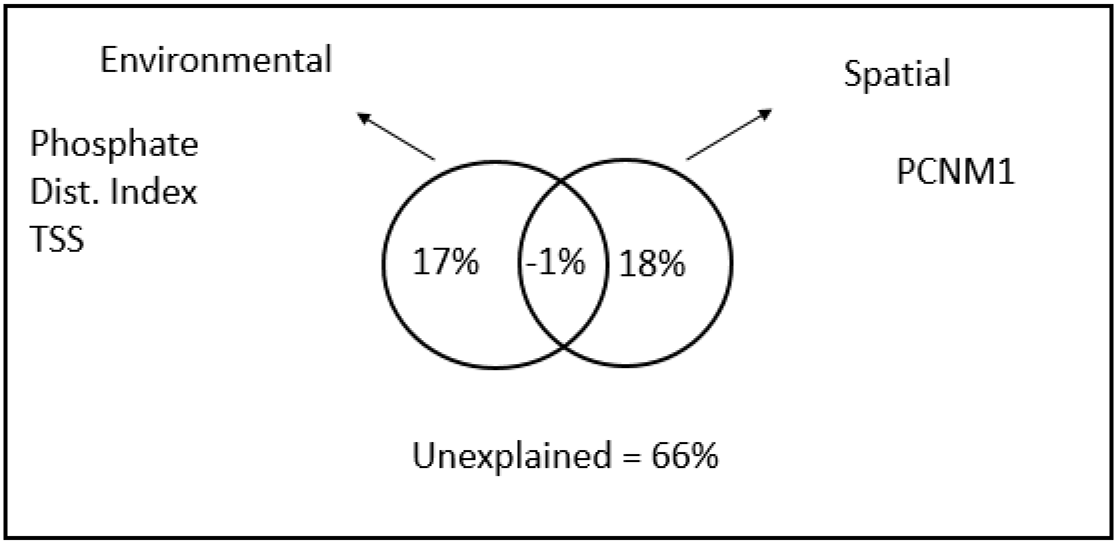

Figure 13: Venn diagram of the variance partitioning analyses of phytoplankton with the selected explanatory variables in dry season**.** Dist. Index = Disturbance index, TSS = Total suspended solids

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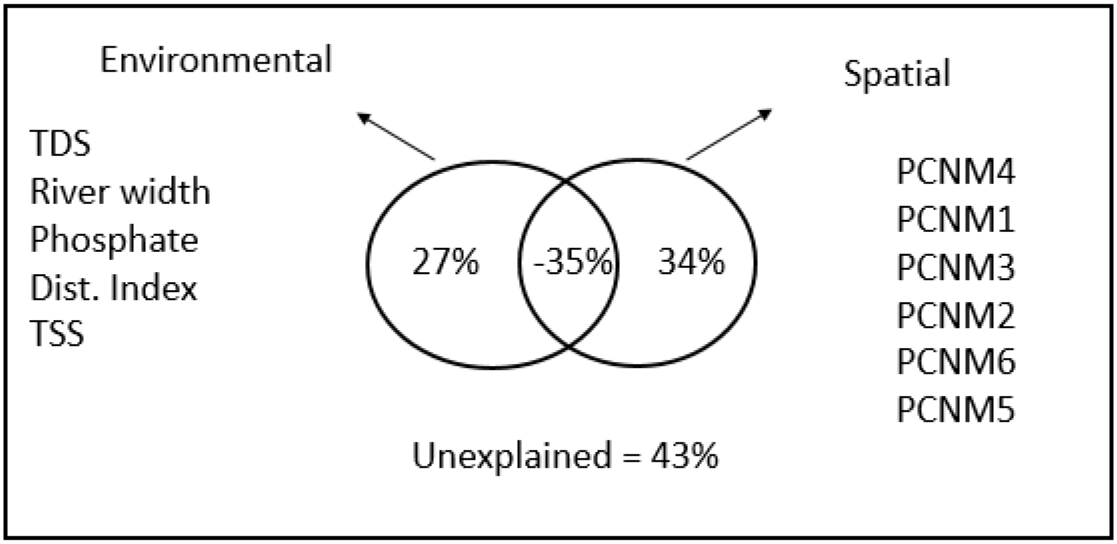

Figure 14: Venn diagram of the variance partitioning analyses of phytoplankton with the selected explanatory variables in rainy season**.** Dist. Index = Disturbance index, TSS = Total suspended solids, TDS = Total dissolved solids

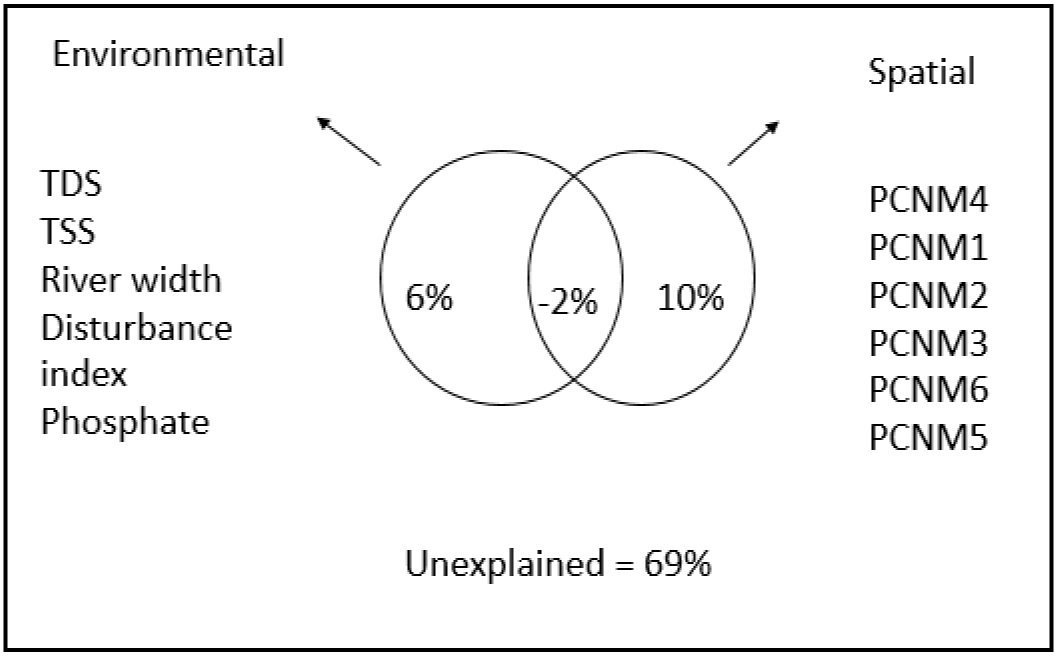

Figure 15: Venn diagram showing the result of variance partitioning analyses of predictors of macroinvertebrate community composition during the dry season. TSS = Total suspended solids, TDS = Total dissolved solids

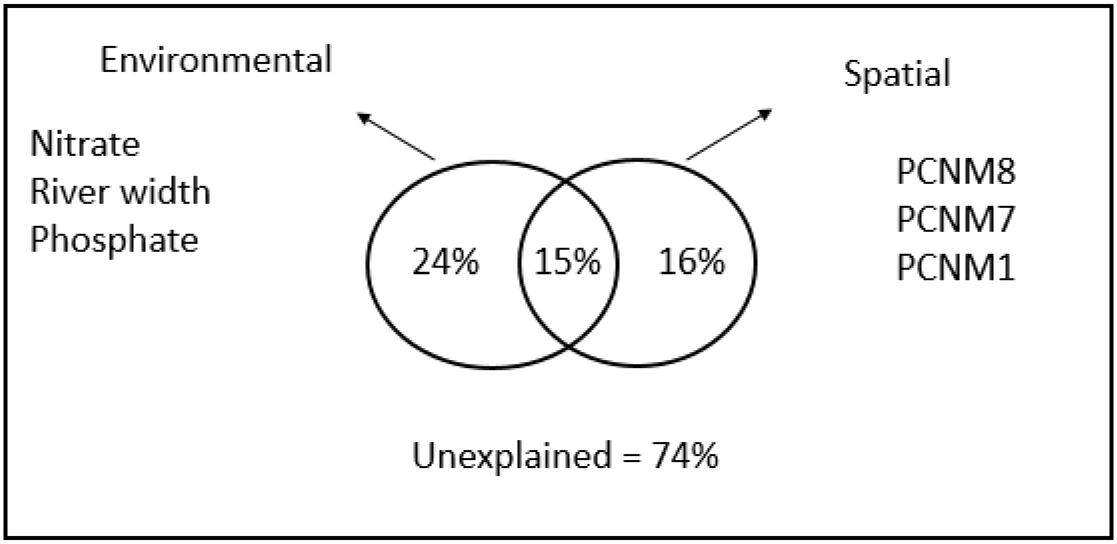

Figure 16: Venn diagram showing the result of variance partitioning analyses of predictors of macroinvertebrates community composition during the rainy season

4.2. Beta diversity decomposition

The result of the beta diversity decomposition into its various components of species replacement and species richness differences, using count based data of fish, macroinvertebrates and phytoplankton show similar overall beta diversity values for each taxa at both basin and reach scale (Table V). Though the beta diversity recorded for the different taxa in this study was low, the result showed that the diversity at basin and reach scale were all dominated by species replacement, which accounted for between 28% to 29% (fish), 22% to 23% (macroinvertebrate) and 24% to 25% (phytoplankton) of beta diversity of the species studied. Thus, reflecting a poorly continuous turnover of species along the longitudinal gradient of the LNRB. According to results from PERMDISP analysis, beta diversity based on distance to centroid of betadisper method, was similar between the upper and lower reaches among the taxa studied (average distance to centroid upper reach = 0.37, average distance to centroid lower reach = 0.33; ANOVA on distance to centroid: F= 0.67, P = 0.44) (fig. 17 to 19).

Table V: Beta diversity and contributions of its components based on the entire basin (Basin) and reach scale for fish, macroinvertebrate and phytoplankton in the LNRB

Species	**Level**	**β**	**Repl**	**RichDiff**	**Repl/BDtotal**	**RichDif/BDtotal**
Fish	**Entire basin**	0.35	0.29	0.06	0.83	0.17
	Upper reach	0.36	0.28	0.08	0.80	0.23
	Low reach	0.33	0.29	0.04	0.88	0.12
Macroinvertebrate	**Entire basin**	0.24	0.23	0.02	0.93	0.07
	Upper reach	0.24	0.22	0.02	0.92	0.08
	Low reach	0.25	0.23	0.02	0.94	0.06
Phytoplankton	**Entire basin**	0.33	0.24	0.09	0.74	0.26
	Upper reach	0.29	0.24	0.05	0.81	0.18
	Low reach	0.28	0.25	0.03	0.90	0.10

β is beta diversity, Repl is species replacement, RichDiff is species richness differences

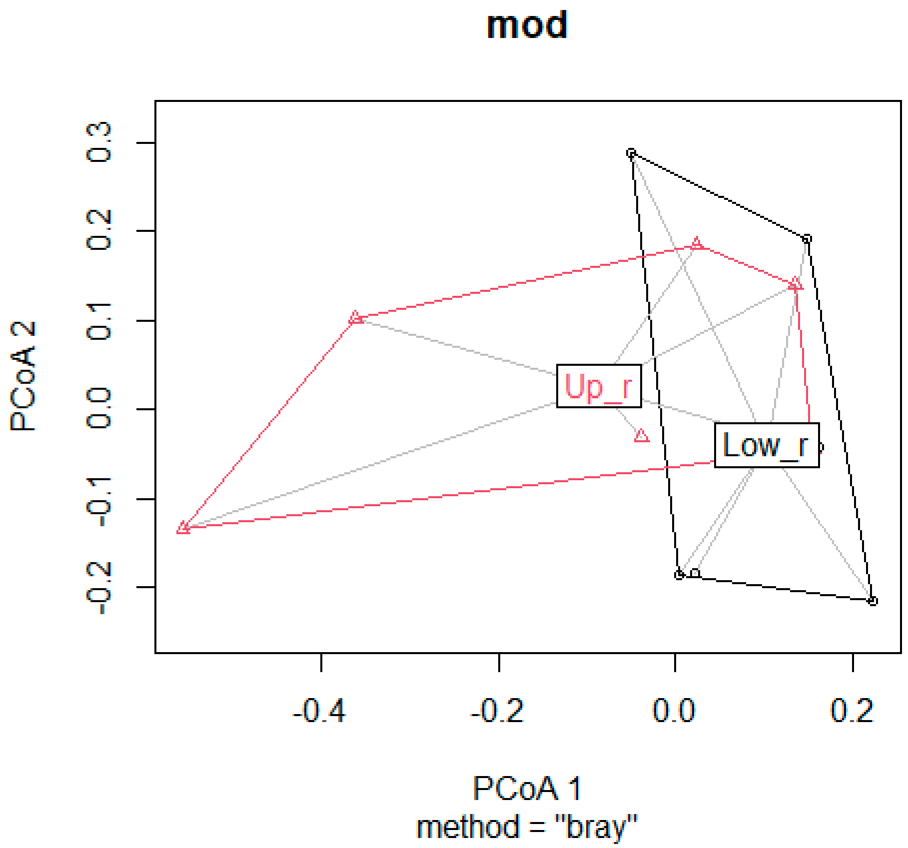

Figure 17: Result for permutational analysis of multivariate dispersion “PERMDISP” for fish beta diversity between upper and lower reaches. Up_r = upper region; Low_r = lower region

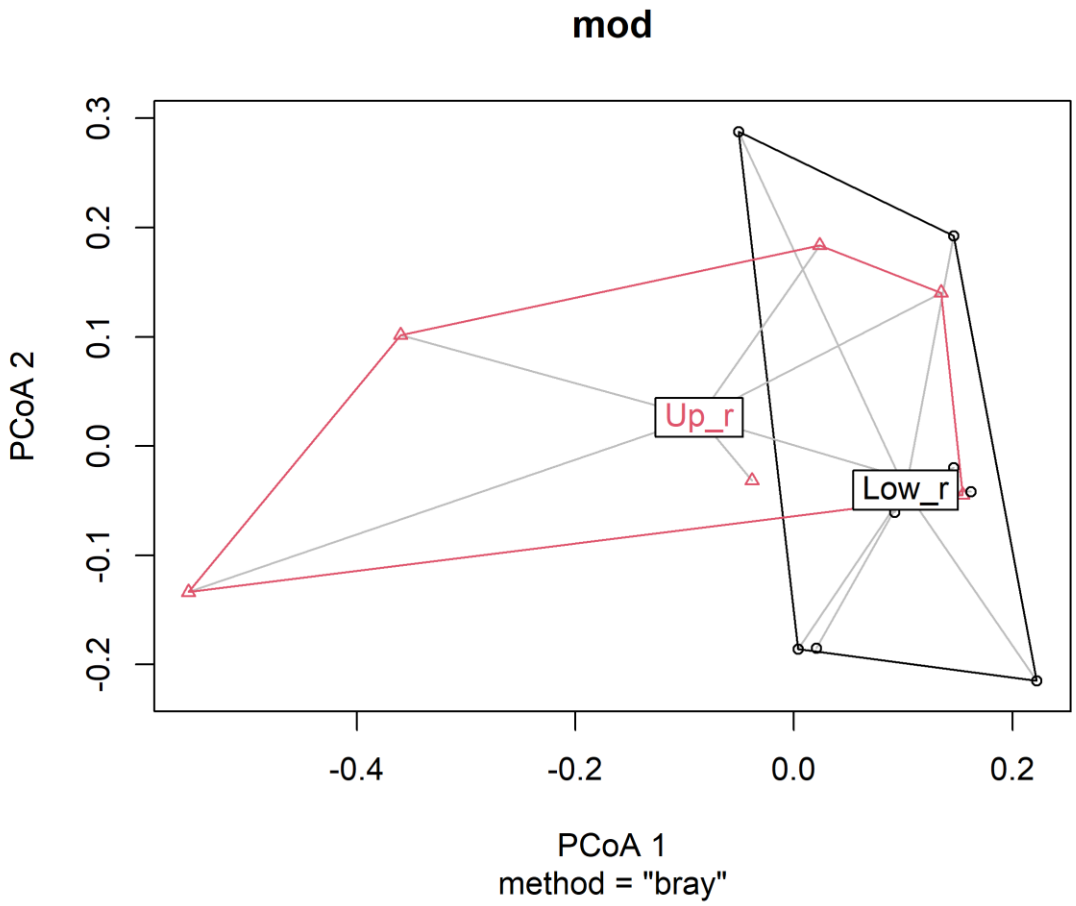

Figure 18: Result for permutational analysis of multivariate dispersion "PERMDISP" for macroinvertebrate beta diversity between upper and lower reaches. Up_r = upper region; Low_r = lower region

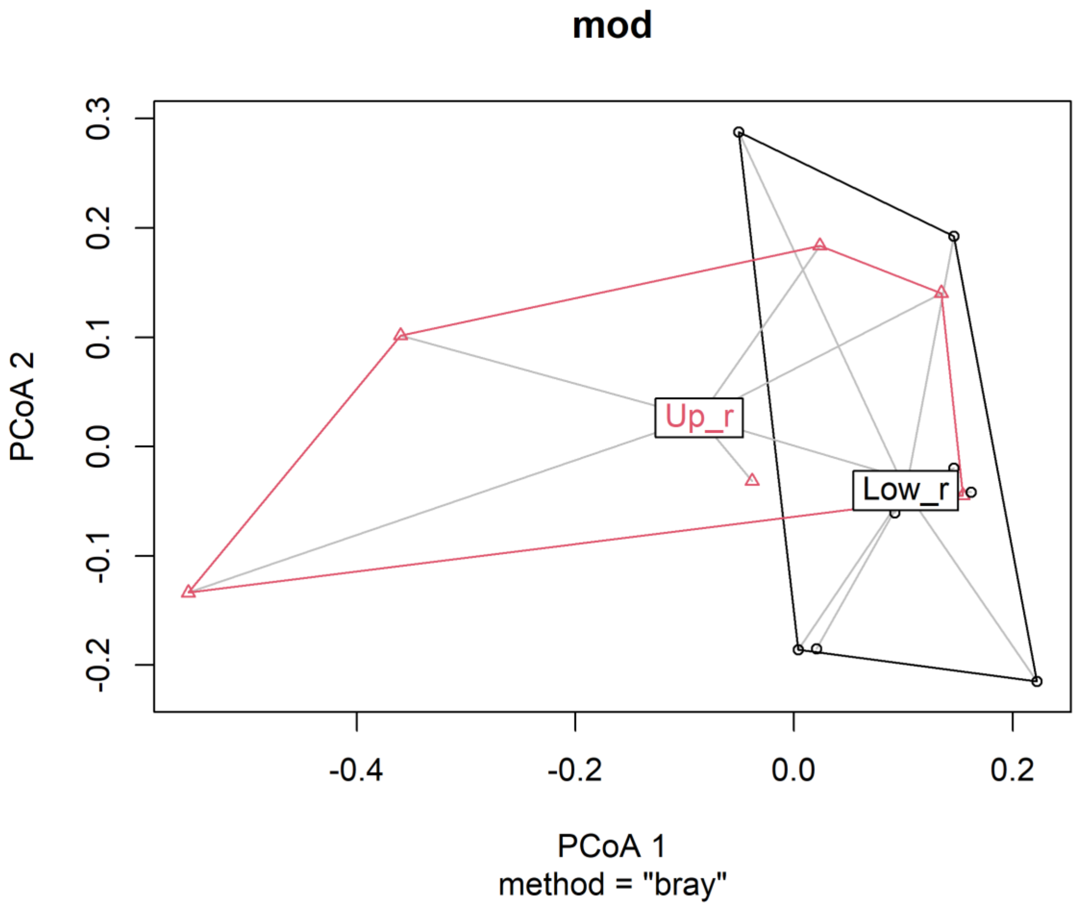

Figure 19: Result for permutation analysis of multivariate dispersion "PERMDISP" for phytoplankton beta diversity between upper and lower reaches. Up_r = upper region; Low_r = lower region

4.2.1. Local contributions of the different sites to beta diversity and its richness difference and species replacement component (LCBD) in the LNRB

LCBD indices were computed for beta diversity and its two components, richness difference and species replacement, using abundance data (Fig. 20 to 22). For fish, whereas, sites E (Fakun), F (Awuru) and G (Jebba) located within the between upper region recorded high values for LCBD contribution to the fish beta diversity, with site F accounting for the highest value, sites C (Shagunu) and M (Onitsha) had the least value. High LCBD values for richness difference values were obtained for site F (Awuru), while most sites at the lower region had lower values. LCBD values for species replacement were high at sites E (Fakun), G (Jebba), H (Lokoja), I (Idah), K (Illushi) and L (Ugbolu) with site G having the highest value. (Fig. 20).

