



Plankton Diversity in Tropical Wetlands Under Different Hydrological Conditions (Lake Tana, Ethiopia)

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Plankton is an integral part of wetland biodiversity and plays a vital role in the functioning of wetlands. Diversity patterns of plankton in wetlands and factors structuring its community composition are poorly understood, albeit important for identifying areas for restoration and conservation. Here we investigate patterns in local and regional plankton richness and taxonomic and functional community composition in riverine papyrus swamps, river mouth wetlands, and lacustrine wetlands in the Lake Tana sub-basin, Ethiopia. Data on phytoplankton, zooplankton, and environmental variables were collected from 12 wetlands during the dry and wet seasons of 2018. Redundancy analysis, and linear mixed effect models, were used to investigate differences in local environmental conditions and variation in plankton community richness and composition between wetland types. We also assessed the ecological uniqueness of the plankton community by calculating the contribution of a single wetland: local contributions to overall beta diversity (LCBD) and contributions of individual species (SCBD) to overall beta diversity (BD_{Total}). Beta regression models were used to investigate the relationships of LCBD and SCBD to environmental variables, wetland, and taxa characteristics. A total of 85 phytoplankton taxa, distributed among 18 Reynolds functional groups, and 57 zooplankton taxa were observed over the entire set of samples. Local plankton taxon richness was significantly higher in riverine papyrus swamps (mean taxa of 30 phytoplankton and 21 zooplankton) compared to river mouth wetlands (mean taxa of 27 phytoplankton and 13 zooplankton). Several local environmental variables and the composition of the plankton community differed significantly between the three wetland types. The highest phytoplankton ecological uniqueness (LCBD) was detected in lacustrine wetlands, whereas the riverine papyrus swamps had the highest zooplankton ecological uniqueness. Based on our analyses, we recommend protecting the wetlands with high LCBD values and stress the importance of various wetland types for preserving the diverse plankton communities of Lake Tana wetlands.

Keywords: Lake Tana, Zooplankton, Phytoplankton, wetlands, community composition, species richness

INTRODUCTION

Wetlands are one of the most productive habitats and are of immense socio-economic and ecological importance (De Groot et al., 2012) because they provide a wide range of ecosystem services such as groundwater recharge, water purification, nutrient cycling, shoreline stabilization, cultural, recreational, and educational resources, flood protection, and carbon storage (Everard et al., 2019). Wetlands also host exceptionally high levels of biodiversity, which is attributed to their high spatial and temporal environmental heterogeneity (Keddy et al., 2009). Wetlands are home to numerous organisms including phytoplankton and zooplankton species (hereafter: plankton) (D'Ambrosio et al., 2016; Gogoi et al., 2019), macroinvertebrates (Mereta et al., 2013; Gezie et al., 2019), aquatic plants (Getnet et al., 2021), fish (Aziz et al., 2021), amphibians (Nagel et al., 2021), waterbirds (Aynalem and Bekele, 2008; Chawaka et al., 2018a; Chawaka et al., 2018b), and mammals (Chatterjee and Bhattacharyya, 2021). Phytoplankton form the base of the food chain in aquatic ecosystems and play an important role in overall wetland productivity (Chengxue et al., 2019), while zooplankton are recognized as the main primary consumers. Due to their short life cycle and thus potentially rapid response to anthropogenic disturbance and environmental changes, planktonic organisms are also regarded as ideal bioindicators for assessing the environmental status of wetlands (Wijeyaratne and Nanayakkara, 2020; Chaparro-Herrera et al., 2021).

The plankton community structure differs between tropical and temperate lakes, but research on wetlands is still limited. One of these differences is that smaller zooplankton species (including rotifers) often predominate in tropical lakes, whereas large cladocerans are dominant in temperate lakes (Fernando, 1980; Green, 1994). However, in some Ethiopian tropical highland lakes, the zooplankton communities are dominated by large Cladocerans (Dejen et al., 2004; Fetahi et al., 2011; Haileeselasie et al., 2012). In temperate lakes, diatoms often dominate the phytoplankton community during winter and phytoflagellates during the summer (Widdicombe et al., 2010). Chlorophyta and Cyanophyta, as well as diatoms in some cases, generally dominate tropical lakes (Ndebele-Murisa et al., 2010). Wide temperature and light intensity fluctuations are widely regarded as the primary drivers of variation in plankton community structure in temperate systems, whereas hydrological conditions are important in the tropical systems (Loverde-Oliveira et al., 2009; Shatwell et al., 2016).

Hydrological conditions, such as water availability and depth in wetlands affect the interchange of water, sediment, nutrients, organic matter, and organisms between the wetlands and their adjacent water bodies (i.e., river, river-lake, or lake; Chaparro et al., 2018; Feng et al., 2021; Rideout et al., 2021). During high water level periods, inputs from the river, and lake water can also modify local environmental conditions in wetlands by altering dissolved oxygen concentration, conductivity, turbidity, and nutrient levels (Alvarez-mieles et al., 2013; Castillo, 2020). Conversely, during periods of isolation or lower exchange with the river and lake, environmental conditions in the wetlands may

be largely driven by autochthonous processes occurring in the water column of the wetland (Cardoso et al., 2012). Thus, variation in hydrological conditions in wetlands results in highly heterogeneous habitats at the wetland scale, ranging from lotic to lentic, turbid to clear water, nutrient-rich to nutrient-poor, frequently disturbed versus relatively stable, and well-vegetated to almost barren conditions (Chaparro et al., 2018). Consequently, plankton communities comprise a huge diversity of life-history traits that vary in response to the environmental conditions in the wetland. These range from small fast-growing phytoplankton taxa adapted to turbulent waters to large slow-growing organisms adapted to more stable conditions (Reynolds, 2002; Padišák et al., 2009; Bhat et al., 2015), and from pelagic filter-feeding to scraping zooplankton taxa associated with vegetation (Gebrehiwot et al., 2017a).

Wetlands can be found in all climatic regions of Ethiopia, with the wetlands of Lake Tana being the second largest in the country after the Gambella wetlands (Menbere and Menbere, 2018). In the Lake Tana sub-basin, wetlands are found mostly along lakeshores, rivers, and stream banks and cover 248 km² of land (Hunegnaw et al., 2013; Stave et al., 2017; Mengistu, 2018). Previous studies in the Lake Tana sub-basin were focused on the abundance and species richness of lake plankton (Dejen et al., 2004; Imoobe and Akoma, 2008; Gashaye, 2016; Melaku, 2017), fish, waterbirds, and mammals (Aynalem and Bekele, 2008; Mengistu, 2018; Zelelew and Archibald, 2021). Specifically for the wetlands in the sub-basin, benthic invertebrates (Gezie et al., 2017; Gezie et al., 2019), fish (Anteneh et al., 2012), macrophytes (Getnet et al., 2021), and water-birds (Aynalem and Bekele, 2008) have been studied. The capacity of these systems for sediment and nutrient retention has also been investigated (Mucheje et al., 2018). They act as a buffering zone, as nurseries for most of the fish populations in the lake, and as breeding and feeding grounds for waterfowl and mammals (Aynalem and Bekele, 2008; Getahun and Dejen, 2012; Zelelew and Archibald, 2021). Lake Tana and most of these wetlands are also a UNESCO Biosphere Reserve (Kalmbach, 2017) due to their high and unique biodiversity.

This study is focused on river-connected riverine papyrus swamps, river mouth wetlands at the interface between river and lake, and lake-connected lacustrine wetlands (Hunegnaw et al., 2013; Aynalem et al., 2017; Getnet et al., 2021). These wetlands are characterized by seasonal water level variations, which are mostly caused by the unimodal rainfall pattern in the area (Jemberie et al., 2015). The river mouth and lacustrine wetlands are increasingly threatened by livestock grazing and crop cultivation (Wondie, 2018; Abera et al., 2021; Chandrasekharan et al., 2021). Additional environmental pressures for river mouth wetlands are the infestation by the non-native floating water hyacinth (*Eichhornia crassipes*) (Asmare et al., 2020) and the accumulation of pollutants from nearby cities and human settlements (Abebe and Minale, 2017). Excessive water abstraction for small-scale irrigation, particularly at river mouth wetlands, is particularly common during the dry season (Abebe et al., 2020). Lake water level fluctuations caused