For macroinvertebrate, whereas, sites C (Shagunu), F (Awuru), H (Lokoja), J (Agenebode) and K (Illushi) contributed the highest LCBD values for total beta diversity and species replacement, sites C (Shagunu), F (Awuru), G (Jebba), K (Illushi), L (Ugbolu) and O (Ogbia) contributed the highest value to the richness differences (Fig. 21).

For phytoplankton, with the exception of sites N and O (located within the lower reaches), most sites (A, B, C and E) within the upper reaches had high LCBD values, thus, contributing the highest to the phytoplankton total beta diversity in the LNRB (Fig. 22). Sites N and O (lower reaches) had the highest LCBD value for species replacement followed by sites A and G at the upper reaches. The LCBD to species richness differences were recorded at the upper reaches (B and C).

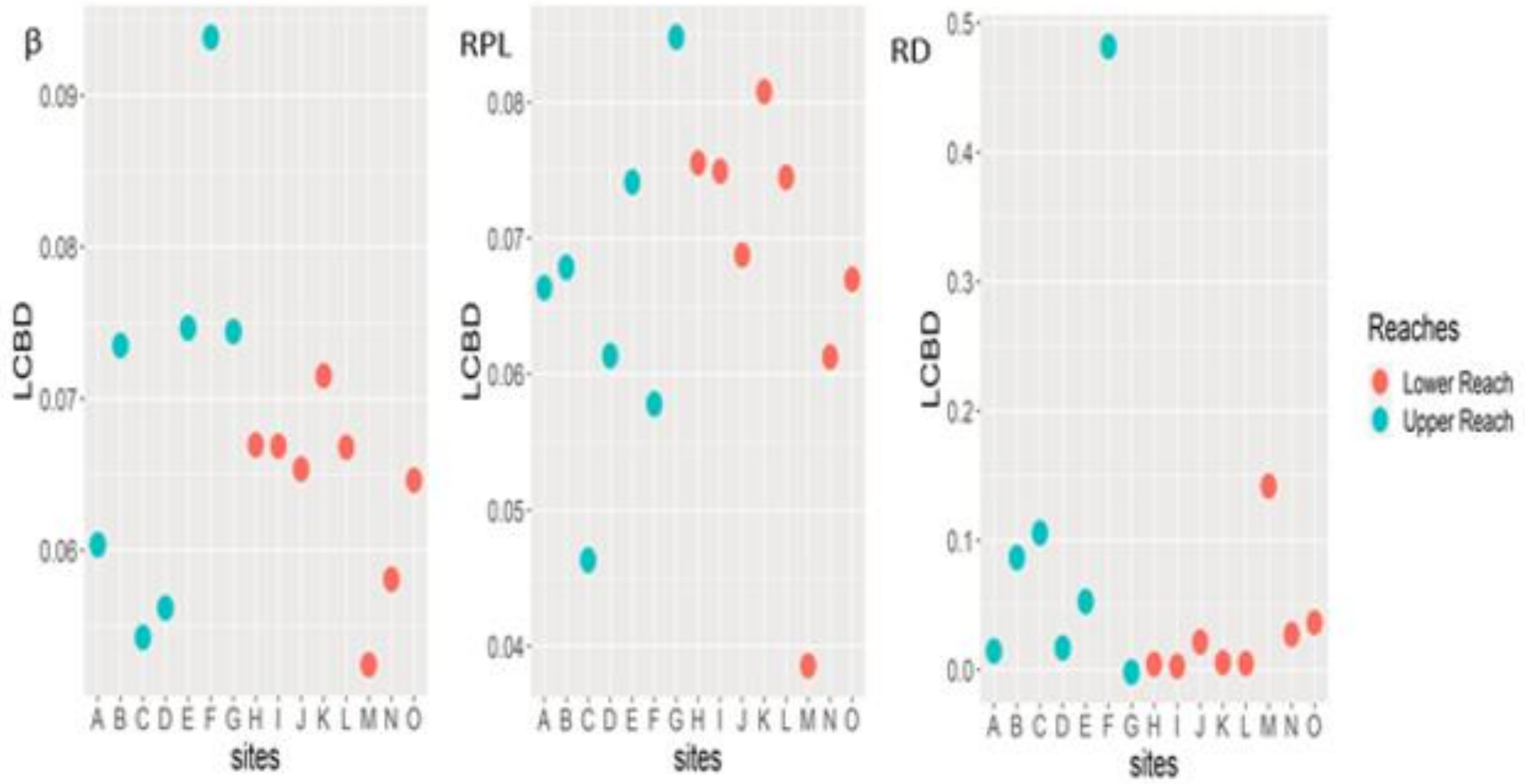

Figure 20: Results of the local contributions to fish beta diversity (LCBD) values for LNRB. β denotes beta diversity; RD is richness differences; RPL is species replacement. Sites A, B, C, D, E, F, G, H, I, J, K, L, M, N and O represents Yauri, Wawu, Shagunu, Yuna, Fakun, Awuru, Jebba, Lokoja, Idah, Agenebode, Ilushi, Ugbolu, Onitsha, Patani and Ogbia respectively

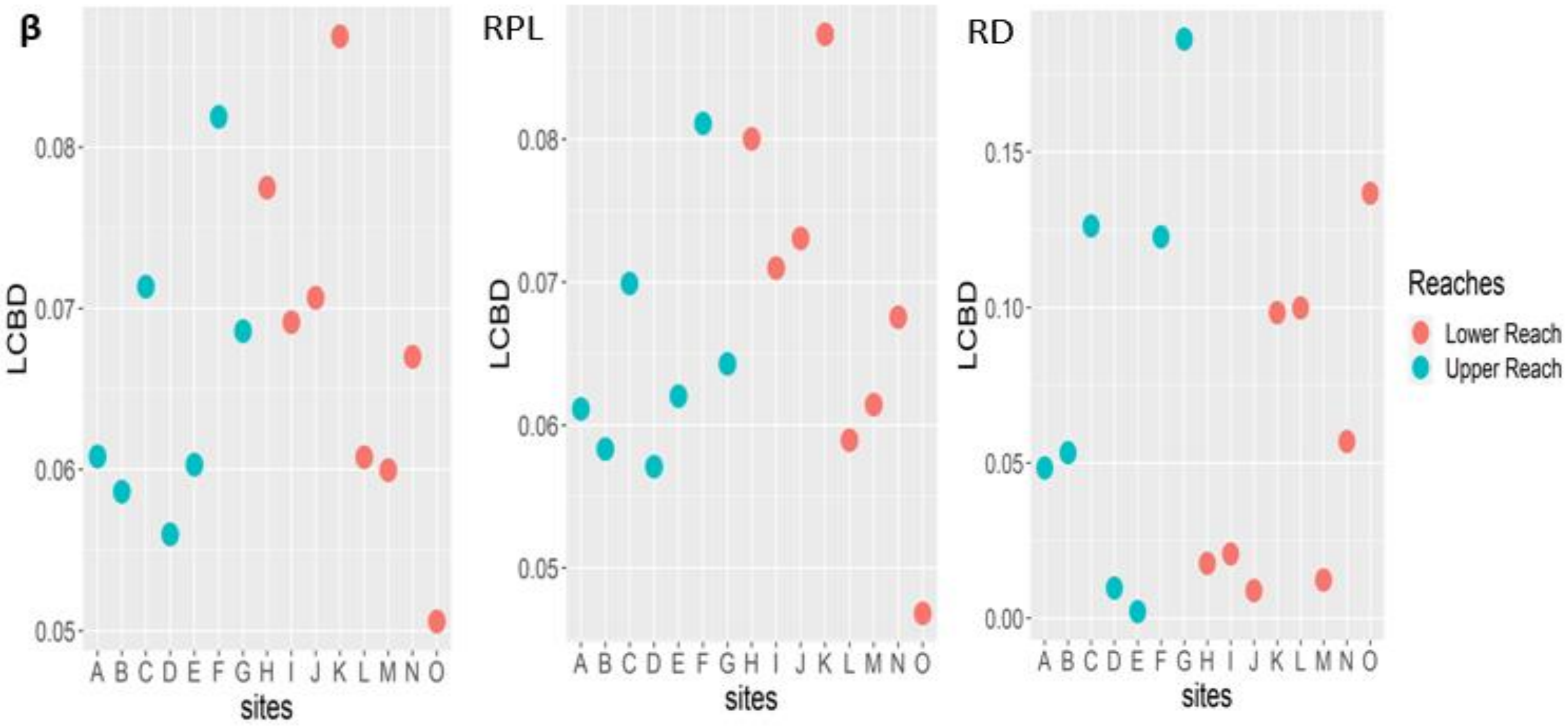

Figure 21: Results of the local contributions to macroinvertebrate beta diversity (LCBD) values for LNRB. β denotes beta diversity; RD is richness differences; RPL is species replacement. Sites A, B, C, D, E, F, G, H, I, J, K, L, M, N and O represents Yauri, Wawu, Shagunu, Yuna, Fakun, Awuru, Jebba, Lokoja, Idah, Agenebode, Ilushi, Ugbolu, Onitsha, Patani and Ogbia respectively

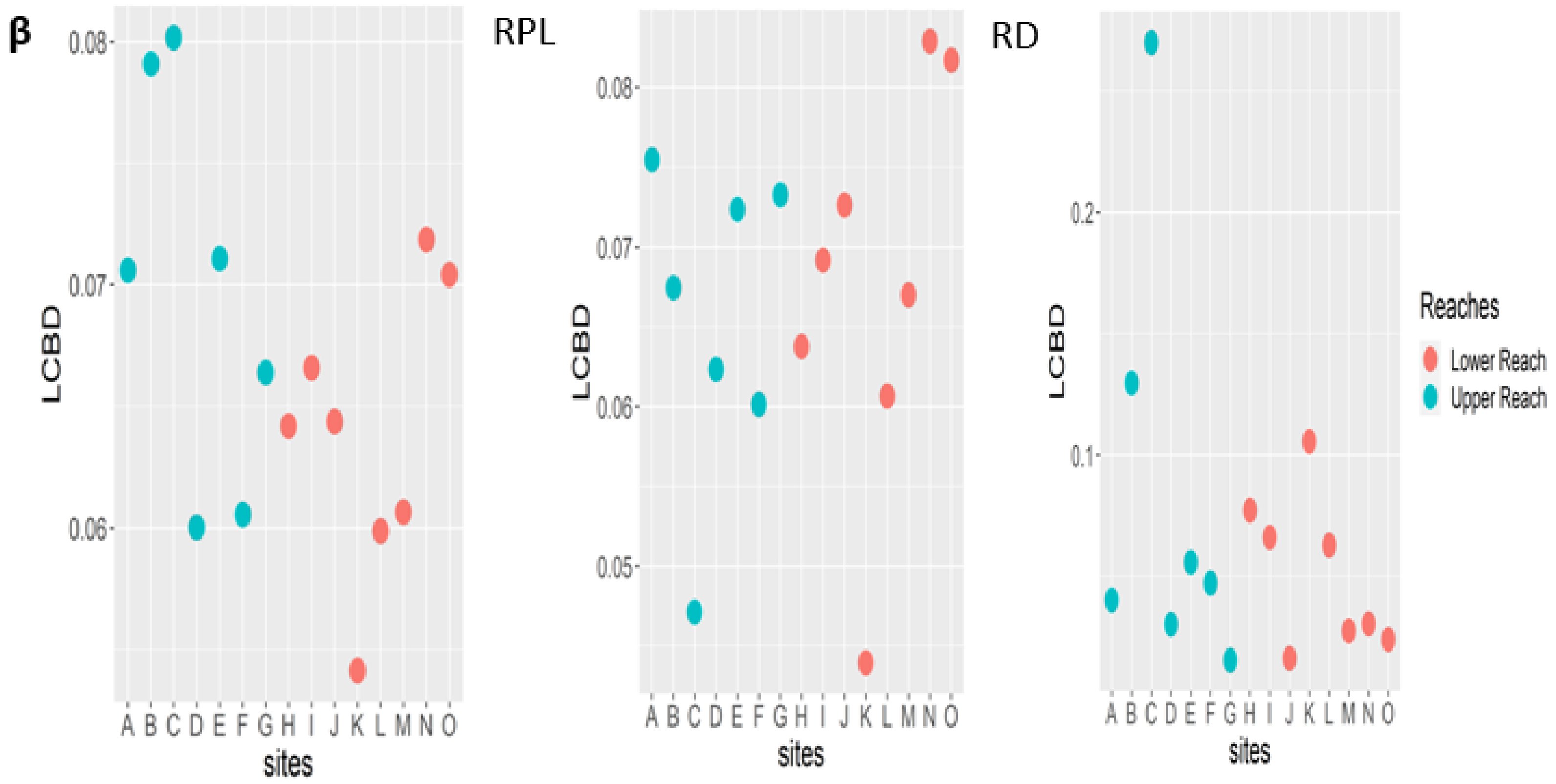

Figure 22: Results of the local contributions to phytoplankton beta diversity (LCBD) values for LNRB. β denotes beta diversity; RD is richness differences; RPL is species replacement. Sites A, B, C, D, E, F, G, H, I, J, K, L, M, N and O represents Yauri, Wawu, Shagunu, Yuna, Fakun, Awuru, Jebba, Lokoja, Idah, Agenebode, Ilushi, Ugbolu, Onitsha, Patani and Ogbia respectively.

4.2.2. Environmental and spatial predictor of beta diversity of the LNRB

Stepwise model selection using permutation tests of dbRDA for environmental and spatial variables with fish count selected six environmental variables (DO, BOD, TSS, TDS, nitrite and total hardness) and four spatial predictors (PCNM1, PCNM3, PCNM4 and PCNM5) as the most important predictor variables influencing fish total beta diversity and species replacement component of the LNRB (Table VI). DO, BOD, alkalinity, nitrite, phosphate and total hardness (environmental), PCNM1, PCNM3, PCNM4 and PCNM6 (spatial) were the selected predictors influencing the species richness difference.

For macroinvertebrate taxa (Table VII), DO, TSS, TDS, nitrite, phosphate, total hardness (environmental), PCNM1, PCNM3, PCNM4, PCNM5 and PCNM6 (spatial) were observed as the most important predictors determining the total beta diversity in the LNRB. Species replacement was shown to be influenced by TSS, nitrite and PCNM6. The species richness difference was associated with predictors such as DO, TSS, TDS, Alkalinity, BOD, nitrite, phosphate, total hardness (environmental), PCNM1, PCNM3, PCNM4 and PCNM6.

dbRDA model selected DO, TSS, TDS, Alkalinity, BOD, nitrite, phosphate, total hardness (environmental), PCNM1, PCNM2, PCNM3, PCNM4 and PCNM5 as the most relevant predictors for phytoplankton total beta diversity in the LNRB. Whereas, DO, TSS, TDS, alkalinity, BOD, phosphate (environmental), PCNM1, PCNM2 and PCNM4 were selected as the most important predictors for species replacement, TSS, PCNM1 and PCNM6 were the major determinant of the phytoplankton species richness differences in the LNRB (Table VIII).

Most of the environmental variable selected by dbRDA model as the most important predictors of the beta diversity for all the studied taxa in the LNRB were mainly associated with nutrients and high concentrations of suspended solids reflecting increased anthropogenic activities in most of the sampled sites. These observed variation in the species assemblage dissimilarity in relation to environmental and spatial predictors are further explained by the dbRDA bi-plots for the various component of the beta diversity in the LNRB.

The dbRDA bi-plots showed the variation in community assemblage dissimilarities of the studied taxa as it relates to environmental and spatial predictors. The fish beta diversity component of most sites at the upper region of the LNRB (Yuna, Wawu, Awuru, Shagunu and Jebba) are positively influenced by nutrient (nitrite) and nutrient related (DO and BOD), PCNM1, PCNM5 (spatial) predictors (Fig. 23). Except for Yauri (located at the upper region), high concentrations of suspended solids are observed to be associated with the beta diversity of most communities at the lower region (Idah, Onitsha, Patani, Ogbia, Itobe and Agenebode) of the basin. Species replacement component and richness differences followed the same trend with beta diversity (Figs. 24 and 25).

Macroinvertebrate total beta diversity of Agenebode, Ugbolu, and Jebba were mostly associated with PCNM1, while, phosphate, total hardness, nitrite, TSS (environmental), PCNM4 and PCNM (spatial) are positively associated with sites such as Onitsha, Yuna, Ogbia, Faku and Shagunu (Fig. 26). Whereas, TSS and PCNM6 are the predictors influencing the species replacement component of macroinvertebrate beta diversity at Yauri, Fakun and Wawu, nutrient (nitrite) was found to be associated with Yuna, Ogbia, Patani and Onitsha (Fig. 27). Phosphate and nitrite are positively associated with the species richness difference of Yauri, Shagunu, Patani and Yuna. TSS influences Ogbia, Wawu and Agenebode (Fig. 28).

For phytoplankton, predictors such as total hardness, alkalinity and TSS are positively associated with the total beta diversity for Awuru, Jebba, Fakun and Wawu sites. Whereas, sites like Agenebode, Ugbolu, Illushi and Onitsha are mainly influenced by spatial predictors (PCNM2, PCNM3, PCNM4 and PCNM5); nutrients (nitrite and phosphate) and nutrient related (DO and BOD) variables are the major determinants of the total beta diversity for Yauri, Shagunu and Yuna sites (Fig. 29). The species replacement component of Fakun, Awuru, Wawu and Jebba are negatively associated with PCNM1, PCNM4, phosphate, nitrite and BOD (Fig. 30). The richness difference for Ogbia and Patani are positively associated to TSS, while Yuna, Onitsha and Agenebode are influenced by PCNM6 (Fig. 31).