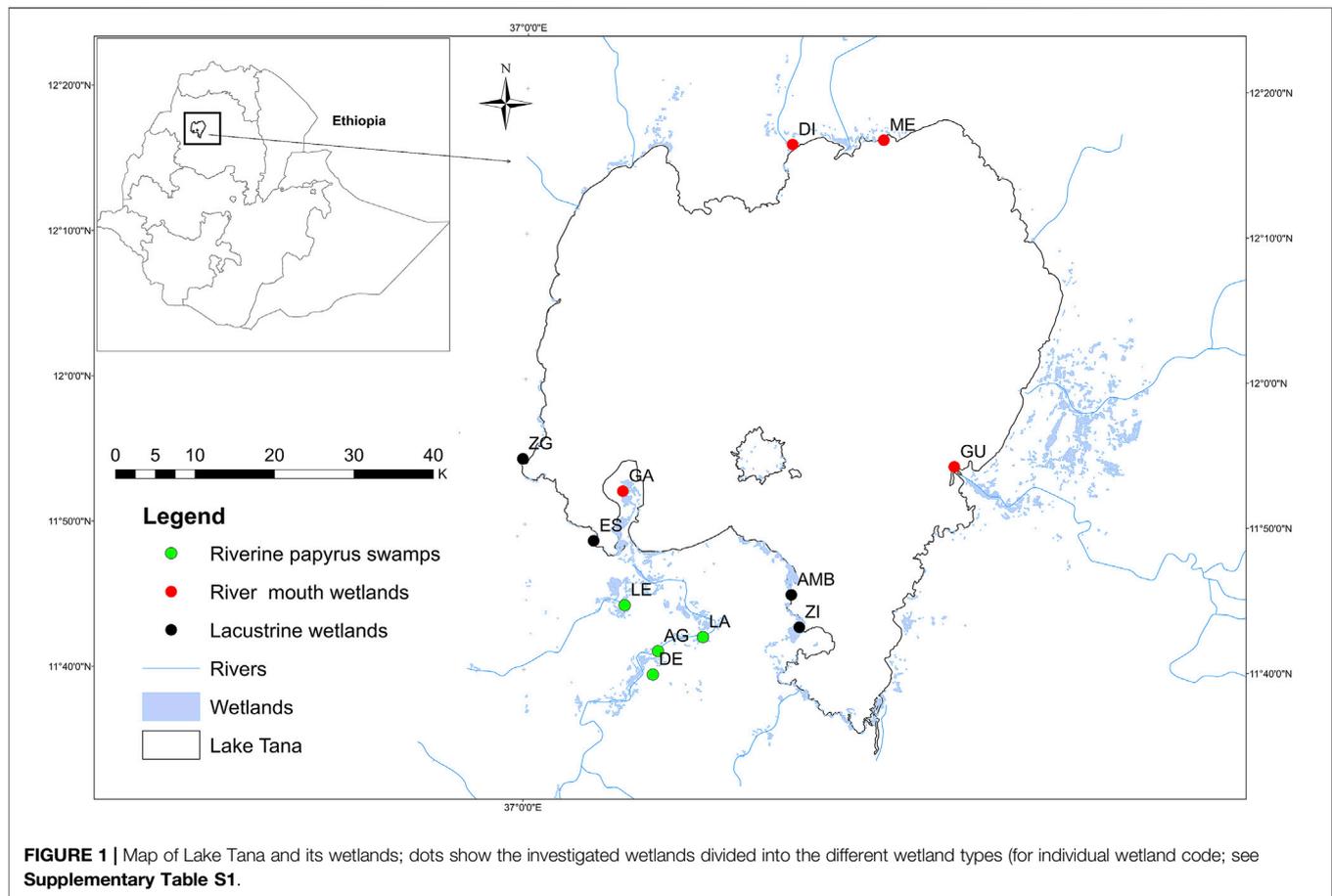


FIGURE 1 | Map of Lake Tana and its wetlands; dots show the investigated wetlands divided into the different wetland types (for individual wetland code; see **Supplementary Table S1**).

by lake water abstractions for major development projects in the sub-basin also had a significant impact on lacustrine wetlands (Alemayehu et al., 2010). These anthropogenic disturbances have been proven to influence the hydrological conditions in other lakes and consequently their plankton diversity (Gownaris et al., 2018; Napiórkowski et al., 2019), and therefore, can be expected to cause both temporal and spatial variation in plankton communities in wetlands of Lake Tana. Generally, plankton communities in wetlands under different hydrological conditions are less studied (but see Cardoso et al., 2012; Rojo et al., 2016; Chaparro et al., 2019). Similarly, plankton communities in Lake Tana wetlands under different hydrological conditions are poorly understood.

In this study, we examined differences in local taxonomic richness and the community composition of plankton, as well as the Reynolds functional phytoplankton composition among wetlands under different hydrological conditions. In addition, we aimed to identify wetlands that support unique plankton communities and therefore require special attention with respect to conservation and restoration. The wetlands studied were (i) riverine papyrus swamps (connected to rivers, R) with substantial papyrus stands, and distant from the lake; (ii) river mouth wetlands at the river-lake interface (connected both to the tributary rivers and the lake, RL), and (iii) lacustrine wetlands (only connected to the lake, L). We hypothesize that plankton

communities from wetlands under various hydrological conditions differ in their taxonomic richness and community composition and that relatively undisturbed wetlands (i.e., riverine papyrus swamps) are more diverse and unique than those influenced by human activities.

MATERIAL AND METHODS

Study Area

The Lake Tana sub-basin is located between 10.95° N to 12.78° N latitude and from 36.98° E to 38.25° E longitude in the highlands of northwestern Ethiopia (**Figure 1**). The sub-basin covers an area of 15,000 km², including the Lake, the largest surface water body in the country, with a total surface area of 3,080.8 km². It is 67 km wide, 84 km long and its mean depth is 9 m (Kebede et al., 2006). The seasonal variation in rainfall is controlled by the northward and southward movement of the intertropical convergence zone resulting in a single rainy season between June and October (Fetene et al., 2018). The hydrogeomorphology of the Lake Tana sub-basin is diverse, with alluvial sediments found in the lower reaches of the tributary rivers (Poppe et al., 2013). Approximately 4.5 million people are living adjacent to the lake and its associated wetlands. More than 500,000 people are directly and indirectly dependent



FIGURE 2 | Field pictures showing the typical habitats for riverine papyrus swamps (R), river mouth wetlands (RL), and lacustrine wetlands (L).

on the lake and its associated wetlands (Vijverberg et al., 2009). The land use in the Lake Tana basin is predominantly cultivated land (7,608.7 km²), water area (2,152.7 km²), bushland (1,438.9 km²), grassland (1,242.1 km²), and forest (546.9 km²) (Tewabe and Fentahun, 2020).

The wetlands of Lake Tana are permanent or seasonal with a total area of 248 km² and distributed from the headwaters of the Guna and Gish-Abay streams to the Fogera and Demba floodplains (Hunegnaw et al., 2013). The majority are located mainly around the lake shores, in the lower reaches of the Gilgel Abay River, and at the river mouths of Gilgel Abay, Ribb, Gumara, and Megech Rivers (Hunegnaw et al., 2013).

The three most common wetland types: riverine papyrus swamps, river mouth wetlands, and lacustrine wetlands in the Lake Tana sub-basin were studied (Figures 1, 2). A total of twelve wetlands (i.e., four wetlands from each wetland type) were selected (Supplementary Table S1). The riverine papyrus swamps sampled are mainly located in the lower reaches of the Gilgel Abay River and are dominated by papyrus (*Cyperus papyrus*) and other less dominant emergent vegetation (Getnet et al., 2021). With little grazing, settlement, or agricultural activity, these wetlands are characterized with >80% vegetation coverage (Wondie, 2018). These wetlands are permanent swamps

with little fluctuation in water level and remain flooded well into the dry season. River mouth wetlands are located at the entrance of the rivers Dirma, Gilgel-Abay, Gumara, and Megech into Lake Tana. The river mouth wetlands are influenced by both lake water levels fluctuation and river flows. During the dry season, most river mouth wetlands have very low water depths due to excessive water abstraction from the inflowing rivers for irrigation by local farmers. River mouth wetlands are characterized by some exotic species and grassy vegetation, with less than 20% cover. The river mouth wetlands included in this study, except the Gilgel Abay wetland, are infested with the non-native water hyacinth (*Eichhornia crassipes*) (Asmare et al., 2020). Rivers input a large amount of sediment into these wetlands, resulting in the formation of deltas in the majority of them (e.g., in the Gilgel Abay and Gumara wetlands) (Abate et al., 2017; Lemma et al., 2020). Lacustrine wetlands are mostly found on the lake's southern shores. Lacustrine wetlands have open water-dominated microhabitats with some emergent, submerged, and freely floating macrophyte species with plant cover ranging from 30 to 50%. The river mouth and lacustrine wetlands are home to 27 fish species, which belong to four families: Cichlidae, Clariidae, Nemacheilidae, and Cyprinidae (Dejen et al., 2017).

Field Sampling and Sample Analysis

Sampling for phytoplankton, zooplankton, and environmental variables was carried out from March to May 2018 (in the dry season) and July to October 2018 (in the wet season) in the 12 selected wetlands. A transect line was drawn using Google Earth in the middle part of each wetland ensuring that the entire width of the wetland was covered. In lacustrine and river mouth wetlands, transects started at the edge of the open water and ended at the most outward part of the emergent vegetation that is associated with the wetland. In the riverine papyrus swamp, transects perpendicular to the flow direction were established. Along each transect, 6 plots of 5 × 5 m, at equal distance from each other, were established and marked using GPS (GPSMAP® ×64). Dissolved oxygen, specific conductance, turbidity, pH, water temperature, water depth, and silt layer (hereafter: sediment depth) were measured from all established plots. Water temperature, pH, specific conductance, and dissolved oxygen were measured *in-situ* using Multi-probe field meter (YSI 556 MPS). Chlorophyll-a concentration was used as a proxy for phytoplankton biomass and was measured *in vivo* in the field using a handheld fluorometer (AquaFluor™, Turner Designs). Similarly, turbidity was measured in the field using an aqualytic Turbidimeter (ALT250-IR). Water depth and sediment depth were measured with a wooden stick and a metal measuring tape. For total nitrogen (TN) and total phosphorus (TP), 50 ml water samples were collected from each plot close to the water surface. Samples from different plots along the transect were pooled. The pooled water samples were kept cool in the dark in the field and frozen (−20°C) in the laboratory until further analysis (American Public Health Association, 2005). TN and TP concentrations were measured using a spectrophotometer (HACH, DR/6000) after alkaline persulfate digestion (American Public Health Association, 2005).