Table VI: Summary statistics of the stepwise model selection in dbRDA, showing significant environmental and spatial variables correlated with fish species turnover in the LNRB

Selected variables	**β**			**Repl**			**RichDiff**		
	AIC	**F**	**P**	**AIC**	**F**	**P**	**AIC**	**F**	**P**
DO	21.9	2.0	<0.01	16.9	1.9	<0.01	-29.7	283.2	<0.01
TSS	21.8	1.9	<0.01	17.5	2.2	<0.01	-78.0	9.4	0.08
TDS	22.5	2.2	<0.01	3.7	5.8	<0.01	-51.0	66.8	0.01
Alkalinity							-29.2	293.3	<0.01
BOD	21.5	1.8	0.02	17.0	2.0	<0.01	-31.7	247.7	<0.01
Nitrite	22.3	2.1	<0.01	17.9	2.4	<0.01	-40.6	136.1	<0.01
Phosphate							-56.4	45.9	0.01
Tot_hard	22.4	2.1	<0.01	18.3	2.5	<0.01	-41.6	127.1	<0.01
PCNM1	23.1	8.2	<0.01	18.7	2.7	<0.01	-28.6	9.6	0.01
PCNM3	21.2	1.7	0.03	17.3	2.1	<0.01	-48.1	43.7	0.003
PCNM4	22.8	2.3	<0.01	17.8	2.3	<0.01	-21.2	18.2	<0.01
PCNM5	21.6	1.8	0.01	17.6	2.2	<0.01			
PCNM6							-30.0	8.4	0.02

DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand; Tot_hard = total hardness; β = total beta diversity; Repl = species replacement; RichDiff = richness differences

Table VII: Summary statistics of the stepwise model selection in dbRDA, showing significant environmental and spatial variables correlated with macroinvertebrate species turnover in the LNRB

Selected variables	**B**			**Repl**			**RichDiff**		
	AIC	**F**	**P**	**AIC**	**F**	**P**	**AIC**	**F**	**P**
DO	4.35	1.85	0.09				-29.7	283.2	<0.01
TSS	11.69	4.90	<0.01	10.0	3.36	<0.01	-78.0	9.4	0.08
TDS	7.01	2.79	0.02				-51.0	66.8	0.01
Alkalinity							-29.2	293.3	<0.01
BOD							-31.7	247.7	<0.01
Nitrite	9.81	3.97	<0.01	7.77	1.38	0.18	-40.6	136.1	<0.01
Phosphate	6.96	2.77	0.01				-56.4	45.9	0.01
Tot_hard	7.48	2.97	0.01				-41.6	127.1	<0.01
PCNM1	6.34	2.53	0.03				-28.6	9.6	0.01
PCNM3	4.89	2.02	0.08				-48.1	43.7	0.003
PCNM4	4.89	2.02	0.07				-21.2	18.2	<0.01
PCNM5	5.25	2.15	0.04						
PCNM6	10.25	4.18	<0.01	8.20	1.74	0.07	-30.0	8.4	0.02

DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand; Tot_hard = total hardness; β = total beta diversity; Repl = species replacement; RichDiff = richness differences

Table VIII: Summary statistics of the stepwise model selection in dbRDA, showing significant environmental and spatial variables correlated with phytoplankton species turnover in the LNRB

Selected variables	**B**			**Repl**			**RichDiff**		
	AIC	**F**	**P**	**AIC**	**F**	**P**	**AIC**	**F**	**P**
DO	5.91	3.15	0.01	8.84	2.37	0.01			
TSS	9.44	4.25	<0.01	11.31	3.69	<0.01	-32.94	3.08	0.08
TDS	5.81	3.12	0.01	8.91	2.40	0.01			
Alkalinity	1.88	2.17	0.08	9.36	2.63	<0.01			
BOD	3.34	2.50	0.03	8.72	2.30	0.01			
Nitrite	0.91	1.97	0.09						
Phosphate	3.30	2.48	0.03	7.36	1.67	0.09			
Tot_hard	3.45	2.52	0.04						
PCNM1	7.48	3.61	<0.01	9.74	2.82	<0.01	-13.26	41.32	<0.01
PCNM2	5.65	3.08	0.01	8.43	2.17	0.01			
PCNM3	2.32	2.26	0.06						
PCNM4	1.20	2.03	0.09	9.20	2.55	0.01			
PCNM5	2.58	2.32	0.05						
PCNM6							-31.22	4.80	0.02

DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand; Tot_hard = total hardness; β = total beta diversity; Repl = species replacement; RichDiff = richness differences

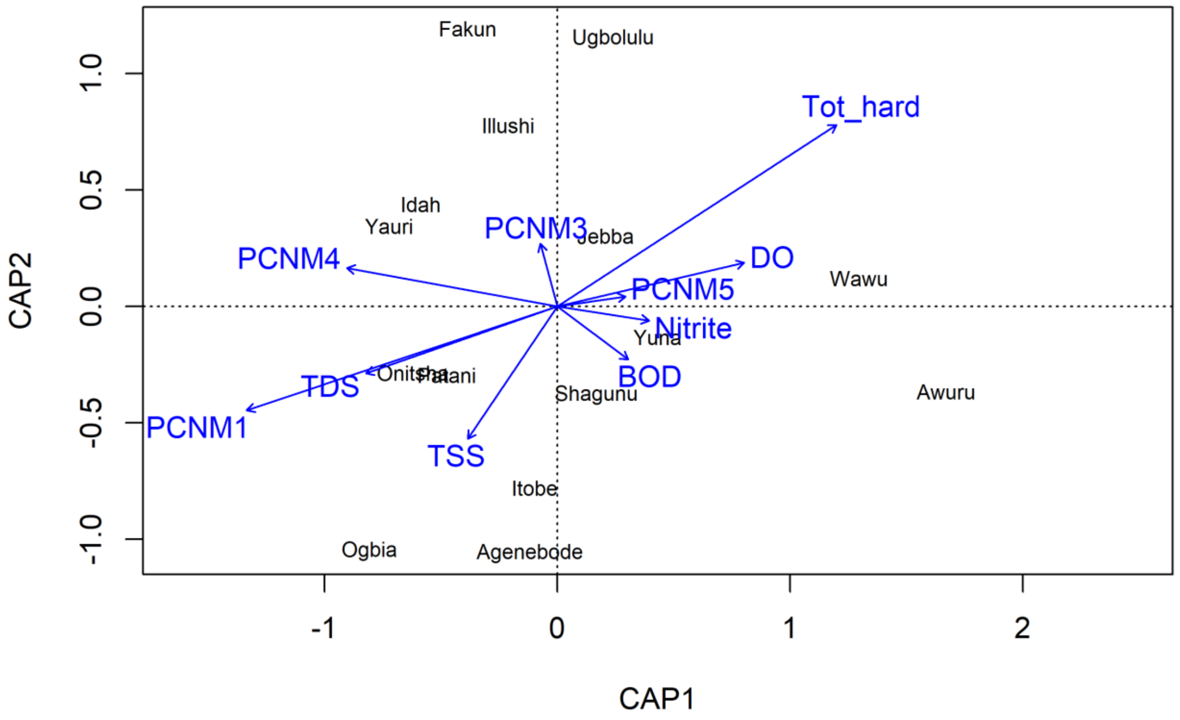

Figure 23: Bi-plot of distance-based redundancy analyses (db-RDA) of fish total beta diversity in relation to environmental and spatial predictors in the LNRB. DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand; Tot_hard = total hardness

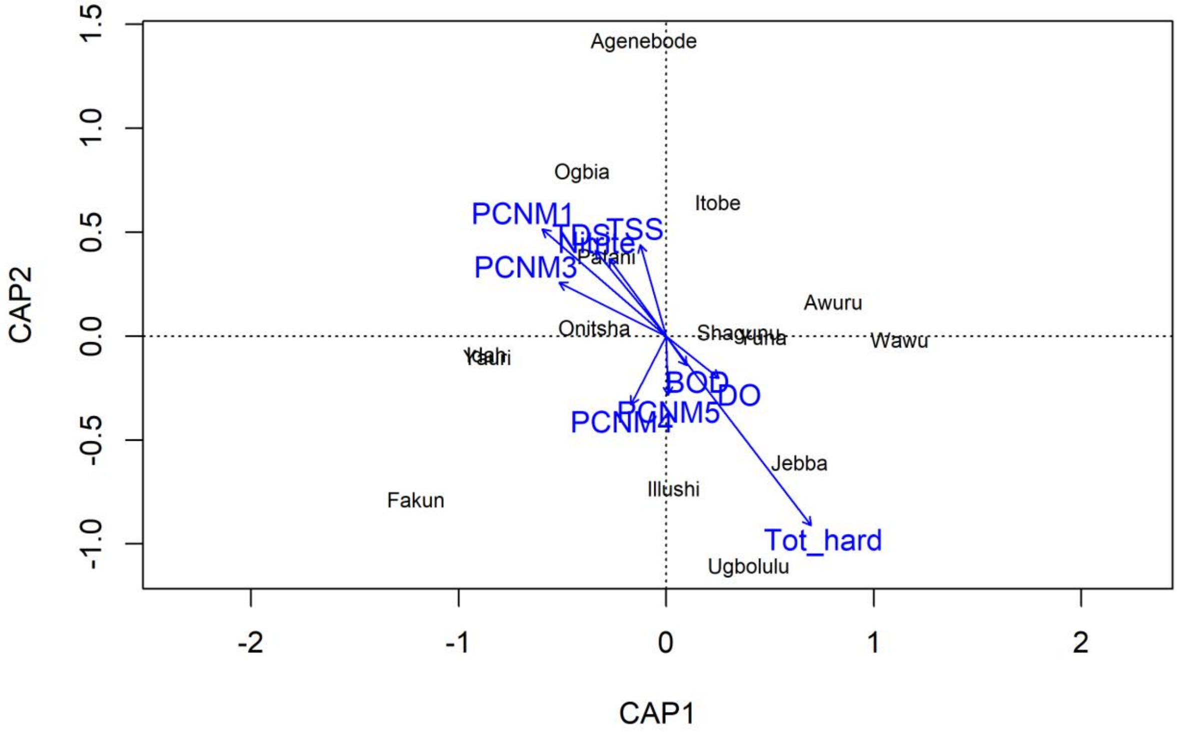

Figure 24: Bi-plot of distance-based redundancy analyses (db-RDA) for fish species replacement in relation to environmental and spatial predictors in the LNRB. DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand; Tot_hard = total hardness

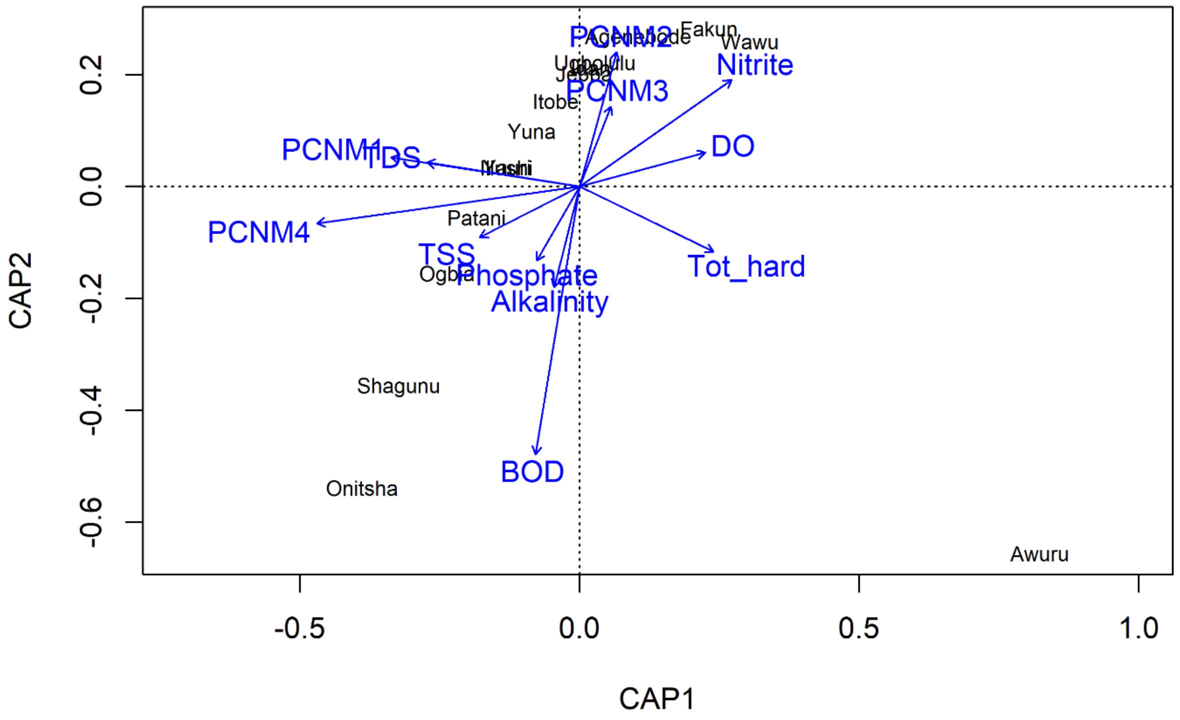

Figure 25: Bi-plot of distance-based redundancy analyses (db-RDA) for fish species richness differences in relation to environmental and spatial predictors in the LNRB. DO = dissolved oxygen; TSS = total suspended solid; BOD_5 = five days biological oxygen demand; Tot_hard = total hardness

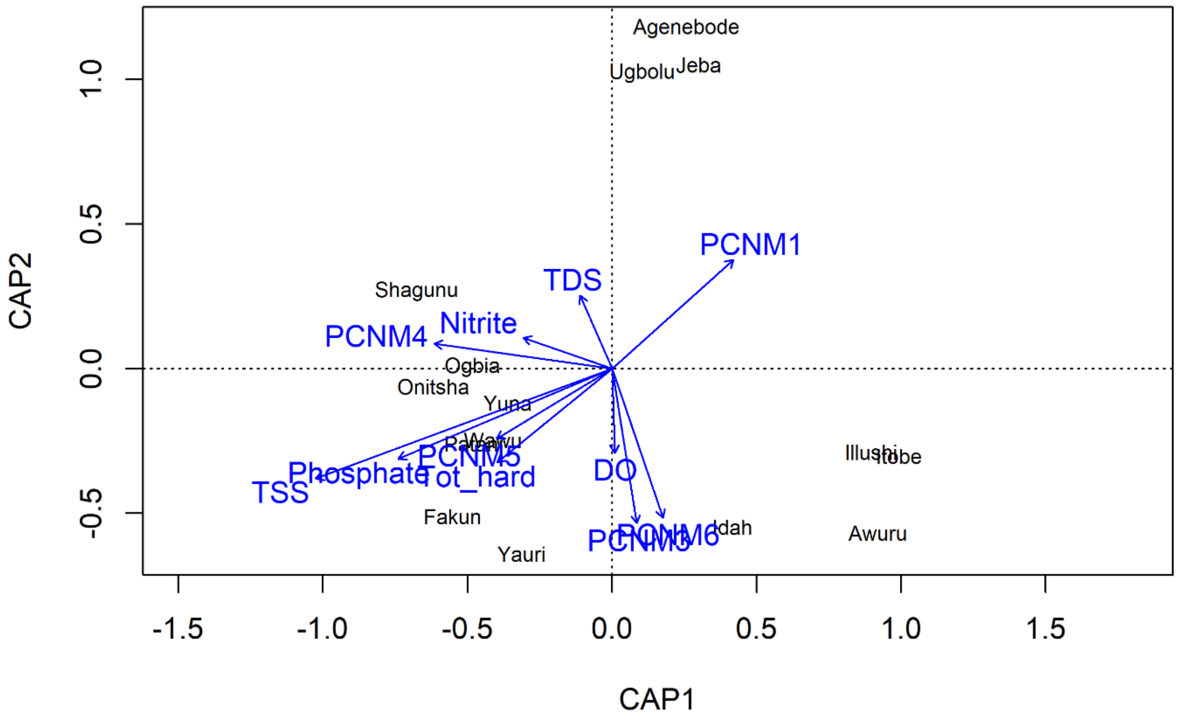

Figure 26: Bi-plot of distance-based redundancy analyses (db-RDA) for macroinvertebrate total beta diversity in relation to environmental and spatial predictors in the LNRB. DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand; Tot_hard = total hardness

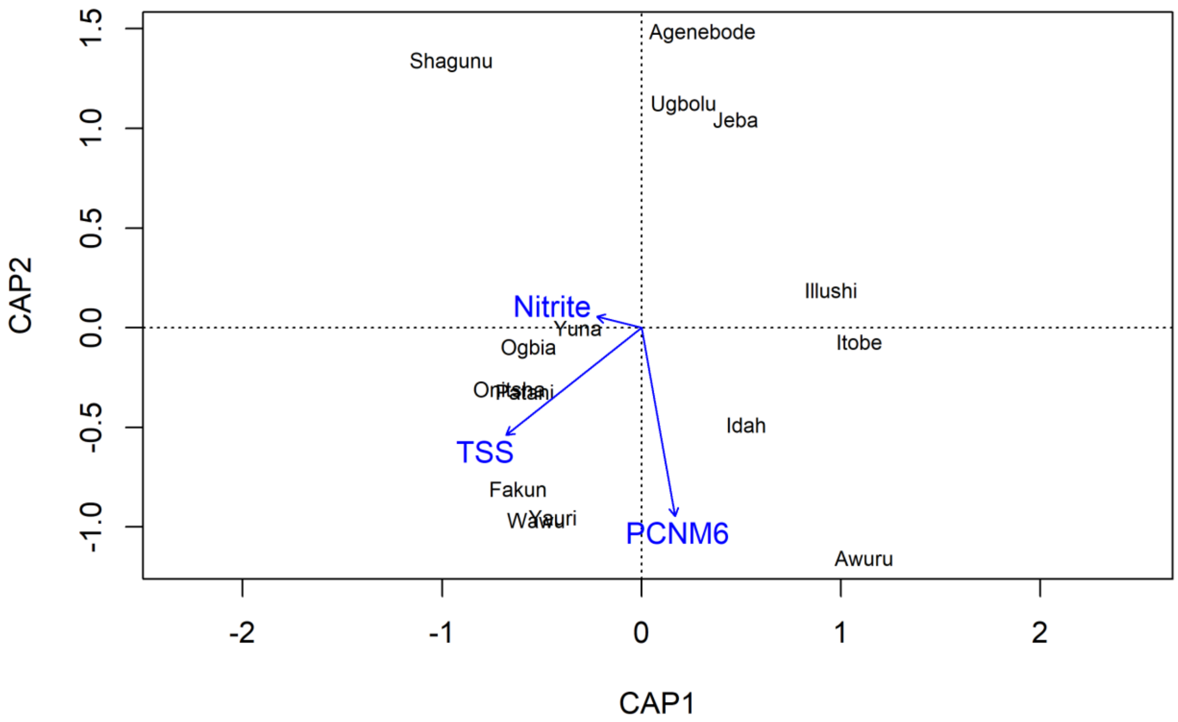

Figure 27: Bi-plot of distance-based redundancy analyses (db-RDA) for macroinvertebrate species replacement in relation to environmental and spatial predictors in the LNRB. TSS = total suspended solid

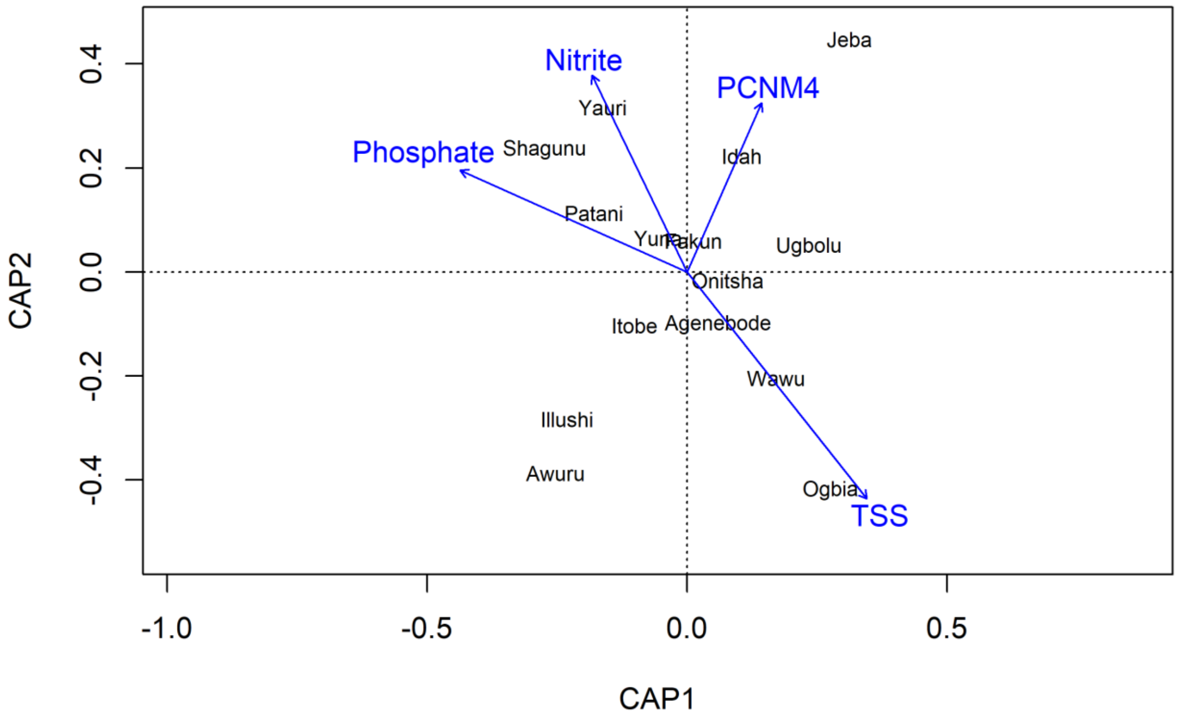

Figure 28**:** Bi-plot of distance-based redundancy analyses (db-RDA) for macroinvertebrate species richness difference in relation to environmental and spatial predictors in the LNRB. TSS = Total dissolved solids.

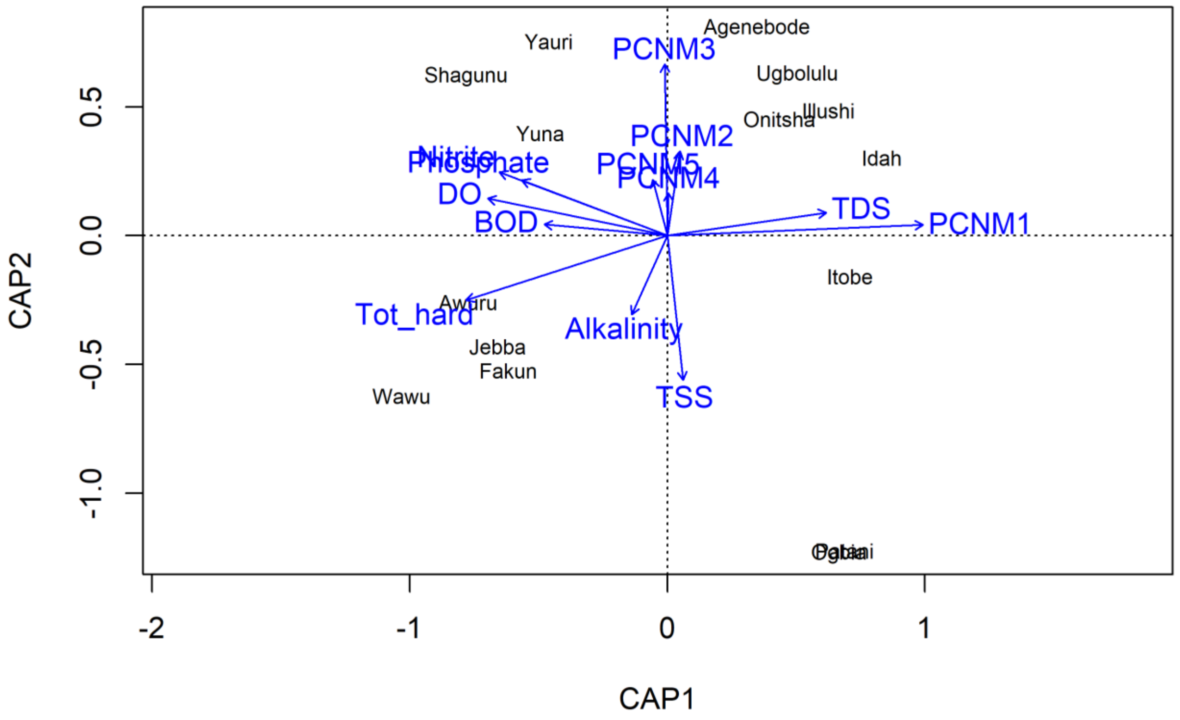

Figure 29: Bi-plot of distance-based redundancy analyses (db-RDA) for phytoplankton total beta diversity in relation to environmental and spatial predictors in the LNRB. DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand; Tot_hard = total hardness

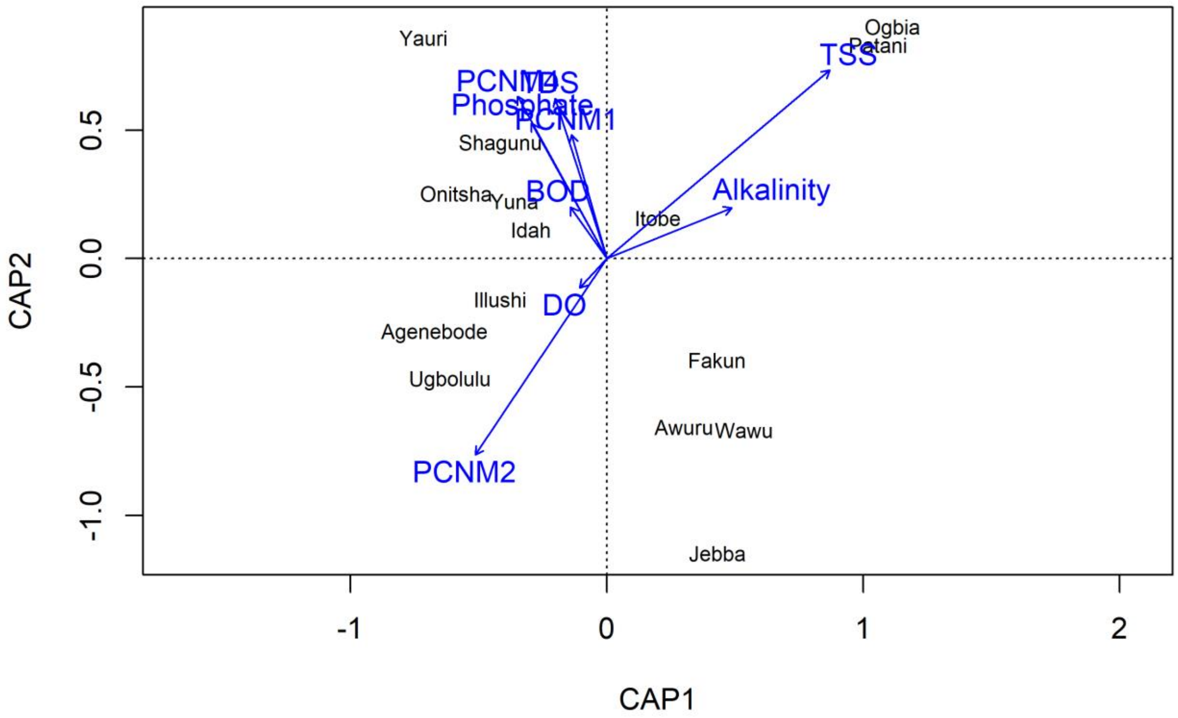

Figure 30: Bi-plot of distance-based redundancy analyses (db-RDA) for phytoplankton species replacement in relation to environmental and spatial predictors in the LNRB. DO = dissolved oxygen; TSS = total suspended solid; BOD_5 = five days biological oxygen demand

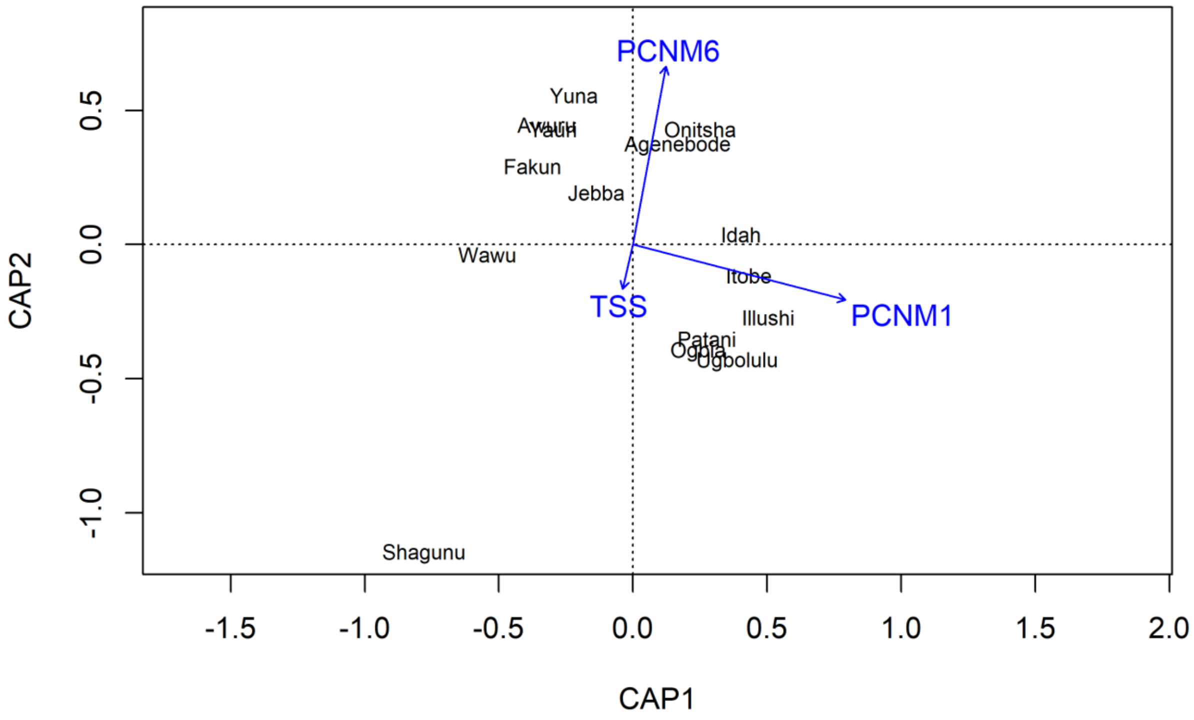

Figure 31: Bi-plot of distance-based redundancy analyses (db-RDA) for phytoplankton species richness difference in relation to environmental and spatial predictors in the LNRB. TSS = Total dissolved solids

4.2.3. Relative contribution of environmental versus spatial predictors to the explained variation in species turnover in the LNRB

The result of the variation partitioning analysis showed that the percentage of variation in fish total beta diversity explained by environmental factors independent of spatial factor (E|S) and spatial factors independent of environmental factor (S|E) were 26% and 32%, respectively (Fig. 32). Whereas, -34% is the shared contribution by environmental and spatial predictor (E ꓵ S) to the explained variation in the total beta diversity, 73% accounted for the unexplained variation [1 – (E + S)]. For species replacement, the overlap between environmental and spatial predictors explained -39% of variation, while, environmental and spatial predictors explained 26% and 35% respectively, with 76% unexplained variation (Fig. 33). For species richness difference, 23% accounted for the unexplained variation while -71% explained the shared contribution of both environmental and spatial predictors. The percentage variation in species richness difference explained by environmental factors independent of spatial factor (E|S) and spatial factors independent of environmental factor (S|E) were 27% and 112% respectively (Fig. 34).

For macroinvertebrate, 34% and 32% are the percentage variation in the total beta diversity explained by E|S and S|E respectively. The overlap between environmental and spatial predictors is – 36% while 71% was the proportion of the unexplained variation in the total beta diversity of macroinvertebrate community in the LNRB (Fig. 35). 5% environmental predictor and 3% spatial predictor are the percentage of the explained variation in the species replacement component of the macroinvertebrate beta diversity in the LNRB. The percentage of unexplained variation is 96% while the overlap between environmental and spatial predictors accounted for – 4% (Fig. 36). High percentage of unexplained variation was recorded for richness difference, while spatial variable alone accounted for 11% of the variation. The overlap between environmental and spatial predictors is 8% (Fig. 37).

The percentage of variation in phytoplankton total beta diversity explained by environmental and spatial factors are 39% and 35%, respectively (Fig. 38). Whereas, - 6% is the shared contribution by environmental and spatial predictor (E ꓵ S) to the explained variation in the total beta diversity, 32% is for the unexplained variation [1 – (E + S)]. For species replacement, the overlap between environmental and spatial predictors to the explained variation is - 23%, while, environmental and spatial predictors explained 34% and 23% respectively, with 67% unexplained variation (Fig. 39).

For species richness difference, 21% accounted for the unexplained variation while - 12% explained the shared contribution of both environmental and spatial predictors. The percentage variation in species richness difference explained by environmental factors independent of spatial factor (E|S) and spatial factors independent of environmental factor (S|E) were 3% and 88% respectively (Fig. 40).

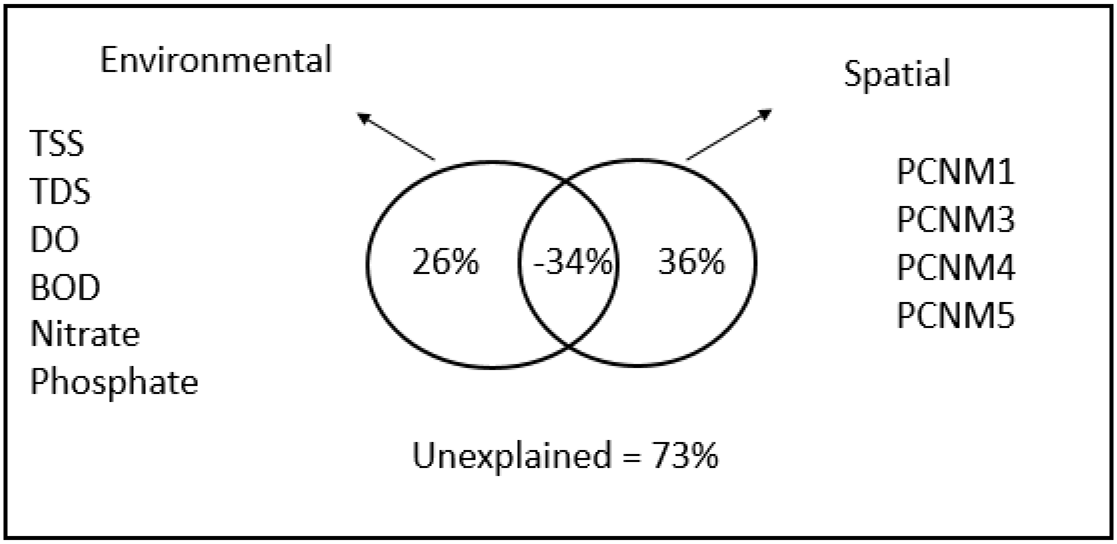

Figure 32: Venn diagram of the variance partitioning analysis of effects of environmental and spatial variables on fish total beta diversity in the LNRB. DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand

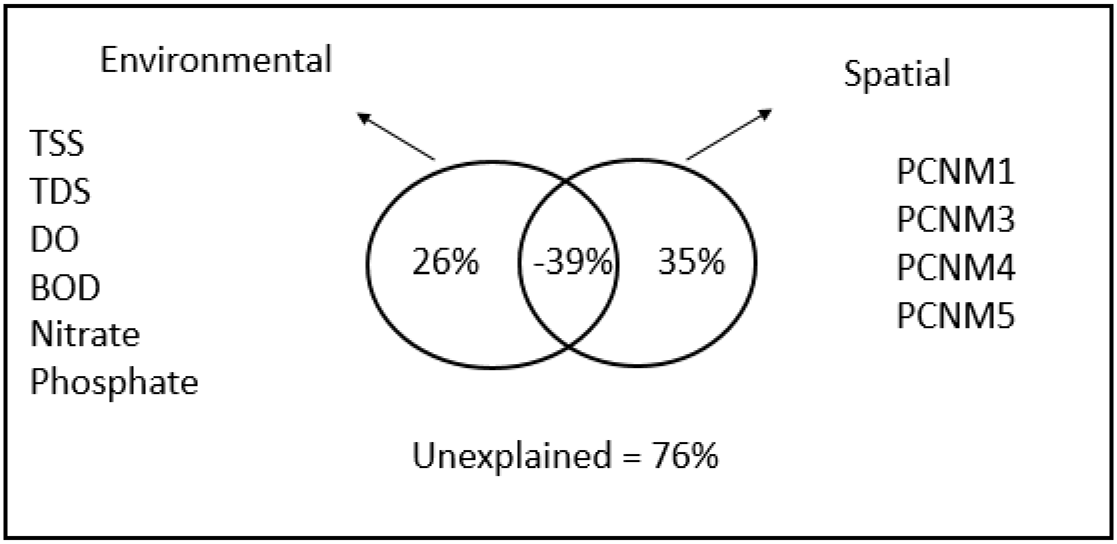

Figure 33: Venn diagram of the variance partitioning analysis of effects of environmental and spatial variables on fish species replacement component of the beta diversity in the LNRB. DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand

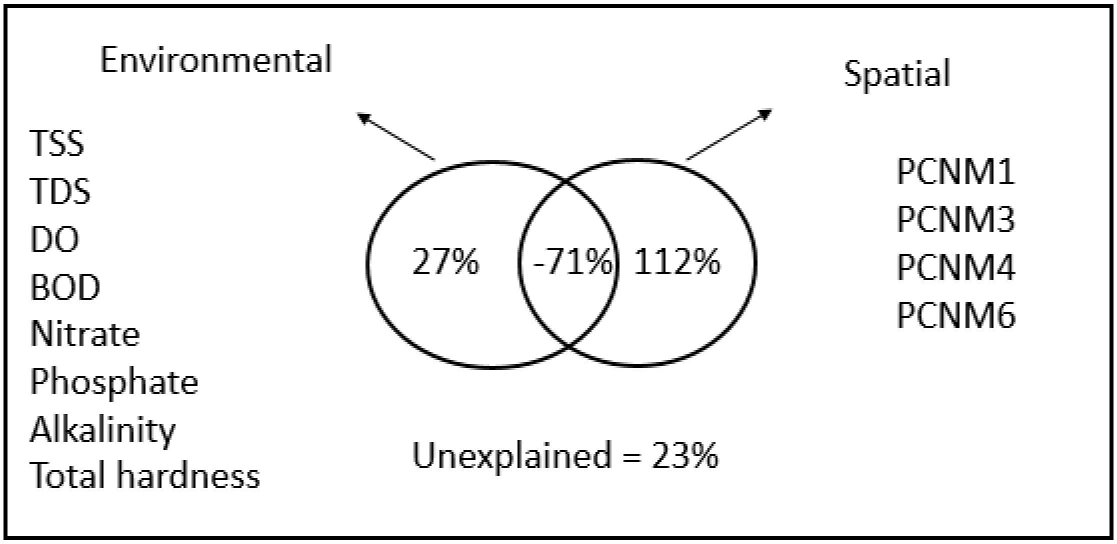

Figure 34: Venn diagram of the variance partitioning analysis of effects of environmental and spatial variables on fish species richness differences component of the beta diversity in the LNRB. DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand

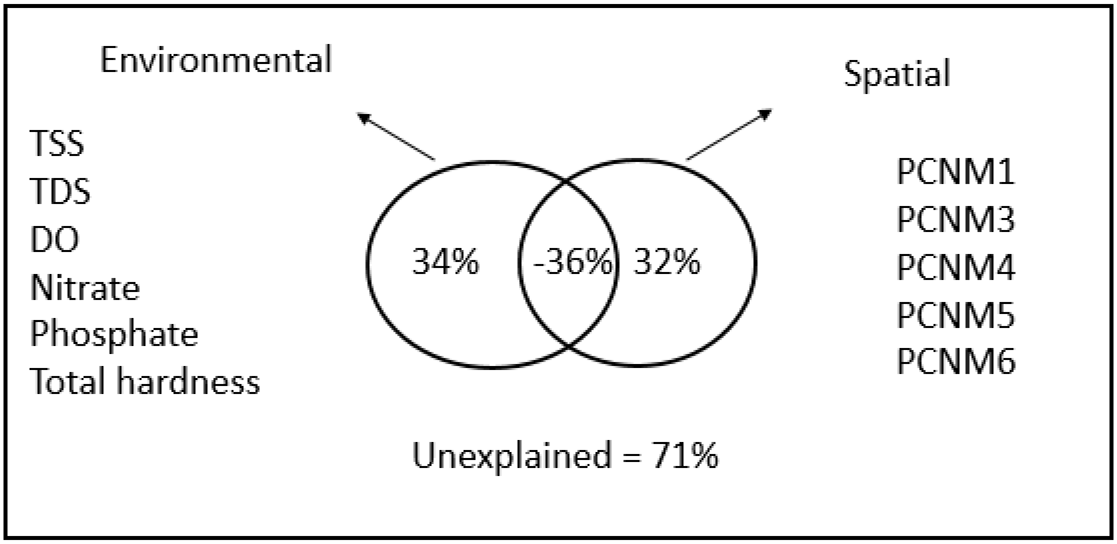

Figure 35: Venn diagram of the variance partitioning analysis of effects of environmental and spatial variables on macroinvertebrate total beta diversity in the LNRB. DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand

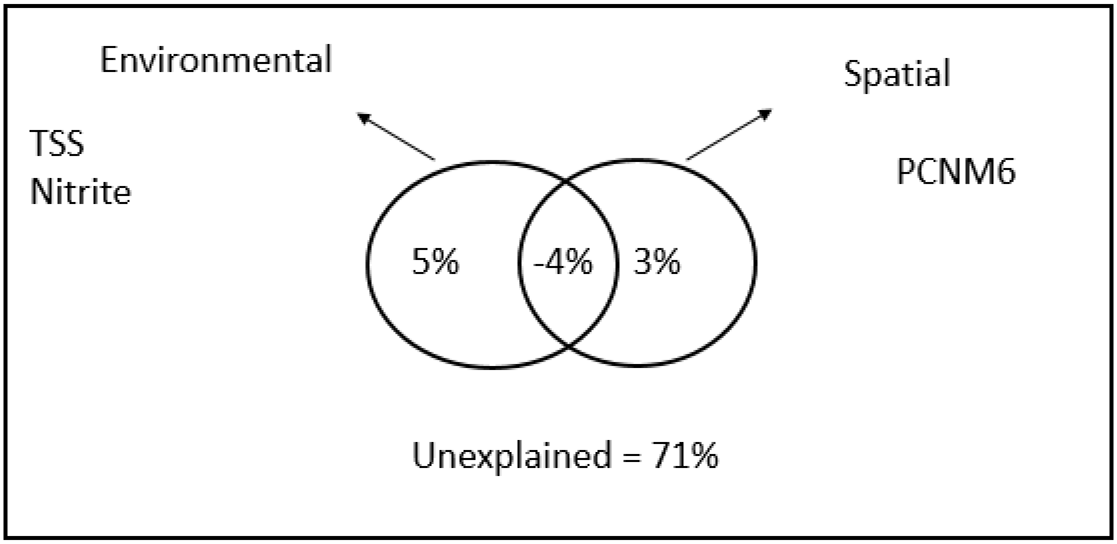

Figure 36: Venn diagram of the variance partitioning analysis of effects of environmental and spatial variables on macroinvertebrate species replacement component of the beta diversity in the LNRB. TSS = Total suspended solids

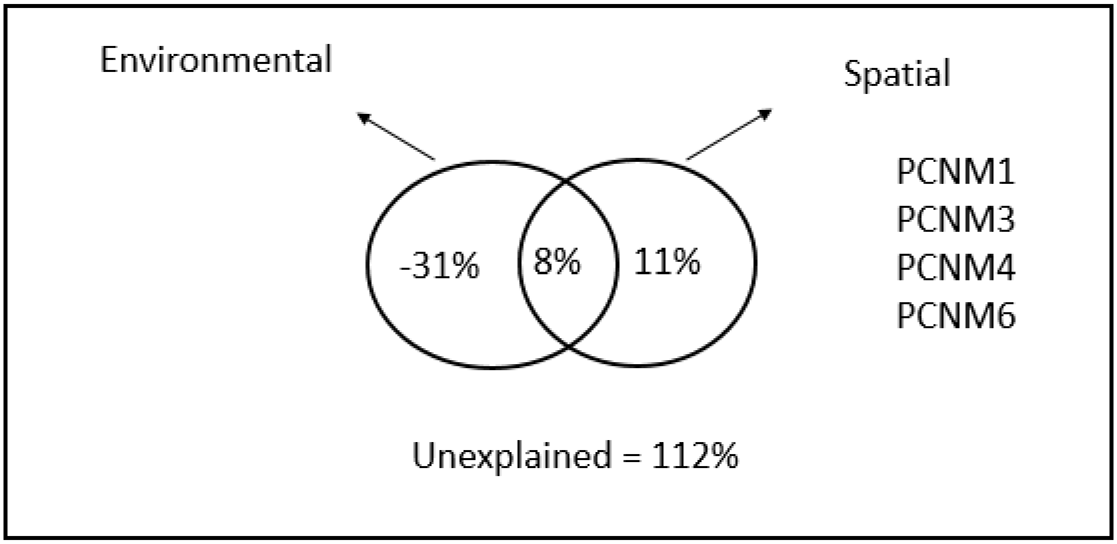

Figure 37: Venn diagram of the variance partitioning analysis of effects of environmental and spatial variables on macroinvertebrate species richness difference component of the beta diversity in the LNRB

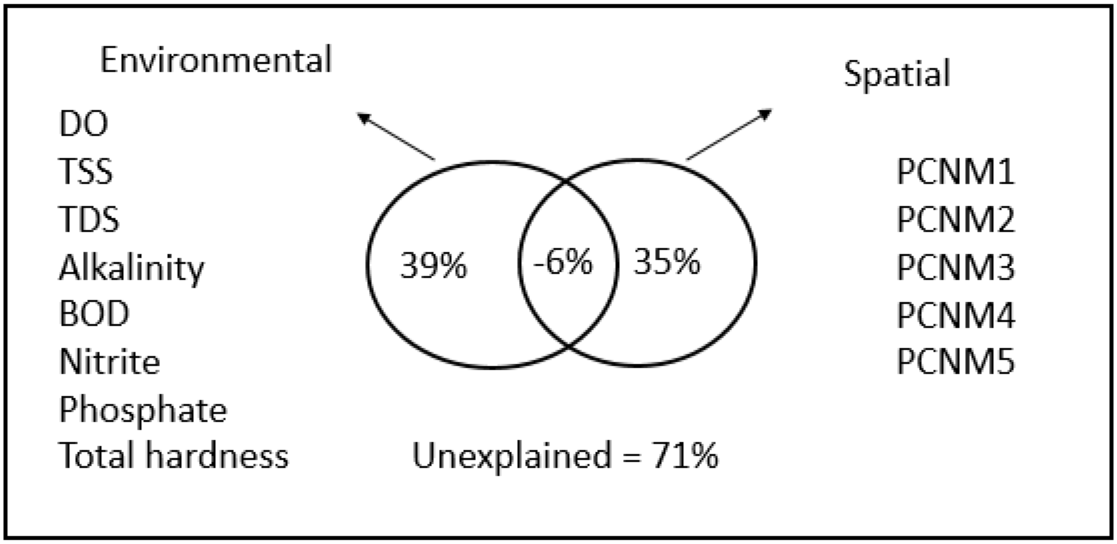

Figure 38: Venn diagram of the variance partitioning analysis of effects of environmental and spatial variables on phytoplankton total beta diversity in the LNRB. DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand

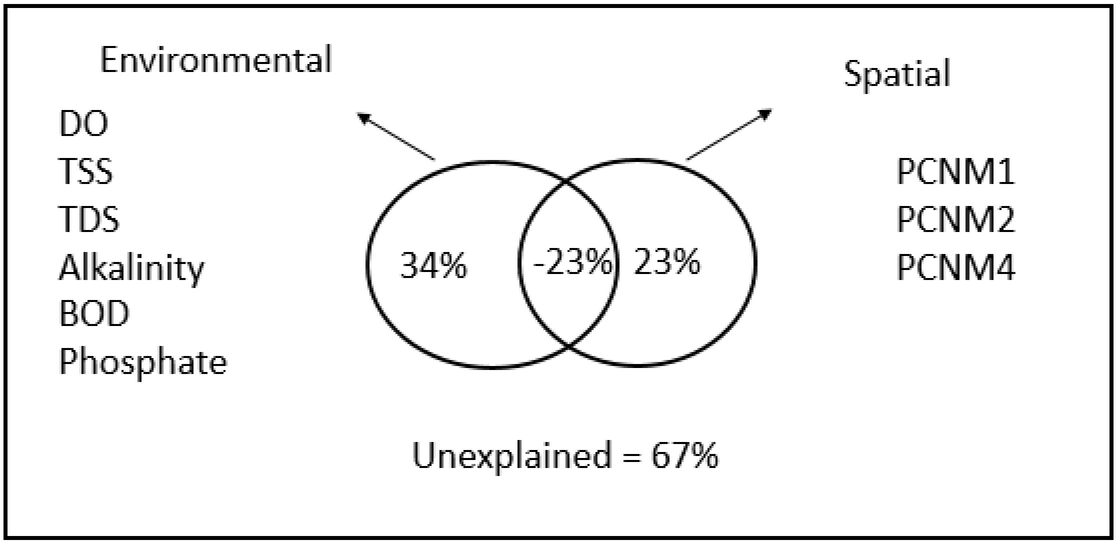

Figure 39: Venn diagram of the variance partitioning analysis of effects of environmental and spatial variables on phytoplankton species replacement component of the beta diversity in the LNRB. DO = dissolved oxygen; TSS = total suspended solid; TDS = total dissolved solid; BOD_5 = five days biological oxygen demand

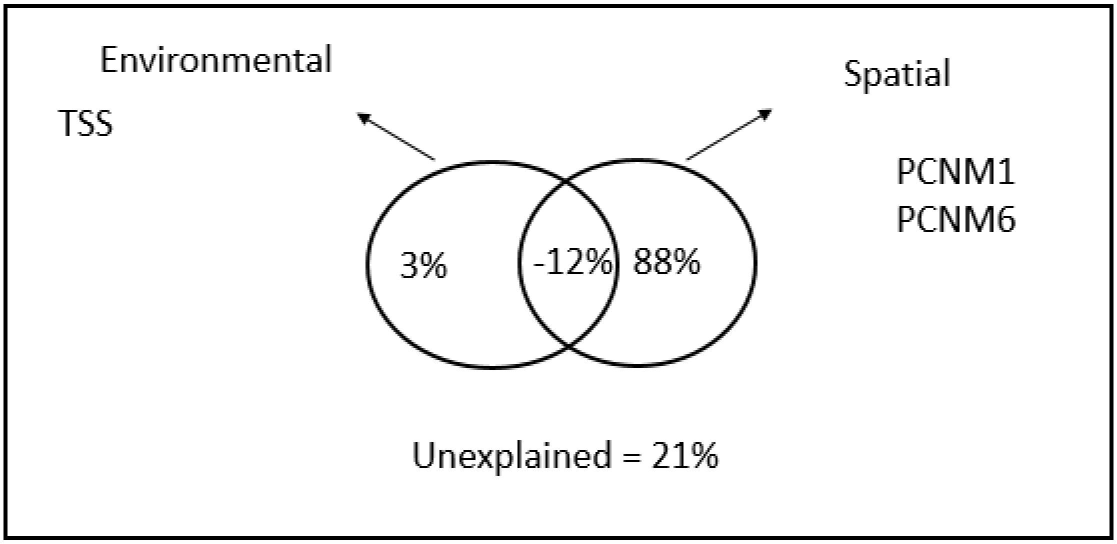

Figure 40: Venn diagram of the variance partitioning analysis of effects of environmental and spatial variables on phytoplankton species richness difference component of the beta diversity in the LNRB. TSS = Total suspended solids

4.3. Discussion

4.3.1. Community structure of the studied taxonomic groups in the LNRB

Relative roles of environmental conditions and regional processes affecting metacommunity structuring have been shown to vary depending on various factors, including niche breadth (**Pandit *et al*., 2009; Szekely and Langenheder, 2014**), biological traits (**Cottenie, 2005; De Bie *et al*., 2012**), taxonomic group (**Vilmi *et al*., 2016**), habitat type (**Cottenie, 2005**), successional stage of the habitat and spatial scale (**Verleyen *et al*., 2009**). The finding of the present study is in agreement with the reports of previous studies (**Vilmi *et al*., 2016; Gothe *et al*., 2017**) that different taxonomic groups with varying dispersal mechanisms are important in shaping the contributions of environmental conditions and spatial processes to metacommunity organization. In this study, the aim is to elucidate the relative importance of spatial and environmental variables in structuring the community assemblages of an Afro-tropical River basin. By comparing responses of three different groups of organisms and using a spatial data set, it was found that whereas, the community compositions of fish and phytoplankton differed between upper and lower regions of the LNRB and between the dry and rainy seasons, macroinvertebrates community structure showed a considerable level of homogenization. This finding negates the prediction of river continuum concept, which describes the longitudinal gradient of physical conditions such as geomorphological and hydrological factors in pristine rivers (**Tornwall *et al*., 2015**). Biological communities are adapted to these gradients and vary predictably along the river from the headwaters to the mouth. According to the River Continuum Concept (**Vannote *et al*., 1980**), the headwater regime (upper reaches) is strongly heterotrophic (the ratio of photosynthesis to respiration [P/R] < 1) and has coarse particular matter and invertivores as the main biological species. The mid-regime is autotrophic (P/R > 1) and has fine particular matter and piscivorous, invertivorous, and planktivorous species. Finally, the downstream regime gradually returns to heterotrophy due to turbidity. Consequently, fish species from the upper river reaches should mostly belong to the insectivore and herbivore-feeding guild as they are expected to depend mainly on allochthonous food sources provided by the riparian vegetation and its associated fauna. In contrast, species from lower river reaches should rely more on autochthonous food sources produced directly in the river, and hence belong to the feeding guilds of carnivores, omnivores, and detritivores. Contrary to these predictions, the result from this study revealed that omnivorous (generalist trophic guild) fishes were the most widely distributed feeding guild along the longitudinal gradient of the LNRB. **Poff and Allan (1995)** suggested that trophic specialists dominate the fish assemblage structure of a stable watercourse, while the abundance of trophic generalists is higher at sites of higher hydrological variability. As observed in this study, the occurrence of generalist species in the river may be caused by the occurrence of two dams that obstruct migration routes, alter sediment transport and water quality, promote biotic homogenization, and favor generalist over specialist fish species (**Araujo *et al*., 2013; Forsberg *et al*., 2019**). Dams interrupt the river continuum altering geomorphology, water quality, temperature regime, and flow regime, thus, resulting in upstream–downstream shifts in biotic and abiotic patterns and processes. The serial discontinuity concept views impoundments as major disruptions to longitudinal resource gradients along river courses (**Ward and Stanford, 1995**).

Furthermore, different species are reported to have their own properties, such as physiological tolerances and dispersal abilities, and similar environments might result in a final homogenization of communities. Microorganisms (e.g. diatoms, bacteria) and organisms with small propagules (e.g. plants, fungi) have been hypothesized to have unlimited dispersal due to their small sizes, large population sizes and potential for high passive dispersal capacity and may therefore show weak spatial structuring along geographical gradients (**Shurin *et al*., 2009; Hajek *et al*., 2011**). Contrary to this hypothesis, this present study found a striking geographical pattern of phytoplankton community between upper and lower region of the LNRB. This observed difference in the community structure of phytoplankton between upper and lower region can be explained by the presence of dams along the longitudinal gradient of the river that may have probably altered the hydrological and geochemical condition of the river after damming (**Wang *et al*., 2018**). Many authors (e.g., **Humborg *et al*., 1997, Jiao *et al*., 2007**) have reported the effect of dams on the phytoplankton community in rivers, estuary, and adjacent sea. For example, phytoplankton community succession in karst cascading reservoirs was reported to be influenced by Si and P stoichiometry (**Wang *et al*., 2014**), whereas in a tributary of the Three Gorges Reservoir, phytoplankton diversity was controlled by hydraulic retention time and nutrient limitation (**Xiao *et al*., 2016**). Furthermore, **Wang *et al*. (2013)** reported that in a river–reservoir unit, dominant Bacillariophyta (diatoms) in rivers change to coexisting Bacillariophyta, Chlorophyta (green algae), and Cyanophyta (blue-green algae) in mesotrophic reservoirs or shift to dominance by

Cyanophyta in eutrophic reservoirs (**Wang *et al.*, 2013**). This phenomenon may be a plausible explanation to the dominance of Chlorophyceae (50.27%) and Cyanophyceae (30.36%) over Baccillarophyceae (18.06%) in the LNRB.

The observed non-significance in the macroinvertebrates community structure between upper and lower region of the LNRB may be attributable to macroinvertebrates dispersal mode (**Gothe *et al.*, 2017**). The dispersal mode of organisms has a key role in determining how communities are spatially structured and how they are interacting with their environment (**Cottenie, 2005**). Passive dispersers (e.g. phytoplankton, clams and mussels) are dispersed by water currents or by larger animals (**Bilton *et al.*, 2001; Vanschoenwinkel *et al.*, 2008**), and they may have limited ability to actively select their habitats (**Vanschoenwinkel *et al.*, 2008**). Active dispersers (e.g. flying insects) can actively select their habitats and oviposition sites to ensure favorable environmental condition for their offspring (**Berendonk, 1999; Resetarits, 2001**). Aerial dispersal is generally the most important mode of dispersal among river littoral macroinvertebrates, and often the majority (56 – 61% of abundance) of species and individuals in macroinvertebrate communities consist of aquatic insects with flying adults (**Tolonen *et al.*, 2001; Tolonen and Hamalainen, 2010**). Therefore, there are higher possibilities that the macroinvertebrates species within the river basin may have tracked suitable environment for their survival irrespective of the barrier created by dams as most of them can disperse by flying. This phenomenon may have explained the homogenization in the community structure between the upper and lower region despite the presence of barrier (dam) along the water channel. Although, this study did not consider the dispersal mode of the macroinvertebrate species of the LNRB, it is a recommended area for further research.