Water samples (200 ml) for phytoplankton analysis were collected from the surface of the wetland in each plot. Samples from different plots within each wetland were pooled and subsequently preserved with Lugol's iodine solution and stored in the dark. In the laboratory, the phytoplankton samples were sedimented for 48–72 h on a heat-free, vibration-free surface, and used for species identification and quantification (Bellinger et al., 2015). A total of 1,190 ml of the supernatant was removed, and the remaining 10 ml concentrated phytoplankton sample was used for further analysis. A 1 ml sub-sample was transferred into the Sedgwick-Rafter cell, which had 1,000 grids, after being fully homogenized by gentle inversion and agitation. Phytoplankton was identified to the species level using taxonomic literature (Tilman et al., 1986; Taylor et al., 2007; Bellinger et al., 2015) and an inverted microscope at a ×1,000 magnification (Krüss, A. Krüss Optronik, Germany). The numbers of phytoplankton cells (single-cell, filament, and colony) of different phytoplankton species in 100 random fields were determined (Hötzel and Croome, 1999).

Samples for zooplankton were collected from the surface of the wetland in each plot by filtering 40 L of water through a 64 µm mesh. Samples from different plots within each wetland were pooled and subsequently preserved in 4% formaldehyde solution

in the field and stored at 4°C. For identification and estimation of density, the concentrated initial sample was mixed homogeneously and a 1 ml subsample was taken with a wide opening Stempel pipette and then poured into a Sedgwick–rafter cell (Wetzel and Likens, 2013). This process was replicated until at least 300 rotifer individuals were counted. Additional subsamples were taken for Copepods and Cladocerans when the number of individuals was less than 50 for at least one species (Mack et al., 2012). Zooplankton was identified to the species level under a stereoscopic microscope at ×400 magnification, by using the relevant taxonomic literature (Idris, 1983; Van de Velde, 1984; Koste and Shiel, 1987; Koste and Shiel, 1989; Defaye, 1988; Sinev, 2016). Calanoids and cyclopoids were enumerated according to their developmental stages (adults, copepodites, and nauplii), whereas for rotifers and cladocerans all stages were counted as one age class.

Data Analysis

Data were analyzed using a combination of univariate and multivariate statistical methods. The environmental variables that were measured at several plots within each wetland were averaged for each wetland for the wet and dry seasons separately. Local diversity was calculated for each wetland as the local number of taxa (α - richness) in a given wetland) during the wet and dry seasons separately. Similarly, we determined regional taxon richness (γ -richness) as the total number of taxa across wetlands for the dry and wet seasons separately (Magurran, 2004). The recorded phytoplankton species were classified into *Reynolds Functional Groups* (RFGs) following Reynolds (2002) and updated by Padišák et al. (2009) to identify dominant functional groups in each wetland.

An ordination plot of a Principal component analysis (PCA) based on standardized and centered environmental data was used to visualize the relationship between environmental variables and wetland types during the dry and wet seasons. The overall effect of wetland type, season, and their interactions on environmental variables, plankton community composition, and Reynolds Functional groups was tested using redundancy analysis (RDA). The significance of RDA models was evaluated with 999 Monte Carlo permutations. The dependency of multiple observations within each wetland type was taken into account by restricting the permutations to blocks (**Supplementary Table S5**). Prior to these analyses, environmental variables were standardized by subtracting their mean and dividing by their standard deviation, whereas plankton communities data were Hellinger transformed (Legendre and Gallagher, 2001). RDA was also used to test the effect of environmental variables on the composition of plankton communities (ter Braak and Schaffers, 2004).

Linear mixed-effects models (LMMs) were constructed with the package lme4 version 1.1–27.1 (Bates et al., 2011) to test for differences between wetland types and seasons for each environmental variable, local taxonomic richness, and Reynolds Functional groups. Wetland type and season were included as fixed factors in these analyses, while wetland ID was included as a random factor to take into account the temporal

dependency of observations from the wet and dry seasons of each wetland. Distributional assumptions of linear models (normality and homoscedasticity of residuals) were checked for each response variable prior to the analyses. Statistical significances of the fixed factors were tested using Satterthwaite's approximation method of the lmerTest R package version 3.1–3 (Kuznetsova et al., 2017). Posthoc tests were implemented in the lsmeans R package version 2.30–0 (Lenth and Lenth, 2018). The relative importance of fixed and random effects in LMMs was assessed using the marginal R^2 and conditional R^2 (Nakagawa and Schielzeth, 2013).

To identify wetlands supporting a unique planktonic community, Local Contribution to Beta Diversity in plankton data sets (LCBD; ecological uniqueness of each wetland in their phytoplankton and zooplankton communities) was calculated following the method proposed by Legendre and De Cáceres (2013). Wetlands with higher LCBD values exhibit substantial dissimilarity in species compositions and may have high or low species richness, which should be given more attention in terms of conservation (Legendre and De Cáceres, 2013; da Silva Brito et al., 2020). In addition, calculations were extended to measure variability in plankton communities (BD_{Total}) and Species Contribution to Beta Diversity (SCBD) (Legendre and De Cáceres, 2013). BD_{Total} varies from zero (totally similar wetlands) to 1 (dissimilar wetlands). The SCBD value denotes the relative importance of each species in affecting BD_{Total} patterns. LCBD, SCBD, and BD_{Total} were calculated for each wetland type and the entire study region from Hellinger transformed plankton abundance data using the beta.div function in the adespatial R package version 0.3–14 (Dray et al., 2018). The significant difference in individual LCBD (each wetland's contribution to BD_{Total}) was tested by permutation (999 runs) for the entire study region according to the procedures described in Legendre and De Cáceres (2013). The significant difference in overall LCBD (wetland types' contribution to BD_{Total}) was tested using the linear mixed effect model. Wetland type and season were included as fixed factors in these analyses, while wetland ID was included as a random factor to take into account the temporal dependency of observations within each wetland type. We used beta regression as our modeling tool to investigate the relationship between LCBD and environmental variables, LCBD, and species data, SCBD and sampling sites, and SCBD and species data because LCBD and SCBD varied between 0 and 1 (Zeileis et al., 2010). We used beta regression with logit link function from the betareg R package version 3.1–4 (Zeileis et al., 2010) for three separate models. First, we related LCBD to species richness, community abundance, and their quadratic terms. Second, we ran beta regression of LCBD using ten environmental variables as predictors (i.e., pH, specific conductance, water temperature, water depth, turbidity, sediment depth, chlorophyll-a, total nitrogen, total phosphorus, and DO). Third, we used beta regression to relate LCBD to the species richness and community abundance (TotAbu). Forth, we used beta regression to relate SCBD to the number of sites occupied (NumSit), the species abundance (SpeAbu), and their quadratic terms.

TABLE 1 | Results of redundancy analysis (RDA) testing for the effect of wetland types, season, and their interactions on the environmental variables, plankton community composition, and Reynolds functional groups.

Environmental variables	R^2 adj:(%)	F	P
Wetland type	38.6	5.12	0.005
Season	4.13	1.91	0.005
Wetland type: Season	2.4	1.3	0.22
Phytoplankton			
Wetland type	37.9	4.18	0.005
Season	0.45	1.16	0.005
Wetland type: Season	1.2	1.2	0.13
Zooplankton			
Wetland type	23.6	2.98	0.005
Season	9.4	2.82	0.005
Wetland type: Season	1.2	1.07	0.22
Wetland type	59.8	8.18	0.005
Season	3.3	2.51	0.005
Wetland type: Season	0.7	1.17	0.32
RFGs abundance			
Wetland type	59.8	8.18	0.005
Season	3.3	2.51	0.005
Wetland type: Season	0.7	1.17	0.32