4.3.2. Environmental versus spatial predictors that explained the variation in the community composition of fish, phytoplankton and macroinvertebrate between upper versus lower region of the LNRB

Evidence from this study shows that the community structure in the upper region appears to be influenced more by high nutrient concentrations, while the sites in the lower region are characterized by high concentrations of suspended solids and high anthropogenic activities (disturbance index). This observation may be explained by the impoundment of the river at the upper region and its subsequent conversion to Kainji and Jebba Lakes. These lakes and its floodplains are strongly used for agricultural production (**Adekolu-John, 1987**), because arable and nomadic farmers take advantage of the lakes as a source of irrigation and drinking water for their cattle. Infiltration and erosion of agro-fertilizers, coupled with release of animal dungs by herders may be plausible explanations for the high nutrient concentrations in the river. However, the level of the nutrient loading did not exceed the level that would trigger off hypoxia (**Almeida *et al*., 2022**), and hence there might be a positive effect of nutrient concentrations on the species composition within upper region of the river. High nutrient concentrations can increase total biomass of phytoplankton, zooplankton, and benthic invertebrates, hence providing more food organisms for fish (**Blumenshine *et al*., 1997; Rose *et al*., 2018**), that may induce higher fish biomass or even increased species diversity of fish.

Furthermore, the increased concentrations of solid particles in the lower region of the basin may partly be due to floods originating from the tributaries (Rivers Benue, Anambra, Ezu etc.) of the LNRB during the rainy season (**Balogun and Ibeun, 1995**). **Adeniji and Mbagwu (1998)** reported that the Niger River when leaving Kainji dam transports about 5 million tons of suspended silt per year. Another plausible explanation for the increased solid concentrations at the sites within the lower region may be sand mining activities within the region. During the field campaign, I observed sand mining in almost all the sites in the lower region of the LNRB. **Kondolf (1993)** reported that instream sand mining and bar scalping increases the turbidity of stream water. **Béjar *et al*. (2017)** reported that the concentrations of suspended sediment associated with sand extraction could be similar to those occurring during peak flow periods and had differing effects on different groups of aquatic organisms. For example, Brown *et al*. (1998) reported that in addition to damaging spawning habitats, mining generates fine sediments that directly impact silt-sensitive fish species.

4.3.3. Relative importance of environmental and spatial predictors in structuring the community composition of fish, phytoplankton and macroinvertebrate in dry and rainy season in the LNRB

Variation partitioning analysis demonstrates that environmental and spatial predictors explained only a limited amount of variability in the community composition of fish, phytoplankton and macroinvertebrates in the LNRB. For example, with the exception of phytoplankton in the rainy season (with 43% of unexplained variation in the community variation), all other organism examined in this study recorded above 60% of unexplained variation in the community composition in both dry and rainy seasons. The explained variations in fish community composition, for instance, (though significant) was smaller than the values reported in tropical river systems in some previous studies (e.g. **Brosse *et al*., 2013; Terra *et al*., 2016**). However, the explained variations reported in this study were corrected for sample size and for the number of variables as recommended by **Peres-Neto *et al*. (2006)**. These authors suggested that although correcting for sample size and for the number of variables may reduce the amount of explained variance, it permits an unbiased measurement of the effect and of the importance of the explanatory variables on species composition. Therefore, the corrections may have contributed to high residual variances in both dry and rainy seasons, in agreement with **Cilleros *et al*. (2017)** who reported 75% unexplained variation of fish community composition in a Neotropical stream ecosystem after correction for sample size and number of variables. Alternatively, the interactive effects of other predictors, such as biotic interactions (e.g. competition), may also cause low percentages of explained variations recorded in this study or environmental variables (e.g. water velocity) not measured in our analyses. **Mehner *et al*. (2013)** had similar report on European rivers.

Furthermore, complete separation of the effects of environmental and spatial variables is never possible in any ecosystem, as different components and process are always interrelated (**Heino *et al*., 2015a**). This should therefore be taken into account when comparing the relative importance of processes working on different scales. In this study, however, the amounts of variances either explained individually by the environmental variables or by the spatial variables for both seasons were substantially higher than the amount of shared variance explained together by these variables. Hence, the separate examination of the effects of the environmental and spatial process in structuring the communities is justified in this Afro-tropical River basin. The results of spatially structured fish communities in the LNRB partly correspond to **Drakou *et al*. (2009)** and **Gothe *et al*. (2017)** who reported a strong correspondence between fish community composition and spatial factors in a temperate freshwater system. Spatial factors seem to have influenced the fish community composition more in the downstream than in the upstream sites, suggesting that dispersal among downstream sites is more limited, in particular during the dry season. Potential explanations are the interrupted connectivity between upper and lower sites as a result of damming, and differences in flow dynamics among sites above (upper region) and below (lower region) the dams as a result of black and white floods in the LNRB. The black flood that occurs during the dry season in the upper region increases the connectivity among sites, and hence enhances dispersal of fish. In contrast, due to damming, the black flood does not reach the lower sites **(Balogun and Ibeun, 1995)**. Owing to reduced rainfall in the dry season and subsequent low flow velocity, the sites within the lower regions are less connected and hence dispersal of fishes is more limited. **Thomaz *et al*. (2007)** concluded that increased connectivity among stream sites during flood periods may lead to homogenized environmental variables and random redistribution of organisms, which decreases the effect of spatial structuring on community composition. Conversely, community structure is expected to be more constrained by reduced connectivity in the dry season, attributable to reduced flow velocity (**Bozelli *et al*., 2015**). The reduced water and nutrient exchange during this period also enhance environmental heterogeneity, and local factors are expected to be the principal driver of community composition at each site (**Benone *et al*., 2018**). Finding from this study is in line with other studies (**Shurin *et al*., 2009; De Bie *et al*., 2012**), emphasizes the importance of dispersal limitation for the structure of fish communities, which may mask effects of environmental filtering, or cause strong spatial structuring not at all related to environmental variation (**Ng *et al*., 2009**). In contrast, **Leibold *et al*. (2004)** reported that one of the prerequisites for efficient local filtering of species is sufficient dispersal, because individuals have to reach the variety of habitats to become sorted along existing environmental gradients. When local habitats are highly connected and/or species have high dispersal abilities, species may even inhabit environmentally less suitable habitats because of the permanent influx of dispersing individuals. Such high-dispersal dynamics can likewise result in spatially shaped communities concealing expected environmental relationships, as already discussed above for dispersal limitation (**Leibold *et al*., 2004; Ng *et al*., 2009**).

In LNRB, damming may have contributed significantly to the spatial structuring of the fish community composition by obstructing migration/dispersal routes of fishes, thereby confining them to a particular habitat and limiting them from dispersing downward or upward even if the environmental conditions are suboptimum for their survival. **Arantes *et al*. (2019)** reported that river impoundment affects environmental conditions by creating a new lentic habitat within the otherwise lotic river upstream and by altering flow regime downstream of the dam. Accordingly, damming fragments the river network longitudinally and laterally. The results of this study suggest that the combined effects of altered environmental conditions and fragmentation of riverscapes coupled with annual flooding events may have resulted in significant changes in the fish community structure of the LNRB. Accordingly, the fish community composition of the LNRB appears to be partially consistent with the Serial Discontinuity Concept (SDC), which views dams as discontinuities within the river continuum. Serial Discontinuity Concept (SDC) views dams as a barrier to the natural continuum of the river, thereby, causing upstream–downstream shifts in abiotic and biotic parameters and processes (**Ward and Stanford, 1995**).

4.3.4. Beta diversity patterns of fish, plankton and macroinvertebrates communities of the LNRB

Beta-diversity links local and regional diversity by measuring the amount of species dissimilarity between communities, and it plays a pivotal role in disentangling the various processes that shapes biodiversity patterns across scales (**Viana *et al*., 2015**). Beta-diversity could be further divided into two components: species richness difference which represent that local communities were formed by subsets of species from regional communities, while species replacement or turnover indicated one species was substituted by another, or the changes of its relative abundance in the community among sites (**Ulrich *et al*., 2009; Yang *et al*., 2018**). In the LNRB, beta-diversity partitioning revealed that species replacement (turnover) rather than species richness difference (nestedness) governed the assembly and biogeographic pattern of fish, phytoplankton and macroinvertebrate community structure at both basin and reach scale. Moreover, the beta diversity recorded in this study is said to be weak at both basin and reach scale.

For fish, this study showed that spatial predictors are the major determinant of the fish beta diversity in the LNRB. A plausible explanation to this observation may be attributable to dispersal limitation between upper and lower region as result of damming coupled with the spatial extent (1200 km) of the studied river. At the section level, I hypothesized that patterns of species replacement and richness difference will vary, depending on location within the longitudinal gradient. The headwater section should have high beta diversity driven mainly by species turnover. Within the downstream section closest to the river mouth, high dispersal rates (strong mass effect) should reduce beta diversity as well as the turnover component (**Tonkin *et al*., 2016, Ferreira *et al*., 2019**). Whereas, the first prediction was not met, the second prediction was supported by results obtained for fish assemblages in the lower region of the LNRB. Beta diversity was low in both upper and lower region of the river, with species replacement (spatial turnover) rather than richness differences driving the community assemblage. The reported low beta diversity in both upper and lower regions in this study may be attributable to “black and white flood” experienced by the upper region and annual flooding of the river at the lower basin from its tributaries (e.g Benue River, Anambra River, Ezu River etc.). **Lopez-Delgado *et al*. (2020)** reported that flooding creates a complex of aquatic habitats with high lateral and longitudinal connectivity. This condition may have increased the opportunities for high-dispersal dynamics leading to mass effects or source-sink dynamics (**Leibold *et al*., 2004**) and may be a plausible explanation of our findings of low beta diversity in both upper and lower region of the river. Furthermore, it is likely that a greater flux of fish species and access to a larger (regional) species pool as a result of flooding in the studied sites may lead to relatively high dispersal among sites, which can – similar to low dispersal (dispersal limitation) – mask the environmental structuring of species communities (**Ng *et al*., 2009; Brown and Swan, 2010; Gothe *et al*., 2013**). Such high dispersal dynamics reduces beta diversity (**Lopez-Delgado *et al*., 2020**). The reported low fish beta diversity in this study is in line with the findings of **Arrington and Winemiller (2006)** in Venezuela's Cinaruco River. The authors reported that the composition of fish assemblages in structurally complex habitats was nonrandom during the low-water period, but during the period of rising water, fish assemblages reflected a strong influence of stochastic colonization dynamics. They found that annual flood pulse promotes fish dispersal, frequent restructuring of fish assemblages over variable spatial scales, homogenization of assemblage composition, and a decline in beta diversity.

In the case of macroinvertebrate, environmental factors alone explained a higher fraction of variation in beta diversity and its components than did spatial factors alone or shared environmental and spatial factors, implying that environmental filters constrain species distributions and abundances, which is consistent with species-sorting metacommunity concept (**Soininen, 2014, Cordova-Tapia *et al*., 2018**). This result is in agreement with the findings of **Lopez-Delgado *et al*. (2020)** who reported that, at the basin level, when among-site environmental heterogeneity is high, species are able to disperse and select suitable environmental conditions, resulting in high beta diversity driven by species replacement. **Heino *et al*. (2015a)** reported that, at the basin level, environmental factors control beta diversity patterns when dispersal rates are intermediate, producing variability in species composition among sites (**Chase and Leibold, 2003; Soininen, 2014**). They also proposed that there should be a positive relationship between beta diversity and environmental heterogeneity. This present study demonstrate similar results, with the most influential environmental variables associated with nutrients and high concentrations of total solids attributable to the structural complexity of instream river habitat, reinforcing the importance of habitat heterogeneity for local macroinvertebrate assemblage structure (**Lopez-Delgado *et al*., 2020**). In the LNRB, habitat features apparently act as a filter that selected macroinvertebrates with particular combination of traits associated with locomotion, feeding and reproduction.

For phytoplankton beta diversity, it is expected that since they are passive dispersers, they would be more strongly related to the spatial factors than environmental conditions. This is because, the unidirectional river flow coupled with "black and white" flood experienced by the LNRB could favor downstream dispersal of species derived from tributaries and the upstream reservoir (**Bortolini *et al*., 2017; Bovo-Scomparin *et al*., 2013**). However, the result of this study showed that, although all beta diversity components were significant, only species richness difference was mostly driven by these processes. Local environmental variables influence total beta diversity and species replacement components of phytoplankton communities. This suggests that continuous downstream passive dispersal through water flow occasioned by flooding, limited the ability of phytoplankton to effectively track environmental variation along the river channel. Although the possibility that unmeasured ecological variables are influential cannot be ruled out (**Peres-Neto and Legendre, 2010**), such as grazing by both zooplankton (**Verreydt *et al*., 2012**) and benthic invertebrates (**Vilmi *et al*., 2017**), this was probably not the case in this present study for three reasons. First, previous studies have shown that the environmental variables selected by the dbRDA model in this study, such as phosphate and nitrite, as well as TSS and TDS, were the main drivers influencing phytoplankton communities (**Gillett *et al*., 2016; Jamoneau *et al*., 2018; Qu *et al*., 2018**). Indeed, nutrient and light availability are considered primary elements for phytoplankton development (**Reynolds, 2002**). Second, the relatively low total proportion of explained variation has been a typical finding in studies of phytoplankton (e.g**. Nabout *et al*., 2009**), which suggests that the community structure of these small passive dispersers shows low predictability. Third, in systems showing high environmental variability, neither species sorting nor dispersal mechanisms may shape aquatic communities (**Datry *et al*., 2016b**). Rather, community structure may display a high degree of stochasticity caused by random colonization and extinction events (**Hubbell, 2001**). This is likely to be the case of phytoplankton inhabiting lotic systems, where the recurrent instability of the water column, continuous downstream flow and high turbulence may impose limits on their colonization, establishment and development (**Bovo-Scomparin *et al*., 2013; Jati *et al*., 2017**). This may, in turn, lead to unexpected absences of some species at sites that are otherwise environmentally suitable, consequently weakening the action of environmental filtering (**Heino *et al*., 2015a**).

4.3.5. Local contributions of sites to beta diversity in the LNRB

The contribution of a single site to overall patterns in beta diversity in a system can be described using local contributions to beta diversity (LCBD; **Legendre and De Cáceres, 2013**). Large LCBD values indicate local assemblages (sites) with strongly divergent species composition compared with the regional average. Relatively undisturbed habitats supporting these local assemblages are particularly important for biodiversity conservation because of their unique features that support species with limited distributions in the riverscape. Conversely, some sites with large LCBD values may represent divergent assemblage structures that reflect impacted habitats that may be candidates for ecological restoration (**Legendre, 2014**).

For fish, large LCBD values were observed for most sites in the upper region (lake section) of the LNRB. Most of the sites had relatively low species richness and fish abundance compared with sites in the lower region, except for site C (Shagunu, often referred to "belly" of Lake Kainji because of its large size) with 28 species. Sites with low species richness might be explained by the influence of human impacts, such as over fishing or local watershed impacts within the upper region. **Ayanda *et al*. (2010)** reported that there are over 275 fishing villages at the Kainji lake section (upper region) of the LNRB, who are actively involved in fishing activities with various unregulated fishing gears. This over fishing may have reduce the diversity and abundance of fish within the lake as evidenced from the reported low richness and abundance compared to reports from earlier studies in the region. For example, **Lelek (1972)** and **Ita (1978)** recorded 99 and 104 fish species, respectively, at the upper region (Kainji Lake) of the river. **Mshelia *et al*. (2010)**, in a relatively recent study in Kainji Lake, recorded about 42 species. Another plausible explanation to the LCBD values recorded by most sites from the upper region may be attributable to damming effect. It has been reported that damming-induced changes affect beta diversity components downstream of the reservoir, which has implications for guiding practical management decisions (**Braghin *et al*., 2018; Chaparro *et al*., 2019**). For example, species may track the environmental gradient along the river, contributing to the dominance of species replacement as observed in this study at the lower region. In contrast, sites closer to the dam may have lower species diversity when compared to more distant ones, since the particular environmental conditions imposed by the impoundment may be unsuitable for many species (**Lansac-Tôha *et al*., 2019**).

In the case of macroinvertebrate, most of the sites that recorded high LCBD values had relatively high species richness and abundance, while some sites have low species richness and abundance compared to others sites along the longitudinal gradient of the LNRB. This finding is in line with the postulation of **Legendre and De Cáceres (2013)** which holds that sites with unique combinations of species are likely to have higher LCBD values and sites that are degraded or species poor are also likely to have higher LCBD values. The high species richness and abundance recorded in some of those sites with high LCBD values could be attributed to relatively lower anthropogenic (human) impacts as well as the presence of suitable habitats for benthic invertebrates that is provided by the diverse nature of the vegetation of the littoral zone of the sites. Mostly the insect groups dominated the macroinvertebrates of those sites, and this is similar to the observations made by **Imoobe (2008)** and **Arimoro *et al*. (2015)**. While, sites with low species abundance were associated with reduced environmental quality, high solid concentrations, nitrite, and phosphate were identified as important variables that influenced the macroinvertebrate beta diversity in this study. For example, site C (Shagunu), H (Lokoja) and K (Illushi) with high LCBD values but with low species abundances were observed to have recorded high values for TSS, TDS, nitrites and phosphates when compared to other sites in the river basin. High concentrations of these environmental variables may indicate early warning signal for eutrophication of the water body, which may lead to oxygen depletion in the water body, and this condition affects macrobenthic invertebrate assemblages since they are reliant on oxygen availability (**Keke *et al*., 2017**). This observation may be a plausible explanation to the finding of reduced species richness and abundance in those sites, thus contributing high values of LCBD to the macroinvertebrate beta diversity in this study. Similar to the results of this study, **Heino and Gronroos (2017)** found that high LCBD values for stream insect assemblages were negatively associated with species richness, suggesting that sites with unique species composition generally had low species richness.

For phytoplankton, large LCBD values were observed for sites in the upper region (lake section) and the last two sites (Patani and Ogbia) in the lower region of the LNRB. The sites in the upper region with high values for LCBD had low species diversity while sites within the lower region with high LCBD had comparable higher species richness. The upper region of the basin is reported to experience two distinct annual flooding (**Balogun and Ibeun, 1995**) with often-high turbulence. **Jati *et al*. (2017)** observed that phytoplankton inhabiting lotic systems with recurrent instability of the water column, continuous downstream flow and high turbulence might experience limited colonization, establishment and development. This phenomenon may lead to unexpected absences of some species at sites that are otherwise environmentally suitable. This phenomenon may be a plausible explanation to the result of this study as there are a lot of species (*Achnanthes clevei*, *Asteronella sp*, *Cylindrotheca closterium*, *Leptocylindrcus danicus*, *Nitzchia sp*., *Merismopedia sp*.) that were absent in the upper regions but were found at sites within the lower region of the LNRB. Conversely, the comparative species richness observed in the lower region may be attributable to heterogeneous environment of the region. Therefore, the unique combination of species at the sites in the lower region and the degraded or species poor sites at the upper region may have explained the higher values of LCBD (**Legendre and De Cáceres, 2013**) recorded in those sites, thus contributing to the phytoplankton dissimilarities in the LNRB.