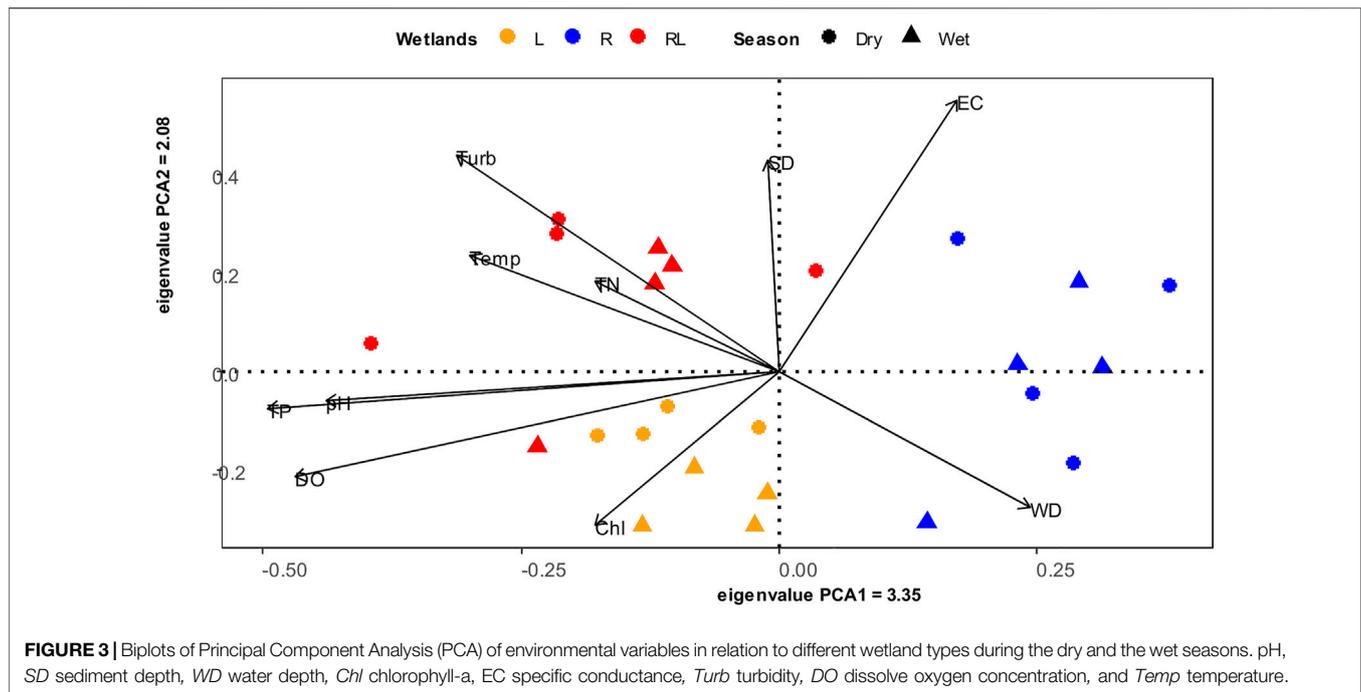
Significant effects ($p < 0.05$) are shown in bold.

All basic statistics were conducted in R (CoreTeam, 2020; Version 3.6.3), ggpubr R package version 0.4.0 (Kassambara, 2020). Figures were produced using the ggplot2 R package version 3.3.5 (Wickham, 2016).

RESULTS

Environmental Variables

RDA analysis revealed that wetland type and season both had a significant effect on the entire set of investigated environmental variables (R^2 adj: = 38.6, 4.13%, respectively; **Table 1**). The first and the second PCA axis jointly explained 54.42% of the overall variation in environmental variables (**Figure 3**). The first axis explained 33.57% of the variation and was positively associated with water depth, and negatively with TP and pH, generally separating the riverine papyrus swamps from the other wetland types. The second axis explained 20.85% of the variation of the environmental variable and was closely associated with turbidity, specific conductance, and sediment depth. The linear mixed model revealed that, except for chlorophyll-a and total nitrogen, the measured environmental variables differed significantly among wetland types (**Supplementary Table S2**). The concentration of dissolved oxygen, pH and concentration of total phosphorus were significantly higher in river mouth wetlands compared to riverine papyrus swamps and lacustrine wetlands (**Figures 4B, D, I**). Water temperature was significantly higher in river mouth wetlands compared to riverine papyrus swamps (**Figure 4C**). Turbidity was significantly higher in river mouth wetlands compared to riverine papyrus swamps and



lacustrine wetlands (Figure 4E). Riverine papyrus swamps had significantly higher sediment depth and electrical conductivity (expressed as specific conductance) compared to lacustrine wetlands (Figures 4F,G). Water depth was significantly higher in riverine papyrus swamps compared to river mouth wetlands (Figure 4H). We also observed considerable differences in water temperature and pH between seasons and the values were higher during the dry season (Supplementary Table S2). Overall, fixed factors (R^2 marginal) explained more variance in local environmental conditions than random factors (R^2 condition- R^2 marginal). However, for chlorophyll-a and total nitrogen concentration, the random factor (Wetland ID) was relatively more than fixed factors (Supplementary Table S2).

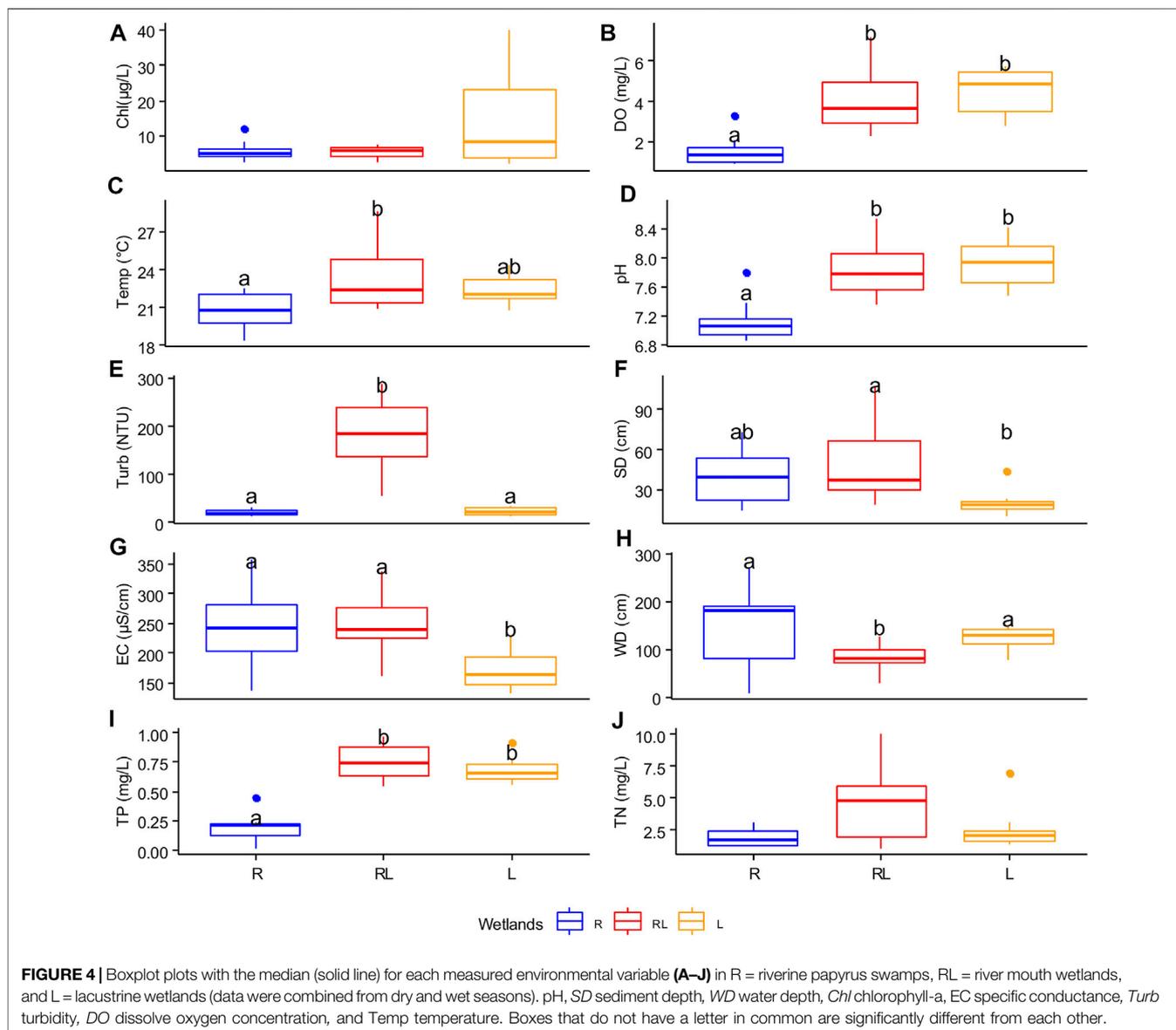
Local, and Regional Taxonomic Richness in Phytoplankton and Zooplankton

A total of 87 phytoplankton taxa belonging to seven main divisions, namely Chlorophyta (43 taxa), Bacillariophyta (25 taxa), Cyanophyta (10 taxa), Euglenophyta (3 taxa), Dinoflagellates (3 taxa), Xanthophyta (2 taxa), and Cryptophyta (1 taxon) were identified as regional taxon richness (Supplementary Table S3). The linear mixed model revealed that phytoplankton local taxonomic richness differed significantly among wetland types (Supplementary Table S2; Figure 5A). Seasonal variation, on the other hand, was insignificant (Supplementary Table S2). The overall mean local taxonomic richness of phytoplankton (data were combined for the dry and the wet seasons) was 29 taxa (25-34 taxa) in the lacustrine wetlands, 30 (20-44 taxa) in the riverine papyrus swamps, and 21 (14-31 taxa) in the river mouth wetlands.

A total of 57 zooplankton taxa representing Cladocerans (24 taxa), Copepods (9 species), and Rotifers (24 taxa) were identified (Supplementary Table S4). Copepods were composed of Cyclopoids and one Calanoid species, i.e., *Thermodiaptomus galebi lacustris*. The linear mixed model revealed that zooplankton local taxonomic richness differed significantly among wetland types and seasons (Supplementary Table S2; Figure 5B). The overall mean local taxonomic richness of zooplankton (data were combined the dry and the wet seasons) was 21 taxa (13-31 taxa) in the lacustrine wetlands, 27 (25-37 taxa) in the riverine papyrus swamps, and 13 (9-17 taxa) in the river mouth wetlands.

Plankton Community Composition

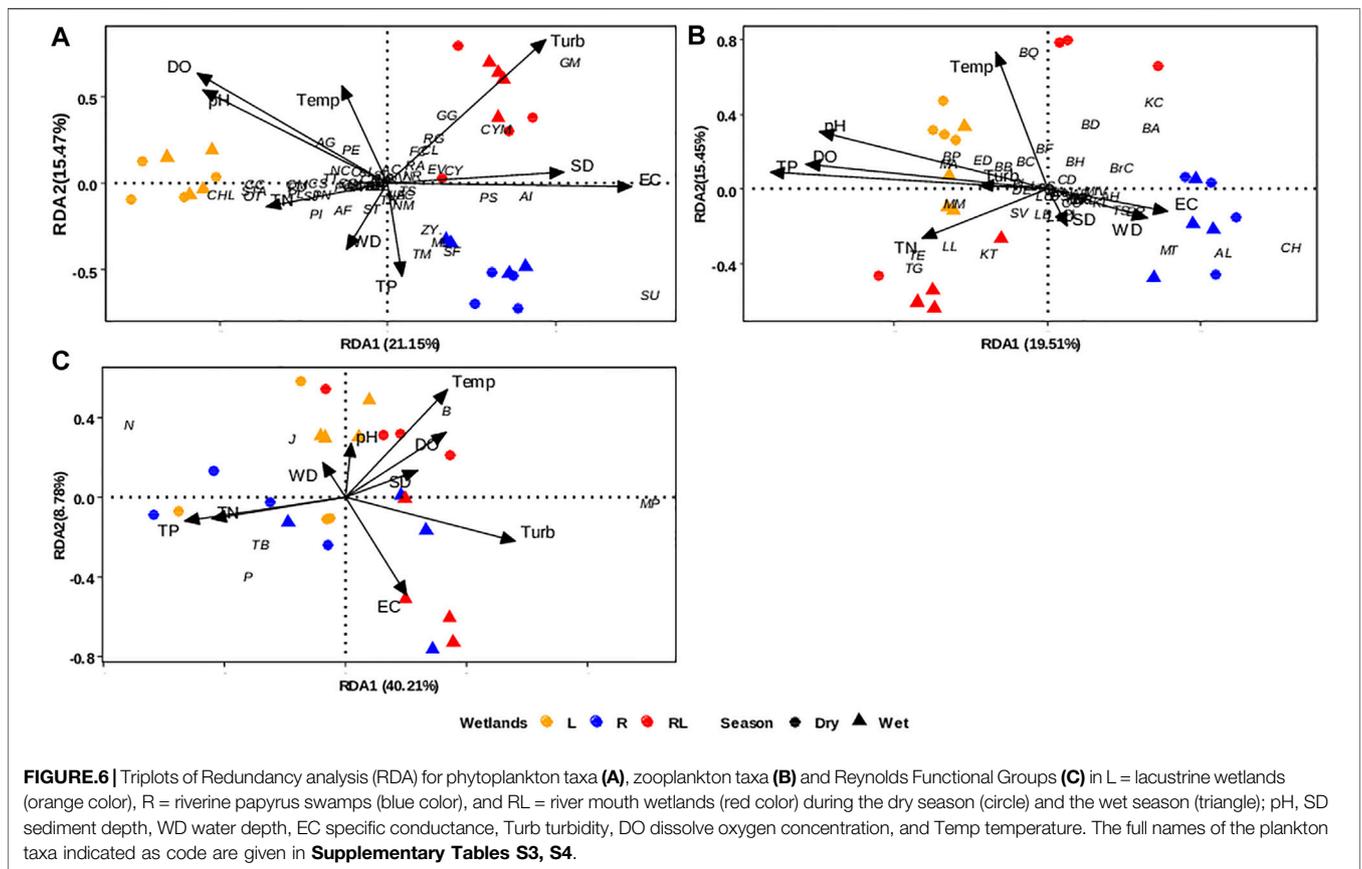
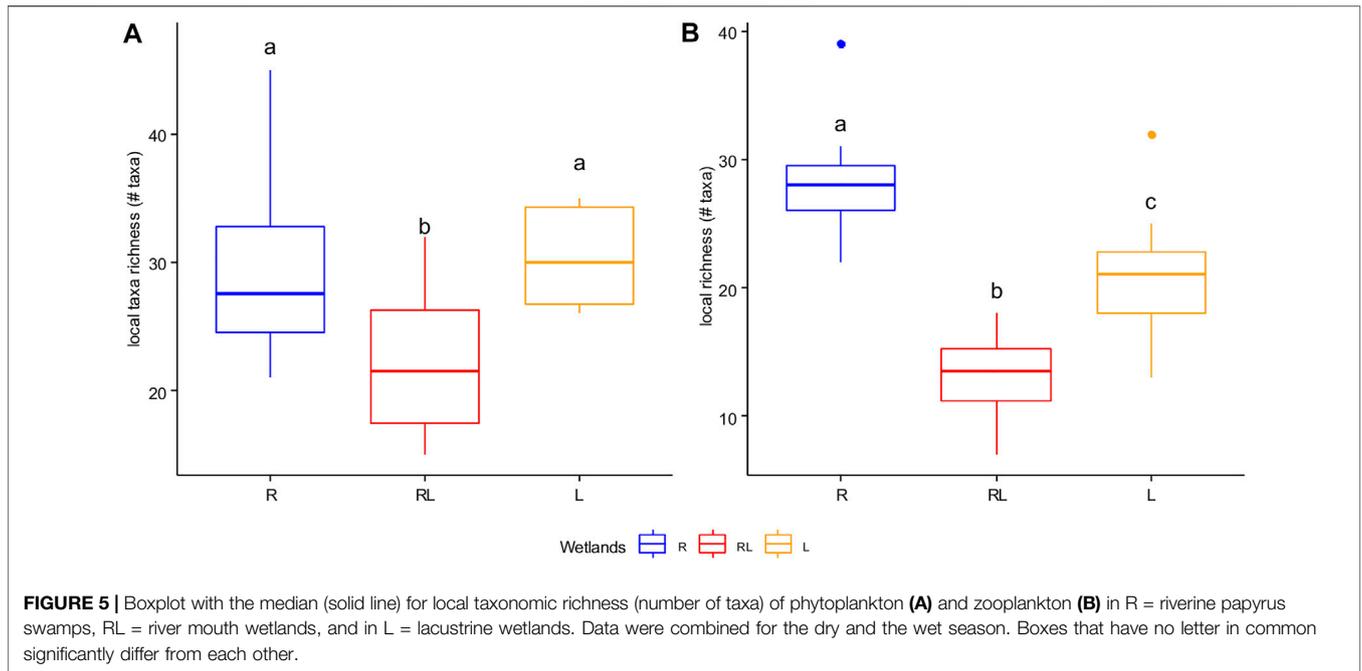
The redundancy analysis (RDA) revealed a significant variation in plankton community composition and Reynolds Functional groups among wetland types and seasons (Table 1). The RDA analyses revealed a significant effect of wetland types on phytoplankton community composition (R^2 adj: = 37.9%; Table 1). The season had a minor impact, despite being statistically significant (R^2 adj: = 0.45%). The first and second axes of the RDA based on phytoplankton, explained 36.62% of the total compositional variation in phytoplankton community (Figure 6A). The first axis explained 21.15% of the total variation and mainly separated river mouth wetlands with high turbidity from lacustrine wetlands and riverine papyrus swamps. The second axis, which explained 15.45% of the total variation, separated riverine papyrus swamps with deep water levels from the lacustrine and river mouth wetlands. Although, the majority of phytoplankton taxa showed a positive association with lacustrine wetland types, *Aulacoseira italica* (AI), *Mougeotia laetevirens* (ML), *Navicula cryptocephala* (NAC), *Nitzschia*