CONCLUSION, RECOMMENDATIONS AND PERSPECTIVES

Understanding the extent to which species distributions at different scales are determined by the dispersal ability or habitat requirements of species is a pivotal task in community ecology. Answering this question may have major implications for how to study and conserve biotic assemblages. Because this simple question challenges two major theoretical concepts in current ecology (dispersal versus niche models; e.g. **Tuomisto *et al*., 2003; McGill *et al*., 2006; Vergnon *et al*., 2009**), recent studies have approached it from a variety of perspectives (e.g. **Girdler and Barrie, 2008; Qian, 2009; Verleyen *et al*., 2009; Heino *et al*., 2010**). One of the most promising theoretical frameworks concerning species distributions, diversity and coexistence is the metacommunity concept, which has developed rapidly in recent years (**Leibold *et al*., 2004; Cottenie, 2005; Ng *et al*., 2009; Pandit *et al*., 2009; Okuda *et al*., 2010**).

Recent metacommunity models (**Cottenie, 2005; Ng *et al*., 2009**) integrate niche explanations (i.e. a process called species sorting or environmental filtering) and spatial explanations (i.e. dispersal processes). While many studies have clearly demonstrated the importance of both kinds of processes in shaping the metacommunity patterns of plants, animals or microorganisms (**Tuomisto *et al*., 2003; Girdler and Barrie, 2008; Heino *et al*., 2010**), it is rare for different groups of organisms to be compared in a single study. In addition, most comparative studies do not perform a direct comparison among organisms in the same landscape context with the same set of sites (**Cottenie, 2005; Soininen *et al*., 2007; Shurin *et al*., 2009**). These methodological differences have limited the ability to draw firm conclusions regarding the relative importance of spatial and environmental effects in different groups of organisms with different dispersal traits and/or different responses to environmental variables (**Soininen *et al*., 2007**). Therefore, the findings of this study illustrate how organism-specific and highly context-dependent patterns in community organization may emerge as a consequence of interactions between local environmental factors (i.e. environmental heterogeneity), habitat connectivity (i.e. at the upper versus the lower region of a large dammed river) and organism dispersal potential (i.e. high versus low). The main findings of this study are:

1. The community structures of fish, phytoplankton and macroinvertebrates in the LNRB clearly showed the influence of damming and flood regimes. The community composition of fish and phytoplankton in the LNRB appears to be partially consistent with the Serial Discontinuity Concept (SDC), which views dams as discontinuities within the river

continuum. Serial Discontinuity Concept (SDC) views dams as a barrier to the natural continuum of the river, thereby, causing upstream–downstream shifts in abiotic and biotic parameters and processes (**Ward and Stanford, 1995**). However, given the lack of reference or pre-impoundment information concerning the biophysical gradients that occurred along the upper and lower region of the LNRB and the degree to which tributaries influence the mainstem, a rigorous test of the SDC's predictions here is compromised. Furthermore, the extent to which anthropogenic effects have affected habitats here may have overwhelmed what underlying patterns researchers might seek to detect. The mode of dam operation (e.g., surface versus deep release and continuous versus regulated flow) is yet another confounding factor. However, given the knowledge of how dams and reservoirs alter lotic fish assemblages (**Pringle *et al*., 2000; Schmutz *et al*. 2000; Agostinho *et al*., 2004; Tiemann *et al*., 2004**), further studies of how dams affect the ecology of the LNRB is needed.

2. Spatial predictor is the determinant of the community structure of fish and phytoplankton thereby, reflecting the effect of dispersal limitation in structuring the community composition of fish and phytoplankton in the LNRB. Macroinvertebrates community composition is structured by environmental predictors, thus, reflecting the importance of species sorting. If this is the case, it suggests that, for example restoration measures applied in headwater reaches would promote recovery of fish and phytoplankton communities, whereas recolonization of macroinvertebrate communities may be substantially delayed (**Pedersen *et al*., 2006**). More studies are, however, needed to assess the generality of these results. To strengthen inference, it would be useful to include trait and genetic approaches to assess dispersal and to take other indicators of isolation into account, such as the specific structure (branching geometry and spatial arrangement) of single stream networks.
3. Regardless of the spatial scale of analysis (basin or reach level) species replacement appeared to be the major mechanism driving the beta diversity and species turnover of fish, phytoplankton and macroinvertebrate in the LNRB, a finding consistent with those from other studies of metacommunities in rivers and streams (**Soininen, 2014; Hill *et al*., 2017; Roa-Fuentes *et al*., 2019**). In the LNRB, spatial variables were strongly associated with beta diversity and its components in the lower region. Strong spatial patterns of species turnover associated with environmental variables, especially factors contributing to habitat

structural complexity, suggest that strategies for biodiversity conservation in the LNRB should focus on protecting areas that encompass diverse habitats that harbor local species assemblages with divergent compositions. Although not evaluated directly here, it nonetheless infers that aquatic habitat connectivity is required to allow intermediate rates of dispersal that facilitate species sorting.

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Appendix 1: Fish species distribution and feeding guilds in upper and lower reaches of the Lower Niger River Basin, Nigeria, 2021

	Dry season		**Rainy season**		**Feeding guild**
	Upper	Lower	Upper	Lower	
Clarias gariepinus	+	+	+	+	Omnivore
Heterobranchus bidorsalis	+	+	+	+	Omnivore
Synodontis membranaceus	+	+	+	+	Omnivore
Synodontis occelifer		+		+	Omnivore
Synodontis schall	+	+	+	+	Omnivore
Synodontis couteti	+			+	Omnivore
Synodontis eupterus				+	Omnivore
Chrysichthys nigrodigitatus	+	+	+	+	Omnivore
Bagrus bayad	+	+	+	+	Invertevore
Bagrus docmac	+	+	+	+	Invertevore
Clarotes laticeps	+	+	+	+	Omnivore
Auchenoglanis occidentalis	+	+	+		Omnivore
Schilbe mystus		+	+	+	Piscivore
Schilbe intermedius	+		+	+	Piscivore
Malapterurus electricus	+	+		+	Invertevore
Citharinus citharus	+	+	+	+	Planktivore
Distichodus rostratus	+	+	+	+	Herbivore
Brycinus nurse	+	+	+	+	Herbivore
Brycinus macrolepidotus	+		+	+	Herbivore
Hydrocynus forskhalii		+	+	+	Piscivore
Alestes baremoze	+	+	+	+	Piscivore
Alestes leuciscus	+	+	+		Piscivore
Paraillia pellucida		+			Invertevore
Tetraodon lineatus		+			Piscivore
Parachanna obscura		+			Piscivore
Polypterus senegalus	+		+	+	Omnivore
Protopterus annectens	+				Omnivore
Lates niloticus	+	+	+	+	Piscivore

Appendix 1. (Continues)

	Dry season		Rainy season		Feeding guild
Gymnarchus niloticus	+				Carnivore
Marcusenius senegalensis	+	+	+		Invertevore
Hyperopisus bebe	+	+	+	+	Omnivore
Mormyrops deliciousus	+	+	+	+	
Mormyrus rume	+	+	+	+	Detritivore
Gnathenomus petersii		+		+	Detritivore
Petrocephalus bane		+			Planktivore
Heterotis niloticus		+			Omnivore
Labeo senegalensis		+	+		Herbivore
Labeo cubie	+	+	+	+	Omnivore
Oreochromis niloticus	+	+		+	Planktivore
Tilapia zillii	+	+		+	Planktivore
Hemichromis fasciatus	+	+			Omnivore
Sarotherodon galilaeus	+	+	+		Omnivore
	31	35	27	29	

Appendix 2: Fish species occurrence in the Lower Niger River basin

Order	**Family**	**Taxon**	**Yauri**	**Wawu**	**Shagun**	**Yuna**	**Fakun**	**Awuru**	**Jebba**	**Itobe**	**Idah**	**Agene**	**Illushi**	**Ugbolulu**	**Onitsha**	**Patani**	**Ogbia**
Siluriformes	Clariidae	*Clarias gariepinus*	+	+	+	+	-	+	+	+	-	+	-	-	+	+	+
		Heterobranchus bidorsalis	+	-	+	+	-	-	+	-	-	-	-	-	+	+	+
	Synodontidae	*S. membranaceus*	+	-	+	+	+	-	+	+	+	+	-	-	+	-	+
		S. occelifer	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
		S. schall	+	-	+	-	+	-	-	+	+	-	+	+	+	+	+
		S.couteti	-	-	-	-	+	-	-	-	-	-	-	-	+	-	+
		S. eupterus	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+
	Bagridae	*Chrysichthys nigrodigitatus*	+	+	+	+	+	-	+	+	+	-	+	+	+	+	+
		Bagrus bayad	+	-	-	-	-	-	-	+	+	+	+	-	+	+	+
		Bagrus docmac	-	-	+	-	-	+	+	+	+	-	-	+	+	-	-
		Clarotes laticeps	-	-	+	+	+	-	+	+	+	-	-	-	+	-	+
		Auchenoglanis occidentalis	-	+	+	-	-	-	+	+	-	+	-	+	-	+	-
	Schilbeidae	*Schilbe mystus*	+	-	+	-	+	-	-	-	-	+	-	-	+	+	+
		Schilbe intermedius	-	-	+	+	-	-	+	+	+	-	+	-	+	-	+
	Malapteruridae	*M. electricus*	+	-	+	-	-	-	-	+	-	-	-	-	-	-	+
Characiformis	Citharinidae	*Citharinus citharus*	+	+	+	+	+	+	-	+	+	+	-	+	+	+	+
		Distichodus rustratus	-	-	+	+	-	-	-	+	+	+	+	-	+	+	+
	Alestidae	*Brycinus nurse*	-	-	+	-	-	-	+	-	-	+	-	-	+	-	+
		B. macrolepidotus	+	-	+	+	+	-	-	-	+	-	-	-	-	+	+
		Hydrocynus forskhalii	+	-	+	+	-	-	+	-	+	-	+	+	+	+	+
		Alestes baremoze	+	+	+	+	+	-	-	-	-	+	+	+	+	+	-
		Alestes leuciscus	+	-	-	-	+	-	-	-	+	-	+	-	-	-	-
		Paraillia pellucida	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Tetraondontiformes	Tetraodontidae	*Tetraodon lineatus*	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+
Anabantiformes	Channidae	*Parachanna obscura*	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-

Appendix 2 (Continues)

Order	**Family**	**Taxon**	**Yauri**	**Wawu**	**Shagun**	**Yuna**	**Fakun**	**Awuru**	**Jebba**	**Itobe**	**Idah**	**Agene**	**Illushi**	**Ugbolulu**	**Onitsha**	**Patani**	**Ogbia**
Polypteriformes	Polypteridae	*Polypterus senegalus*	-	-	+	-	-	-	-	-	-	-	+	-	-	+	-
Lepidosireniformes	Protopteridae	*Protopterus annectens*	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Perciformes	Centropomidae	*Lates niloticus*	+	+	+	+	+	+	+	+	-	-	+	+	+	+	+
Osteoglossiformes	Gymnarchidae	*Gymnarchus niloticus*	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-
	Mormyridae	*Marcusenius senegalensis*	+	-	+	+	-	+	+	-	+	-	+	+	+	-	-
		Hyperopisus bebe	+	-	+	+	+	+	+	-	-	-	+	+	-	+	+
		Mormyrops deliciousus	-	+	-	-	+	-	+	+	-	-	+	+	+	-	+
		Mormyrus rume	+	+	+	+	-	-	+	+	+	+	+	+	+	+	+
		Gnathenomus petersii	-	+	-	-	-	-	-	-	+	-	-	+	+	+	-
		Petrocephalus bane	-	-	+	-	-	-	-	-	-	-	+	+	+	-	-
	Osteoglosidae	*Heterotis niloticus*	-	-	-	-	-	-	-	+	-	-	-	-	+	+	+
Cypriniformes	Cyprinidae	*Labeo senegalensis*	+	-	+	-	+	-	+	-	+	+	+	-	+	+	-
		Labeo coubie	-	+	+	+	+	-	+	+	-	+	+	+	+	+	+
Cichliformes	Cichlidae	*Oreochromis niloticus*	+	+	+	+	+	+	-	-	+	+	+	+	+	+	-
		Tilapia zillii	-	-	+	+	-	-	-	+	-	+	+	-	+	-	+
		Hemichromis fasciatus	-	-	+	+	-	-	-	-	+	-	-	-	-	-	-
		Sarotherodon galilaeus	-	+	+	+	-	+	+	+	-	-	-	-	-	-	-

Appendix 3: Fish species composition and abundance at the upper region of the LNRB during the dry season

Order	Family	Taxon	Number	Abundance (%)
Siluriformes	Clariidae (5.09%)	*Clarias gariepinus*	25	2.77
		Heterobranchus bidorsalis	21	2.32
	Synodontidae (8.75 %)	*Synodontis membranaceus*	62	6.87
		Synodontis occelifer	0	0
		Synodontis schall	2	0.22
		Synodontis couteti	15	1.66
		Synodontis eupterus	0	0
	Bagridae (7.74 %)	*Chrysichthys nigrodigitatus*	31	3.43
		Bagrus bayad	30	3.32
		Bagrus dormac	3	0.33
		Clarotes laticeps	4	0.44
		Auchenoglanis occidentalis	2	0.22
	Schilbeidae (4.43 %)	*Schilbe mystus*	0	0
		Schilbe intermedius	40	4.43
	Malapteruridae (0.55 %)	*Malapterurus electricus*	5	0.55
Characiformes	Citharinidae (12.18 %)	*Citharinus citharus*	103	11.41
		Distichodus rustratus	7	0.77
	Alestidae (7.31 %)	*Brycinus nurse*	12	1.33
		Brycinus macrolepidotus	24	2.66
		Hydrocyanus forskhalii	0	0
		Alestes baremoze	28	3.10
		Alestes leuciscus	2	0.22
		Paraillia pellucida	0	0

Appendix 3 (Continues)

Order	**Family**	**Taxon**	**Number**	**Abundance (%)**
Tetraodontiformes	Tetraodontidae	*Tetraodon lineatus*	0	0
Anabantiformes	Channidae	*Parachanna obscura*	0	0
Polypteriformes	Polypteridae (0.11 %)	*Polypterus senegalus*	1	0.11
Lepidosireniformes	Protopteridae (0.33 %)	*Protopterus annectens*	3	0.33
Order	Families	Taxa	Number	Abundance (%)
Perciformes	Centropomidae (3.76 %)	*Lates niloticus*	34	3.76
Osteoglosiformes	Gymnarchidae (0.55 %)	*Gymnarchus niloticus*	5	0.55
	Mormyridae (11.95 %)	*Marcusenius senegalensis*	6	0.66
		Hyperopisus bebe	50	5.54
		Mormyrops deliciousus	15	1.66
		Mormyrus rume	33	3.65
		Gnathenomus petersii	4	0.44
		Petrocephalus bane	0	0
	Osteoglosidae	*Heterotis niloticus*	0	0
Cypriniformes	Cyprinidae (4.32 %)	*Labeo senegalensis*	4	0.44
		Labeo cubie	35	3.88
Cichliformes	Cichlidae (32.79%)	*Oreochromis niloticus*	182	20.17
		Tilapia zillii	34	3.76
		Hemichromis fasciatus	5	0.55
		Sarotherodon galilaeus	75	8.31
			902	**100**

Appendix 4: Fish species composition and abundance at the upper region of the LNRB during the rainy season

Order	Family	Taxon	Number	Abundance (%)
Siluriformes	Clariidae (1.63%)	*Clarias gariepinus*	10	1.49
		Heterobranchus bidorsalis	1	0.14
	Synodontidae (17.45 %)	*Synodontis membranaceus*	88	13.13
		Synodontis occelifer	0	0
		Synodontis schall	29	4.32
		Synodontis couteti	0	0
		Synodontis eupterus	0	0
	Bagridae (12.81 %)	*Chrysichthys nigrodigitatus*	41	6.11
		Bagrus bayad	7	1.04
		Bagrus dormac	4	0.59
		Clarotes laticeps	9	1.34
		Auchenoglanis occidentalis	32	4.77
	Schilbeidae (14.17 %)	*Schilbe mystus*	53	7.91
		Schilbe intermedius	42	6.26
	Malapteruridae	*Malapterurus electricus*	0	0
Characiformes	Citharinidae (5.21 %)	*Citharinus citharus*	28	4.17
		Distichodus rustratus	7	1.04
	Alestidae (11.91 %)	*Brycinus nurse*	29	4.32
		Brycinus macrolepidotus	1	0.14
		Hydrocyanus forskhalii	34	5.07
		Alestes baremoze	13	1.94
		Alestes leuciscus	3	0.44
		Paraillia pellucida	0	0
Tetraodontiformes	Tetraodontidae	*Tetraodon lineatus*	0	0
Anabantiformes	Channidae	*Parachanna obscura*	0	0
Polypteriformes	Polypteridae (0.29 %)	*Polypterus senegalus*	2	0.29
Lepidosireniformes	Protopteridae	*Protopterus annectens*	0	0

Appendix 4 (Continues)

Order	Families	Taxa	Number	Abundance (%)
Perciformes	Centropomidae (4.77%)	*Lates niloticus*	32	4.77
Osteoglosiformes	Gymnarchidae	*Gymnarchus niloticus*	0	0
	Mormyridae (15.79 %)	*Marcusenius senegalensis*	17	2.53
		Hyperopisus bebe	49	7.31
		Mormyrops deliciousus	6	0.89
		Mormyrus rume	29	4.32
		Gnathenomus petersii	0	0
		Petrocephalus bane	5	0.74
	Osteoglosidae	*Heterotis niloticus*	0	0
Cypriniformes	Cyprinidae (11.78 %)	*Labeo senegalensis*	34	5.07
		Labeo cubie	45	6.71
Cichliformes	Cichlidae (2.97%)	*Oreochromis niloticus*	0	0
		Tilapia zillii	0	0
		Hemichromis fasciatus	6	0.89
		Sarotherodon galilaeus	14	2.08
			670	**100**

Appendix 5: Fish species composition and abundance at the lower region of the LNRB during the dry season

Order	Family	Taxon	Number	Abundance (%)
Siluriformes	Clariidae (5.11%)	*Clarias gariepinus*	73	4.61
		Heterobranchus bidorsalis	8	0.5
	Synodontidae (14.39 %)	*Synodontis membranaceus*	90	5.68
		Synodontis occelifer	44	2.78
		Synodontis schall	94	5.93
		Synodontis couteti	0	0
		Synodontis eupterus	0	0
	Bagridae (16.54 %)	*Chrysichthys nigrodigitatus*	73	4.61
		Bagrus bayad	76	4.80
		Bagrus dormac	35	2.21
		Clarotes laticeps	36	2.27
		Auchenoglanis occidentalis	42	2.65
	Schilbeidae (5.49 %)	*Schilbe mystus*	87	5.49
		Schilbe intermedius	0	0
	Malapteruridae (0.18 %)	*Malapterurus electricus*	3	0.18
Characiformes	Citharinidae (12.81 %)	*Citharinus citharus*	169	10.67
		Distichodus rustratus	34	2.14
	Alestidae (10.64 %)	*Brycinus nurse*	66	4.16
		Brycinus macrolepidotus	0	0
		Hydrocyanus forskhalii	23	1.45
		Alestes baremoze	40	2.52
		Alestes leuciscus	12	0.75
		Paraillia pellucida	28	1.76
Tetraodontiformes	Tetraodontidae (0.31 %)	*Tetraodon lineatus*	5	0.31
Anabantiformes	Channidae (0.18 %)	*Parachanna obscura*	3	0.18
Polypteriformes	Polypteridae	*Polypterus senegalus*	0	0
Lepidosireniformes	Protopteridae	*Protopterus annectens*	0	0