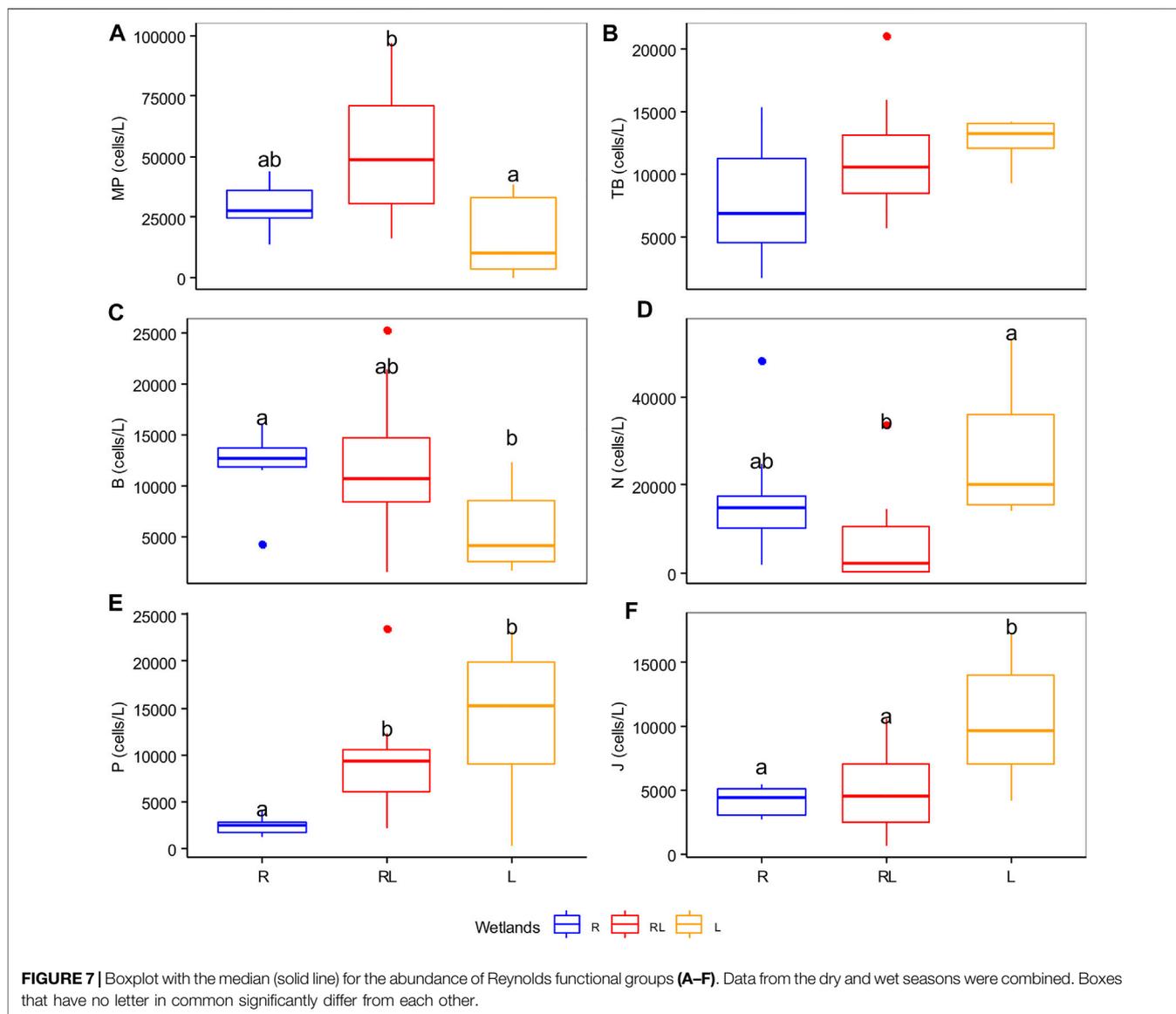


minuta (NM), *Spirogyra fluviatilis* (SF), *Synedra ulna* (SU), *Pediastrum simplex* (PS), and *Tribonema minus* (TM) tended to be slightly more abundant in riverine papyrus swamps. In river mouth wetlands, *Cymbella minuta* (CM), *Gomphonema minutum* (GM), *Fragilaria capucina* (FC), *Gomphonema gracile* (GG), *Nitzschia reversa* (NR), *Rhoicosphenia abbreviate* (RA), and *Rhopalodia gibba* (RG) were more abundant.

The phytoplankton species were grouped into 18 Reynolds functional groups (Supplementary Table S3). The functional groups B, MP, N, P, J, and TB accounted for more than 85% of the total phytoplankton abundance. Group B represented by the diatom *Aulacoseira italica* was the most dominant species comprising 29.4% of the total abundance followed by groups P (15.6%), J (13.71%), MP (12.11%), N (12.02%), and TB (5.97%). Differences in Reynolds functional groups abundance were especially strong between wetland types ($R^2_{adj} = 59.8\%$),

whereas season explained a relatively small proportion of variation ($R^2_{adj} = 3.3\%$; Table 1). The first and the second RDA axis jointly explained 48.99% of the overall variation in Reynolds functional groups abundance (Figure 6C). The first axis comprised 40.21% of the compositional variation in the Reynolds functional groups. The first axis clearly differentiated the river mouth wetlands from the lacustrine wetlands and riverine papyrus swamps (Figure 6C). Groups B and MP were dominant in river mouth wetlands (towards the positive side of the first axis), which was correlated with turbidity. Groups N and P were dominant in lacustrine wetlands (towards the negative side of the first axis), which was correlated with TP and TN concentrations. The second RDA axis accounted for 8.78% of the variation in Reynolds functional groups. Linear mixed models revealed that the abundances of groups B, J, N, MP, and P differ significantly among wetland types, while only group TB





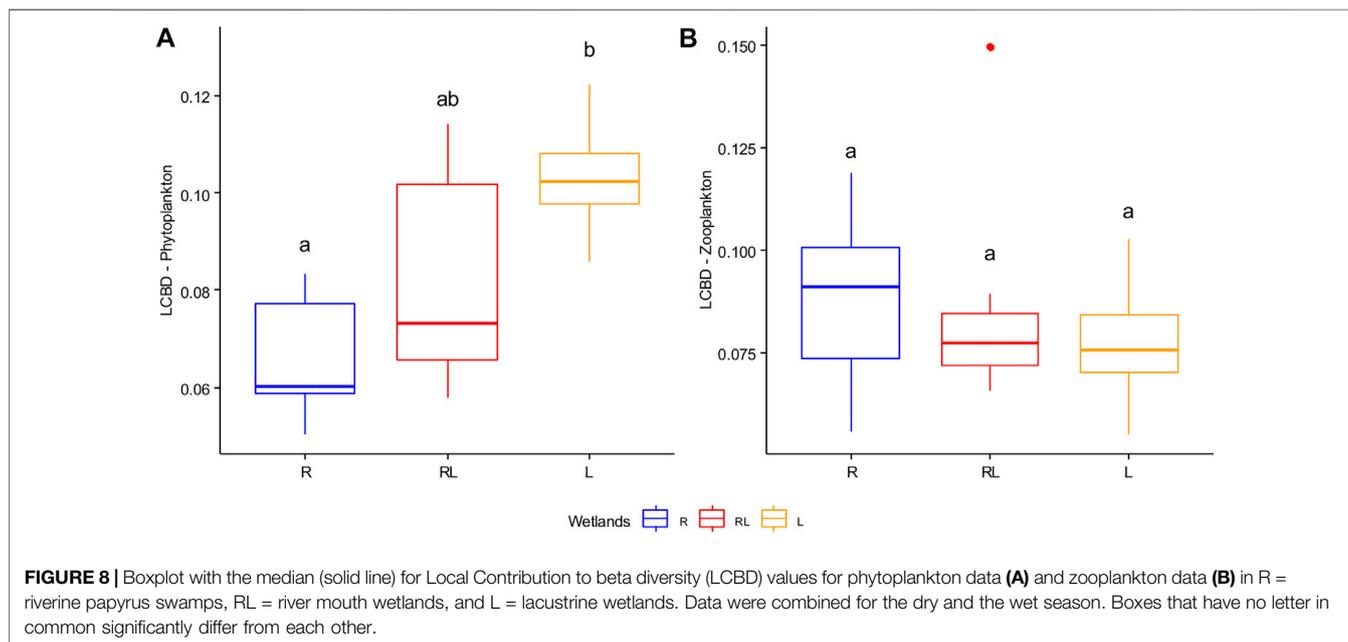
significantly varied between seasons (**Supplementary Table S2**). The group MP was significantly higher in river mouth wetlands compared to lacustrine wetlands (**Figure 7A**). The group TB did not differ between wetland types (**Figure 7B**). Group B was significantly higher in riverine papyrus swamps compared to lacustrine wetlands (**Figure 7C**). The group N was significantly higher in lacustrine wetlands compared to river mouth wetlands (**Figure 7D**). The groups P and J were slightly higher in lacustrine wetlands compared to the other two wetland types (**Figures 7E,F**). Except for group B, where wetland identity was more relevant, wetland types and season (Marginal R^2) explained more variance in most RFGs (**Supplementary Table S2**). The habitat preferences, representative taxa, tolerance, and sensitivity of dominant phytoplankton RFGs in the studied wetland types are shown in **Table 2**.

Zooplankton community composition differed between wetland types (R^2 adj = 23.6%) and season. However, season only explained a

relatively small proportion of variation (R^2 adj = 9.4%; **Table 1**). The first and the second RDA axis jointly explained 34.56% of the overall variation in zooplankton community composition (**Figure 6B**). The first axis comprised 19.51% of the compositional variation in the zooplankton community and differentiated riverine papyrus swamps from the lacustrine and river mouth wetlands. Zooplankton taxa associated with these riverine papyrus swamps were *Acroporus harpae* (AH), *Alona* spp. (AL), *Chydorus* spp. (CH), *Ectocyclops rubescens* (ER), *Mesocyclops kieferi* (MK), *Microcyclops varicans* (MV), *Macrothrix triserialis* (MT), and *Kurzia longirostris*. In river mouth wetlands, *Brachionus caudatus* (BC), *Brachionus diversicornis* (BD), *Brachionus quadridentatus* (BQ), and *Brachionus calyciflorus* (BrC) tended to be slightly more abundant during the dry season, while *Thermocyclops ethiopiensis* (TE), *Thermodiaptomus galebi* (TG), *Keratella tropica* (KT), *Lecane bulla* (LB), and *Lecane luna* were abundant during the wet season.