Appendix 5 (Continues)

Order	Family	Taxon	Number	Abundance (%)
Perciformes	Centropomidae (1.07 %)	*Lates niloticus*	17	1.07
Osteoglosiformes	Gymnarchidae	*Gymnarchus niloticus*	0	0
	Mormyridae (10.96 %)	*Marcusenius senegalensis*	31	1.95
		Hyperopisus bebe	18	1.13
		Mormyrops deliciousus	7	0.44
		Mormyrus rume	75	4.73
		Gnathenomus petersii	25	1.57
		Petrocephalus bane	34	2.14
	Osteoglosidae (1.13 %)	*Heterotis niloticus*	18	1.13
Cypriniformes	Cyprinidae (9.02 %)	*Labeo senegalensis*	2	0.12
		Labeo cubie	141	8.90
Cichliformes	Cichlidae (10.65 %)	*Oreochromis niloticus*	69	4.04
		Tilapia zillii	72	4.54
		Hemichromis fasciatus	3	0.18
		Sarotherodon galilaeus	30	1.89
			1583	**100**

Appendix 6: Fish species composition and abundance at the lower region of the LNRB during the rainy season

Order	Families	Taxa	Number	Abundance (%)
Siluriformes	Clariidae (1.07%)	*Clarias gariepinus*	4	0.61
		Heterobranchus bidorsalis	3	0.46
	Synodontidae (25.8 %)	*Synodontis membranaceus*	42	6.45
		Synodontis occelifer	2	0.31
		Synodontis schall	117	17.97
		Synodontis couteti	2	0.31
		Synodontis eupterus	5	0.76
	Bagridae (14.11 %)	*Chrysichthys nigrodigitatus*	16	2.45
		Bagrus bayad	65	9.98
		Bagrus dormac	6	0.92
		Clarotes laticeps	5	0.76
		Auchenoglanis occidentalis	0	0
	Schilbeidae (8.75 %)	*Schilbe mystus*	4	0.61
		Schilbe intermedius	53	8.14
	Malapteruridae (0.46 %)	*Malapterurus electricus*	3	0.46
Characiformes	Citharinidae (9.36 %)	*Citharinus citharus*	31	4.76
		Distichodus rustratus	30	4.6
	Alestidae (10.58 %)	*Brycinus nurse*	7	1.07
		Brycinus macrolepidotus	6	0.92
		Hydrocyanus forskhalii	34	5.22
		Alestes baremoze	22	3.37
		Alestes leuciscus	0	0
		Paraillia pellucida	0	0
Tetraodontiformes	Tetraodontidae	*Tetraodon lineatus*	0	0
Anabantiformes	Channidae	*Parachanna obscura*	0	0
Polypteriformes	Polypteridae (1.53 %)	*Polypterus senegalus*	10	1.53
Lepidosireniformes	Protopteridae	*Protopterus annectens*	0	0

Appendix 6 (Continues)

Order	Families	Taxa	Number	Abundance (%)
Perciformes	Centropomidae (1.69 %)	*Lates niloticus*	11	1.69
Osteoglosiformes	Gymnarchidae	*Gymnarchus niloticus*	0	0
	Mormyridae (9.36 %)	*Marcusenius senegalensis*	0	0
		Hyperopisus bebe	6	0.92
		Mormyrops deliciousus	14	2.15
		Mormyrus rume	34	5.22
		Gnathenomus petersii	7	1.07
		Petrocephalus bane	0	0
	Osteoglosidae	*Heterotis niloticus*	0	0
Cypriniformes	Cyprinidae (8.44 %)	*Labeo senegalensis*	28	4.30
		Labeo cubie	27	4.14
Cichliformes	Cichlidae (8.75 %)	*Oreochromis niloticus*	45	6.91
		Tilapia zillii	12	1.84
		Hemichromis fasciatus	0	0
		Sarotherodon galilaeus	0	0
			651	**100**

Appendix 7: Phytoplankton species composition and abundance at the upper region of the LNRB during the dry season

Families	Taxon	Total (cell/L)	Abundance (%)
Baccillanophyceae	*Synedra* sp	800	2.07
	Achnanthes clevei	0	
	Asteronella sp.	0	
	Cymbella similis	0	
	Cylindrotheca closterium	0	
	Leptocylindrus danicus	0	
	Melosira granulate	830	2.15
	Fragillana sp.	500	1.29
	Navicula sp.	330	0.85
	Nitzchia sp.	0	
	Surirella angustata	100	0.25
	Pinnularia gibba	0	
	Pleurosigma delicatula	0	
	Meridion circulare	0	
	Meuniera membranaceae	0	
	Ophiocytium parculum	20	0.05
	Diatomella sp.	400	1.03
		2980	**7.73**
Chlorophyceae	*Tetraspora* sp.	3600	9.33
	Zygnema sp.	0	
	Microspora sp.	500	1.29
	Actinastrum gracilum	0	
	Cerastrias staurastria	0	
	Cosmarium sp.	0	
	Hematococcus lacustria	0	
	Ulothrix sp.	0	
	Pediastrum simplex	500	1.29
	Chlorella sp.	7900	20.49
	Selenastrium sp.	0	0
	Hormidium sp.	1700	4.40
	Staurastrum sp.	300	0.75
	Volvox sp.	220	0.57
	Spirogyra sp.	2600	6.74
	Mougeotia sp.	0	
	Scenedesmus incrasatucus	100	0.25
	Haematococcus lacustria	0	
	Quadrigula closteriopsis	0	
		17420	**45.18**

Appendix 7 (Continues)

Families	Taxon	Total (cell/L)	Abundance (%)
Cyanophyceae	*Spirulina* sp	180	0.46
	Chrooccus sp	0	
	Durvilla Antarctica	0	
	Merismopedia sp	0	
	Anabeana sp	200	0.50
	Aphanocapsa sp	100	0.25
	Oscillatoria sp	700	1.81
	Anacytis sp	2600	6.74
	Athrospira sp	9500	24.64
	Microcytis sp	4500	11.67
		17780	**46.12**
Pyrrophyceae	*Amphidinium sphenoides*	50	0.12
	Micracanthodium claytonii	220	0.57
	Ceratulinia pelagica	100	0.25
		370	**0.95**
		38,550	**100**

Appendix 8: Phytoplankton species composition and abundance at the upper region of the LNRB during the rainy season

Family	Taxon	Total (cell/L)	Abundance (%)
Baccillanophyceae	*Synedra* sp	700	3.79
	Achnanthes clevei	0	
	Asteronella sp.	0	
	Cymbella similis	0	
	Cylindrotheca closterium	0	
	Leptocylindrus danicus	50	0.27
	Melosira granulate	330	1.78
	Fragillana sp.	550	2.97
	Navicula sp.	250	1.35
	Nitzchia sp.	150	0.81
	Surirella angustata	50	0.27
	Pinnularia gibba	0	
	Pleurosigma delicatula	0	
	Meridion circulare	0	
	Meuniera membranaceae	0	
	Ophiocytium parculum	70	0.27
	Diatomella sp.	400	2.16
		2550	**13.81**
Chlorophyceae	*Tetraspora* sp.	2300	12.45
	Zygnema sp.	0	
	Microspora sp.	300	1.62
	Actinastrum gracilum	0	
	Cerastrias staurastria	0	
	Cosmarium sp.	0	
	Hematococcus lacustria	0	
	Ulothrix sp.	0	
	Pediastrum simplex	230	1.24
	Chlorella sp.	2400	13.00
	Selenastrium sp.	120	0.65
	Hormidium sp.	450	2.43
	Staurastrum sp.	100	0.54
	Volvox sp.	270	1.46
	Spirogyra sp.	1150	6.22
	Mougeotia sp.	0	
	Scenedesmus incrasatucus	110	0.59
	Haematococcus lacustria	0	
	Quadrigula closteriopsis	0	
		8000	**43.33**

Appendix 8 (Continues)

Family	Taxon	Total (cell/L)	Abundance (%)
Cyanophyceae	*Spirulina* sp	130	0.70
	Chrooccus sp	0	
	Durvilla Antarctica	0	
	Merismopedia sp	0	
	Anabeana sp	100	0.54
	Aphanocapsa sp	0	
	Oscillatoria sp	300	1.62
	Anacytis sp	1070	5.79
	Athrospira sp	3550	19.23
	Microcytis sp	2510	13.59
		7660	**41.19**
Pyrrophyceae	*Amphidinium sphenoides*	250	1.35
	Micracanthodium claytonii	60	0.32
	Ceratulinia pelagica	10	0.05
		320	**1.73**
		18460	**100**

Appendix 9: Phytoplankton species composition and abundance at the lower region of the LNRB during the dry season

Families	Taxon	Total (cell/L)	Abundance (%)
Baccillanophyceae	*Synedra* sp	1300	2.86
	Achnanthes clevei	300	0.66
	Asteronella sp.	1150	2.53
	Cymbella similis	770	1.69
	Cylindrotheca closterium	450	0.99
	Leptocylindrus danicus	300	0.66
	Melosira granulate	690	1.52
	Fragillana sp.	600	1.30
	Navicula sp.	700	1.54
	Nitzchia sp.	700	1.57
	Surirella angustata	700	1.54
	Pinnularia gibba	100	0.22
	Pleurosigma delicatula	350	0.77
	Meridion circulare	280	0.61
	Meuniera membranaceae	410	0.90
	Ophiocytium parculum	300	0.66
	Diatomella sp.	700	1.54
		9800	**21.59**
Chlorophyceae	*Tetraspora* sp.	4700	10.35
	Zygnema sp.	1050	2.31
	Microspora sp.	2700	5.94
	Actinastrum gracilum	400	0.88
	Cerastrias staurastria	450	0.99
	Cosmarium sp.	300	0.66
	Hematococcus lacustria	980	2.15
	Ulothrix sp.	500	1.10
	Pediastrum simplex	300	0.66
	Chlorella sp.	7700	16.96
	Selenastrium sp.	100	0.22
	Hormidium sp.	760	1.67
	Staurastrum sp.	600	1.30
	Volvox sp.	510	1.12
	Spirogyra sp.	3200	7.05
	Mougeotia sp.	200	0.44
	Scenedesmus incrasatucus	330	0.72

Appendix 9 (Continues)

Families	Taxon	Total (cell/L)	Abundance (%)
	Haematococcus lacustria	100	0.22
	Quadrigula closteriopsis	300	0.66
		25280	**55.69**
Cyanophyceae	*Spirulina* sp	300	0.66
	Chrooccus sp	500	1.10
	Durvilla Antarctica	350	0.77
	Merismopedia sp	1580	3.48
	Anabeana sp	560	1.23
	Aphanocapsa sp	250	0.55
	Oscillatoria sp	260	0.57
	Anacytis sp	2700	5.94
	Athrospira sp	200	0.44
	Microcytis sp	3100	6.82
		9800	**21.59**
Pyrrophyceae	*Amphidinium sphenoides*	220	0.48
	Micracanthodium claytonii	280	0.61
	Ceratulinia pelagica	110	0.25
		610	**1.34**
		45390	**100**

Appendix 10: Phytoplankton species composition and abundance at the lower region of the LNRB during the rainy season

Families	Taxon	Total (cell/L)	Abundance (%)
Baccillanophyceae	*Synedra* sp	1700	3.17
	Achnanthes clevei	450	0.98
	Asteronella sp.	750	1.64
	Cymbella similis	970	2.12
	Cylindrotheca closterium	590	1.29
	Leptocylindrus danicus	500	1.09
	Melosira granulate	750	1.64
	Fragillana sp.	850	1.85
	Navicula sp.	600	1.31
	Nitzchia sp.	800	1.74
	Surirella angustata	600	1.31
	Pinnularia gibba	50	0.10
	Pleurosigma delicatula	700	1.57
	Meridion circulare	500	1.09
	Meuniera membranaceae	450	0.98
	Ophiocytium parculum	50	0.10
	Diatomella sp.	700	1.57
		11010	**24.07**
Chlorophyceae	*Tetraspora* sp.	4300	9.40
	Zygnema sp.	580	1.26
	Microspora sp.	3250	7.10
	Actinastrum gracilum	600	1.31
	Cerastrias staurastria	450	0.98
	Cosmarium sp.	200	0.42
	Hematococcus lacustria	800	1.74
	Ulothrix sp.	550	1.20
	Pediastrum simplex	200	0.42
	Chlorella sp.	8800	19.24
	Selenastrium sp.	0	0
	Hormidium sp.	730	1.59
	Staurastrum sp.	700	1.57
	Volvox sp.	260	0.56
	Spirogyra sp.	2250	4.92
	Mougeotia sp.	100	0.21
	Scenedesmus incrasatucus	410	0.89

Appendix 10 (Continues)

Families	Taxon	Total (cell/L)	Abundance (%)
	Haematococcus lacustria	100	0.21
	Quadrigula closteriopsis	250	0.54
		24530	**53.64**
Cyanophyceae	*Spirulina* sp	200	0.43
	Chrooccus sp	380	0.83
	Durvilla Antarctica	400	0.87
	Merismopedia sp	600	1.31
	Anabeana sp	560	1.22
	Aphanocapsa sp	570	1.24
	Oscillatoria sp	250	0.54
	Anacytis sp	3200	6.99
	Athrospira sp	300	0.65
	Microcytis sp	3100	6.77
		9560	**20.90**
Pyrrophyceae	*Amphidinium sphenoides*	270	0.59
	Micracanthodium claytonii	220	0.48
	Ceratulinia pelagica	140	0.30
		630	**1.37**
		45730	**100**

Appendix 11: Phytoplankton species of the entire basin of LNRB, Nigeria

Family	Taxon	Total (cell/L)	% Abundance
Baccillanophyceae	*Synedra sp*	2100	**18.06**
	Achnanthes clevei	300	
	Asteronella sp.	1150	
	Cymbella similis	770	
	Cylindrotheca closterium	450	
	Leptocylindrus danicus	300	
	Melosira granulate	1520	
	Fragillana sp.	1100	
	Navicula sp.	1030	
	Nitzchia sp.	700	
	Surirella angustata	800	
	Pinnularia gibba	100	
	Pleurosigma delicatula	350	
	Meridion circulare	280	
	Meuniera membranaceae	410	
	Ophiocytium parculum	320	
	Diatomella sp.	1100	
		26830	
Chlorophyceae	*Tetraspora sp.*	8300	**50.27**
	Zygnema sp.	1050	
	Microspora sp.	3200	
	Actinastrum gracilum	400	
	Cerastrias staurastria	450	
	Cosmarium sp.	300	
	Hematococcus lacustria	980	
	Ulothrix sp.	500	
	Pediastrum simplex	800	
	Chlorella sp.	15600	
	Selenastrium sp.	200	
	Hormidium sp.	2460	
	Staurastrum sp.	900	
	Volvox sp.	730	
	Spirogyra sp.	5800	
	Mougeotia sp.	200	
	Scenedesmus incrasatucus	430	
	Haematococcus lacustria	100	
	Quadrigula closteriopsis	300	
		74660	
Cyanophyceae	*Spirulina sp*	480	**30.36**
	Chrooccus sp	500	

Appendix 11 (Continues)

Family	Taxon	Total (cell/L)	% Abundance
	Durvilla Antarctica	350	
	Merismopedia sp	1580	
	Anabeana sp	760	
	Aphanocapsa sp	350	
	Oscillatoria sp	1160	
	Anacytis sp	5300	
	Athrospira sp	9800	
	Microcytis sp	7600	
		45100	
Pyrrophyceae	*Amphidinium sphenoides*	270	**1.30**
	Micracanthodium claytonii	500	
	Ceratulinia pelagica	210	
		1930	
		148,520	**100**

Appendix 12: Macroinvertebrate species of the LNRB, Nigeria

Order	Family	Taxon	Number	Abundance (%)
Ephemeroptera	Beatidae	*Pseudocloeon sp*	76 (3.1%)	411 (16.73)
		Bugillisia sp	105 (4.27%)	
		Cloen sp	65 (2.64%)	
		Crassabwa sp	49 (2%)	
		Afroaetis sp	117 (4.76%)	
	Leptophilebiidae	*Thraulus sp*	51 (2.1%)	450 (18.32)
		Adenophleboides sp	84 (3.42%)	
		Choroterps sp	58 (2.36%)	
	Tricorythidae	*Diceromyzon sp*	69 (2.81%)	
		Tricorythus sp	33 (1.34%)	
	Caenidae	*Caenis sp*	96 (3.91%)	
	Oligoneuridae	*Oligoneux sp*	59 (2.40%)	
Oligochaeta	Naididae	*Dero digitate*	73 (2.97%)	177 (7.20)
		Stylaria lacustris	104 (4.23%)	
Gastropoda	Thiaridae	*Melanoides tuberculata*	71 (2.89%)	156 (6.34)
	Sphaeriidae	*Shaerudux sp*	85 (3.46%)	
Araneae	Pisauridae	*Thalassius sp*	47 (1.91%)	47 (1.91)
Trichoptera	Leptoceridae	*Leptocerina sp*	24 (0.97%)	45 (1.83)
	Hydroptillidae	*Leptonema sp*	21 (0.85%)	
Hemiptera	Belostomatidae	*Apassus sp*	65 (2.65%)	169 (6.87)
	Gerridae	*Naboandelus africanus*	44 (1.79%)	
	Neptidae	*Ranatra sp*	38 (1.55%)	
	Naucoridae	*Macrocoris sp*	22 (0.90%)	
Coleoptera	Dystiscidae	*Hyphydrus sp*	80 (3.26%)	449 (18.27)
		Cybister sp	40 (1.63%)	

Appendix 12 (Continues)

Order	**Family**	**Taxon**	**Number**	**Abundance (%)**
		Philaccolus sp	72 (2.93%)	
	Hydrophilidae	*Amphiops sp*	113 (4.60%)	
	Notonectidae	*Hydrocanthus sp*	50 (2.04%)	
	Gyrinidae	*Orectogyrus sp*	94 (3.83%)	
Diptera	Chironomidae	*Chironomus sp*	156 (6.36%)	386 (15.71)
		Pentaneura sp	75 (3.05%)	
		Tanypus sp	83 (3.38%)	
	Simulidae	*Simulium sp*	21 (0.85%)	
	Athericidae	*Atherix sp*	28 (1.14%)	
	Ceratopogonidae	*Alladomyia sp*	23 (0.94%)	
Odonata	Calapteryggidae	*calapteryx sp*	27 (1.10%)	166 (6.76 %)
	Libellulidae	*Orthetrum sp*	37 (1.51%)	
		Zyxoma sp	42 (1.83%)	
	Gomphidae	*Lestigomphus sp*	25 (1.02%)	
	Coenagrionidae	*Enattagma sp*	35 (1.42%)	
			2457	**100 %**