TABLE 2 | Description of the main phytoplankton RFGs (with >3% contribution) in wetlands of lake Tana and representative taxa (Reynolds, 2002; Padišák et al., 2009).

RFG	Habitat	Representative phytoplankton species in lake tana wetlands	Tolerance	Sensitivity
MP	Inorganically turbid shallow lakes	<i>Cymbella minuta</i> , <i>Cymbella ventricosa</i> , <i>Gomphonema gracile</i> , <i>Gomphonema minutum</i> , <i>Navicula cuspidata</i> , <i>Oscillatoria brevis</i> , <i>Synedra ulna</i>	—	—
TB	Highly lotic environments	<i>Nitzschia Closterium</i> , <i>Nitzschia reversa</i> , <i>Rhoicosphenia abbreviata</i>	—	—
B	Vertically mixed, mesotrophic small-medium lakes	<i>Aulacoseira italica</i> , <i>Cyclotella comta</i> , <i>Cyclotella radiosa</i>	Light deficiency	pH rise, Si depletion, stratification
N	Mesotrophic epilimnia	<i>Cosmarium circulare</i> , <i>Cosmarium sexangulare</i> , <i>Staurastrum johnsonii</i> , <i>Sta. urastrum gracile</i> , <i>Staurodesmus convergens</i>	Nutrient deficiency	pH rise, stratification
P	Eutrophic epilimnion	<i>Aulacoseira granulate</i> , <i>Closterium acutum</i> , <i>Closterium kuetzingii</i> , <i>Closterium kuetzingii</i>	Mild light and C	Stratification, Si deficiency depletion
J	Shallow enriched ponds	<i>Coelastrum microporum</i> , <i>Pediastrum boryanum</i> , <i>Pediastrum simplex</i> , <i>Pediastrum duplex</i>		Settling under low light
T	Deep, well-mixed epilimnia	<i>Mougeotia laetevirens</i> , <i>Tribonema minus</i>	Light deficiency	Nutrient deficiency
X1-X3	Shallow mixed layers in enriched conditions	<i>Ankistrodesmus falcatus</i> , <i>Ankistrodesmus angustus</i> , <i>Treubaria crassispina</i>	Low base status, stratification	Mixing, grazing, filter-feeding



Local Contribution and Species Contribution to Beta Diversity (BD_{Total}) of Plankton

The total beta diversity (BD_{Total}) of phytoplankton for the entire data set was 0.61 and 0.62 during the dry and the wet season, respectively (Supplementary Table S6). LCBD values of phytoplankton for the entire data set ranged between 0.05 and 0.12 during the dry season and between 0.06 and 0.11 during the wet season. Lacustrine wetlands' contribution to phytoplankton LCBD was significantly higher compared to riverine papyrus swamps (Supplementary Table S2; Figure 8A). For all data, the Zegie-yiganda lacustrine wetland was statistically significant for single wetland contribution (LCBD) of phytoplankton ($P_{adj} = 0.037$). The BD_{Total} of zooplankton for the entire data set was 0.56 and 0.47 for the dry and the wet seasons, respectively

(Supplementary Table S6; Figure 8B). LCBD of zooplankton for the entire data set ranged between 0.06 and 0.15 during the dry season and between 0.07 and 0.10 during the wet season. Although three of the four wetlands of riverine papyrus swamps (Amba-giorgis, Dehna-mesenta, and Legdiya) contributed more than the average to zooplankton BD_{Total} (LCBD), there was no significant difference between wetland types (Supplementary Table S2; Figure 8B). For all data, the Megech river mouth wetland was statistically significant for single wetland contribution (LCBD) of zooplankton ($P_{adj} = 0.003$).

The LCBD of phytoplankton data was significantly related to pH (Estimate = 0.27; $z = 2.08$, $p = 0.04$), whereas the LCBD of zooplankton data was significantly related to water depth (Estimate = 0.00; $z = 2.76$, $p = 0.005$) and sediment depth (Table 3; Estimate = 0.00; $z = 2.41$, $p = 0.02$). Also, pseudo R^2 values of these models were moderate, 56% of the variation in

TABLE 3 | Results of beta regression analyses when the response variable, local contributions to beta diversity (LCBD), was explained by local environmental variables.

Phytoplankton	Estimate	Se	z	p	Model pseudo R ²
(Intercept)	-4.51	1.05	-4.28	0.00***	0.56
DO (mg/L)	0.04	0.03	1.05	0.29	
Water temperature (0°C)	0.01	0.02	0.45	0.65	
pH	0.27	0.13	2.08	0.04*	
Specific conductance (μS/cm)	0.00	0.00	-0.82	0.41	
Water depth (cm)	0.00	0.00	-0.37	0.71	
Sediment depth (cm)	0.00	0.00	-1.4	0.16	
Turbidity (NTU)	0.00	0.00	-0.83	0.41	
Total Phosphorus (mg/L)	0.02	0.02	1.22	0.22	
Total Nitrogen (mg/L)	0.01	0.01	1.16	0.25	
Zooplankton	Estimate	SE	z	p	Model pseudo R ²
(Intercept)	-3.97	1.16	-3.41	<0.001***	0.41
Chlorophyll-a (μg/L)	0.00	0.02	-0.15	0.88	
DO (mg/L)	0.06	0.04	1.68	0.09	
Water temperature (0°C)	-0.03	0.02	-1.36	0.17	
pH	0.19	0.15	1.33	0.18	
Specific conductance (μS/cm)	0.00	0.00	1.01	0.31	
Water depth (cm)	0.00	0.00	2.76	0.005**	
Sediment depth (cm)	0.00	0.00	2.41	0.02*	
Turbidity (NTU)	0.00	0.00	-0.48	0.63	
Total Phosphorus (mg/L)	0.01	0.02	0.99	0.32	
Total Nitrogen (mg/L)	-0.02	0.01	-1.36	0.17	

Significant effects ($p < 0.05$) are shown in bold.

LCBD of phytoplankton and 41% in LCBD of zooplankton was explained by all environmental variables included (Table 2). However, there was no significant relationship between LCBD values and taxa richness, abundance, or quadratic terms in either of the plankton communities (Supplementary Table S7).

The SCBD values for the entire data set of phytoplankton ranged from 0 to 0.108 and 15 out of 80 phytoplankton taxa had an above average (0.0125) contribution to BD_{Total} during the dry season. The SCBD for the wet season ranged from 0 to 0.12, with 21 out of 81 phytoplankton taxa contributing more than the average (Supplementary Table S8). Zooplankton SCBD values for the entire data set during the dry season ranged between 0 and 0.08, and 15 out of 55 zooplankton taxa contributed above the mean (0.018) to BD_{Total} . SCBD during the wet season ranged between 0.00027 and 0.074, and 11 out of 57 zooplankton taxa contributed above the average (0.017) (Supplementary Table S6).

The SCBD of phytoplankton was related to the number of sites occupied and its quadratic term, which accounted for 29% of the variation, whereas abundance and its quadratic term accounted for 62% of SCBD variation of phytoplankton (Table 4). SCBD of Zooplankton was found to be significantly related to the number of sites occupied and its quadratic term, which accounted for 47% of the variation. The SCBD of Zooplankton was also significantly related to abundance and its quadratic term, which accounted for 43% of the variation (Table 4).

DISCUSSION

Wetlands in Lake Tana are heterogeneous, as evidenced by differences in environmental conditions such as the water

TABLE 4 | Results of beta regression analyses when species contributions to beta diversity (SCBD) was explained by species abundance, site occupancy, and their quadratic terms.

Phytoplankton	Estimate	Se	z	p	Model pseudoR ²
(Intercept)	-5.68	0.27	-20.68	< 0.001 ***	0.29
NumSit	0.39	0.10	4.01	<0.001 ***	
NumSit2	-0.02	0.01	-2.23	0.03 *	
SCBD (Intercept)	-5.40	0.11	-49.45	< 0.001 ***	
SpeAbu	0.00	0.00	13.21	< 0.001 ***	
SpeAbu2	0.00	0.00	-8.51	< 0.001***	
Zooplankton	Estimate	SE	z	p	Model pseudoR ²
(Intercept)	-5.38	0.23	-23.14	< 0.001***	0.47
NumSit	0.37	0.08	4.65	<0.001***	
NumSit2	-0.01	0.01	-2.54	0.01**	
SCBD (Intercept)	-4.66	0.10	-48.47	< 0.001***	
SpeAbu	0.00	0.00	10.88	< 0.001***	
SpeAbu2	0.00	0.00	-7.30	<0.001***	

NumSit number of sites occupied, SpeAbu a species abundance in the whole data set. Significant statistical values are indicated by bold font and as follows: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

depth, pH, dissolved oxygen, and turbidity of the water, as well as by the differences in the local richness and composition of the planktonic communities in the different wetland types. These differences could be attributed to differences in local habitat conditions as well as in variation in hydrological conditions between wetlands. In our study, river mouth wetlands were highly turbid, warmer, and shallower, whereas riverine papyrus swamps and lacustrine wetlands were

characterized by extended areas of emergent macrophytes, low turbidity, and deeper water levels.

The observed lower phytoplankton local taxa richness in river mouth wetlands compared to riverine papyrus swamps and lacustrine wetlands might be related to the higher turbidity in the former wetland type. Increased turbidity results in lower light availability for wetland phytoplankton (Allende et al., 2009), which in turn might select for a lower number of taxa specifically adapted to low light intensities. This is in line with earlier studies (Sharma and Singh, 2018; Gogoi et al., 2019), which found low phytoplankton richness in turbid aquatic ecosystems. Many authors suggested that water depth is the primary hydrological factor influencing phytoplankton species richness and community composition in wetlands (Casali et al., 2011; Chaparro et al., 2018; Xiao et al., 2020). This is because water depth influences the wetland's persistence, stability, and size (Chaparro et al., 2018), and local environmental conditions (Xiao et al., 2020), which, in turn, have an impact on phytoplankton communities. Our findings revealed that water depths were shallower in river mouth wetlands than in riverine papyrus swamps and lacustrine wetlands, which might be another reason for the lower phytoplankton richness in the former wetland type. Similarly, phytoplankton species richness was found to be lower during the low water phase than during the high water phase in one of Brazil's wetlands (Cardoso et al., 2012). This, however, contradicted the broader paradigm, which holds that low water levels in wetlands result in heterogeneous microhabitats as the wetlands become more isolated from one another and disconnected from the main river channel (Tockner et al., 2000). In addition to variation in water depth, the presence of macrophytes in riverine papyrus swamps might have benefited the shade-tolerant species of Bacillariophyta and small-sized species of Chlorophyta that were dominant in these wetlands (Padisák et al., 2009). Macrophytes have also been shown to promote the growth of periphytic phytoplankton species such as *Spirogyra fluviatilis*, *Mougeotia laetevirens*, *Aulacoseira italica*, *Gonatozygon monotaenium*, and *Oedogonium* spp. (Rodríguez et al., 2012), which were also dominant in the riverine papyrus swamps in our study.

The high local taxa richness of zooplankton in riverine papyrus swamps might be attributed to the varying water depth (30–300 cm depth) observed in these wetlands. In general, variation in water depth within wetlands promotes different niches that support many zooplankton species (Adamczuk, 2014; Chaparro et al., 2018). Thus, various species can be seen along a water depth gradient, which can be related to UV exposure, thermal properties, and food resources associated with varying water depths. Here as well, the extensive macrophyte cover in riverine papyrus swamps might also provide a complex habitat (e.g., space and food resources) for zooplankton but especially for epibenthic generalists (Bolduc et al., 2016; Gebrehiwot et al., 2017a; Gogoi et al., 2018) such as *Alona* spp., *Chydorus* spp., and *Macrothrix triserialis* which were dominant zooplankton species in these wetlands. Epibenthic generalists attach to substrates such as underwater stems or leaf surfaces and their low activity makes them less likely to be detected by macrophyte-associated predators compared to planktonic species (Gogoi et al., 2018).

The regional taxonomic richness in the plankton of the Lake Tana wetlands is difficult to compare with other wetlands because the number of species is strongly dependent on the number of samples analyzed and the taxonomic accuracy in the analysis. However, the 85 phytoplankton taxa found was higher than the 36 phytoplankton species in the wetlands of India's Sundarbans wetlands (Gogoi et al., 2019), 53 species in India's Chatla wetlands (Laskar and Gupta, 2013), and 36 species in Diyawannawa wetland of Sri Lanka (Wijeyaratne and Nanayakkara, 2020). However, the regional phytoplankton taxa richness in our wetlands was lower than the 360 phytoplankton species in the Bhoj wetland of India (Bhat et al., 2015), 97 species in of Pantanal wetland of South America (Cardoso et al., 2012), and 200 species in Danube Riverine wetlands of Austria (Chaparro et al., 2018). Similarly, the regional taxon richness of zooplankton in our study was higher than the 32 species reported from the wetland of Opa Reservoir (Adebayo et al., 2021), but lower than the 128 species reported from the Yangtze River floodplain (Lu et al., 2021).

In addition to differences in local taxonomic richness, we also found significant differences in plankton community composition, studied at the functional (RFG) and taxonomic level, and the zooplankton communities between the different wetland types. The phytoplankton in riverine papyrus swamps was dominated by Reynolds functional group B, which was represented by *Aulacoseira italica*; a member of a cosmopolitan genus with a tychoplanktonic live style (Denys et al., 2003; Bicudo et al., 2016). The phytoplankton communities in the river mouth wetlands were dominated by the MP group, which corroborates its presence in inorganically turbid lakes and rivers elsewhere (Padisák et al., 2009; Stević et al., 2013; Udovic et al., 2014). This group was also dominant within the macrophyte stands in Lake Ziway (Gebrehiwot et al., 2017b), a lake that is highly turbid and heavily impacted by intensive agricultural activities and urbanization (Gebrehiwot et al., 2017a; Merga et al., 2020). In addition, species that predominantly contributed to the Reynolds functional group MP, such as *Rhopalodia gibba*, *Gomphonema minutum*, *Rhicosphenia abbreviate*, *Nitzschia reversa*, *Gomphonema gracile*, *Cymbella minuta*, and *Nitzschia closterium* have been reported from running waters elsewhere (Leira et al., 2017; Shen et al., 2018). The lacustrine wetlands are dominated by the J, P, and N groups which prefer shallow enriched water bodies with continuous or semi-continuous mixed layers of 2–3 m in thickness (Reynolds, 2002). The zooplankton communities in the riverine papyrus swamps were dominated by the cladoceran functional groups. This is most likely due to the high density of macrophyte stands dominated by *Cyperus papyrus*, which may have served as a foraging and attachment site for non-active epiphytic zooplankton (e.g., *Alona* and *Chydorus* spp.; Choi et al., 2015). This is consistent with what was found in other studies in Lake Ziway (Gebrehiwot et al., 2017a) and Lake Tana (Wudneh 1998). In the present study, a considerably higher diversity of rotifers was recorded in river mouth wetlands. The most abundant species found in these wetlands (*B. caudatus*, *B. diversicornis*, *B. quadridentatus*, *B. calyciflorus*, *K. tropica*, *L. bulla*, and *L. luna*) were cosmopolitan planktonic species that are generalists that feed on bacteria, detritus, and flagellates (Yin

et al., 2018; García-Chicote et al., 2019). Some of these species are also known to be tolerant of differences in temperature, dissolved oxygen, and turbidity (Segers and De Smet, 2007). As a result, some of these species are expected to predominate in river mouth wetlands, which have higher turbidity, higher temperature, and low dissolved oxygen concentrations.

The phytoplankton in the lacustrine wetlands and particularly that in the Zegie-yiganda wetland, with its deep open water and diverse microhabitats, appeared to be relatively unique. The positive correlation between pH and LCBD values for phytoplankton in our study confirms that pH is one of the environmental factors that affect phytoplankton directly or through its influence on the bioavailability of nutrients (Chakraborty et al., 2011). The zooplankton in the Megech river mouth wetland, but particularly the communities in the riverine papyrus swamps, were relatively unique. For the Megech river mouth wetland, this is due to its low richness and severely degraded state and therefore restoration actions are recommended. The zooplankton in the riverine papyrus swamps consisted of unique communities. This, together with the presence of unique taxa in waterbirds in these wetlands (e.g., Zelelew et al., 2020) underlines the need that these wetlands require special protection (Brito et al., 2020). The LCBD values of zooplankton were found to be positively related to sediment and water depth. Indeed, water depth is likely to influence zooplankton community composition by altering the other environmental variables such as turbidity, dissolved oxygen, specific conductance, and nutrient concentrations, as well as the cover and structure of macrophytes in wetlands (Chaki et al., 2021). Water depth in wetlands is known to be directly related to the establishment and survival of different macrophyte types (Rolon et al., 2010), which are very important for zooplankton as a refuge, substrate, and food source, resulting in distinct zooplankton communities (Nevalainen, 2012; Adamczuk, 2014). The positive relation between LCBD and sediment depth might be related to some taxa being present in the riverine papyrus swamps wetlands with deep sediments, such as several bottom-dwelling Cladoceran species (Gogoi et al., 2018).

Finally, the effect of wetland type was more prominent than the effect of season on environmental variables, plankton communities, and RFGs. However, because only one-time sampling per season was used, the insignificance of the seasonal effect could be attributed to our under-sampling efforts.

CONCLUSION

Understanding local taxon richness, as well as variation in community composition, in combination with ecological uniqueness analysis (LCBD), could aid in the wetland restoration and conservation activities. The observed significant variation in plankton community composition among the three wetland types suggests that all the wetlands included in this study must be conserved, which may be difficult due to limited resources. Therefore, wetlands with a high plankton local taxon richness and a high LCBD (high ecological uniqueness) are worth special attention. Thus,

conserving riverine papyrus swamps is critical for preserving the majority of phytoplankton and zooplankton taxa, as well as the most valuable sites. However, the taxa poor, degraded Megech river mouth wetland, which contributed significantly to zooplankton LCBD, requires restoration. Although we believe our findings can serve as a foundation for any conservation and restoration plans, we recommend more research is needed on the diversity, and community composition of other organisms in these wetlands to make better decisions and preserve the Lake Tana regional biodiversity.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

AK contributed to data collection, analysis, and manuscript writing. AK, AW, IS, and PL designed the study and developed a data collection protocol. EV, IS, LT, and PL contributed to the critical revision of the manuscript for important intellectual content. EA, LDM, and MK contributed to the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2022.816892/full#supplementary-material>

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